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Validation of *Eleutherodactylus crepitans* Bokermann, 1965, notes on the types and type locality of *Telatrema heterodactylum* Miranda-Ribeiro, 1937, and description of a new species of *Eleutherodactylus* from Mato Grosso, Brazil (Amphibia: Anura: Leptodactylidae)

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Abstract.—Examination of the types of *Eleutherodactylus crepitans* Bokermann, 1965, indicates that they represent a valid species, which should be removed from the synonymy of *Eleutherodactylus fenestratus* (Steindachner 1864). *Eleutherodactylus crepitans* is only known from the type material. Certain features of the types of *Telatrema heterodactylum* Miranda-Ribeiro, 1937, are described and the type locality clarified. Analysis of the advertisement call and morphology of a series of specimens from Chapada dos Guimarães indicates that the specimens represent a species distinct from *E. fenestratus* (Steindachner 1864), for which no name is available. We describe this new species as *Eleutherodactylus dundeei.* The frog fauna of Chapada dos Guimarães contains four distinct historical units: cerrado, chaco, Amazonian hylaea, and endemic.

The advertisement call of what has been identified as *Eleutherodactylus fenestratus* from Chapada dos Guimarães, Mato Grosso, Brazil, was recently recorded by WRH as part of PRODEAGRO. PRODEAGRO is an ecological-agricultural survey of the State of Mato Grosso, undertaken by the State Secretariat of Planning, funded by the World Bank, and contracted to the São Paulo firm of consultants "Consorcio Nacional de Engenheiros Consultores" (CENEC). As part of the National Museum of Natural History's Research Training Program, AMM analyzed the advertisement call of the Chapada dos Guimarães form and compared it to the advertisement call of *Eleutherodactylus fenestratus* from the Amazon basin. The results indicate that the Chapada dos Guimarães form is a different species from the Amazonian *E. fenestratus.* To determine whether there is an available name for the Chapada dos Guimarães form and whether it has a distribution beyond the region of the town of Chapada dos Guimarães, we examined other specimens of *Eleutherodactylus* from Mato Grosso, including the type material of *Telatrema heterodactylum* Miranda-Ribeiro, 1937 and *Eleutherodactylus crepitans* Bokermann, 1965. The purpose of this paper is to report our findings.

Methods and Materials

The first recording of the Chapada dos Guimarães form is from USNM Tape 320, Cut 2, Brazil, Mato Grosso, Chapada dos Guimarães, Estancia Monarca, recorded 30 September 1996, between 1835–1930 h, air temperature 21.6°C, unvouchered, by WRH, one call recorded and analyzed. The second recording of the Chapada dos Guimarães form is from USNM Tape 320, Cut 3, same data as Cut 2, except recorded at

1930 h, voucher USNM 507899, one call recorded and analyzed. The recordings for *Eleutherodactylus fenestratus* are from USNM Tape 206, Cut 2, Peru, Madre de Dios, Tambopata, recorded 6 January 1989, 1850 h, air temperature 24.0°C, voucher USNM 342993, by Reginald B. Cocroft III, four calls analyzed, and USNM Tape 266, Cut 19, Peru, Madre de Dios, Tambopata, recorded 15 November 1990, 1815 h, air temperature 27.0°C, unvouchered, by Reginald B. Cocroft III, six calls analyzed.

Call recordings were digitized using Sound Image software at a sampling frequency of 22.05 KHz and 16-bit resolution. The digitized calls were converted into audio data files using a wave converter package and analyzed as audiospectrograms and wave forms using Computerized Speech Research Environment software (AVAAZ Innovations Inc., Version 4.2).

Eleven parameters were analyzed for each call following the definitions of Heyer et al. (1990): call duration, call rate, notes per call, note duration, note repetition, note pulsation, fundamental frequency, dominant frequency, change in dominant frequency, peak frequency, and characterization of harmonics.

The audiospectrograms used in Fig. 1 were produced using Canary software (Cornell Laboratory of Ornithology, Version 1.2).

Color pattern and external morphological data were recorded using a system of sketches to represent all distinctive patterns or states. These data were then summarized and categorized into written character states. Measurements were taken with dial calipers and recorded to the nearest 0.1 mm following Heyer (1984). Adult males were determined by presence of vocal slits. Adult females were determined by presence of mature ova visible through the body wall. Unclear sex determinations based on external examination were verified by dissection. Multivariate discriminant function analyses were performed using SYSTAT 7.0 for Windows.

Specimens examined are listed in Appendix 1. Museum abbreviations follow Leviton et al. (1985).

Results

Advertisement calls.—The ideal calls to compare the Chapada dos Guimarães form with are those from topotypic *Eleutherodactylus fenestratus* males. *Eleutherodactylus fenestratus* (Steindachner 1864) was described from specimens from Rio Mamoré, Rondônia and Borba, Amazonas, Brazil. The geographically most proximate adequate recordings we know for Amazonian *E. fenestratus* are from Tambopata, Peru. We use these recordings to represent *E. fenestratus* for our comparisons.

As there is some variation among the four individual frogs recorded from Peru and Brazil, the data are summarized by individual caller (Table 1).

The frog from Tambopata, USNM Tape 206, Cut 2, has a mean call duration of 0.31 sec; 2.75 mean notes per call; and a mean note duration of 0.07 sec. The dominant frequency is the second harmonic; additional harmonics are present, but weak. (Fig. 1a).

The second frog from Tambopata, USNM Tape 266, Cut 19, has a mean call duration of 0.18 sec; and a mean note duration of 0.07 sec. The dominant frequency is the second harmonic; additional harmonics are present, but weak.

The single call of the frog from Chapada dos Guimarães, USNM Tape 320, Cut 2, has a relatively short (0.02 sec) and weak first note, the other 4 notes are stronger and have a duration range of 0.03–0.04 sec. The notes are pulsatile. The dominant frequency is the second harmonic; additional harmonics are present, but weak.

The single call of the second frog from Chapada dos Guimarães, USNM Tape 320, Cut 3, has a relatively short (0.02 sec) and weak first note, all other notes are stronger with a duration of 0.04–0.05 sec. The notes are pulsatile. The dominant frequency is the

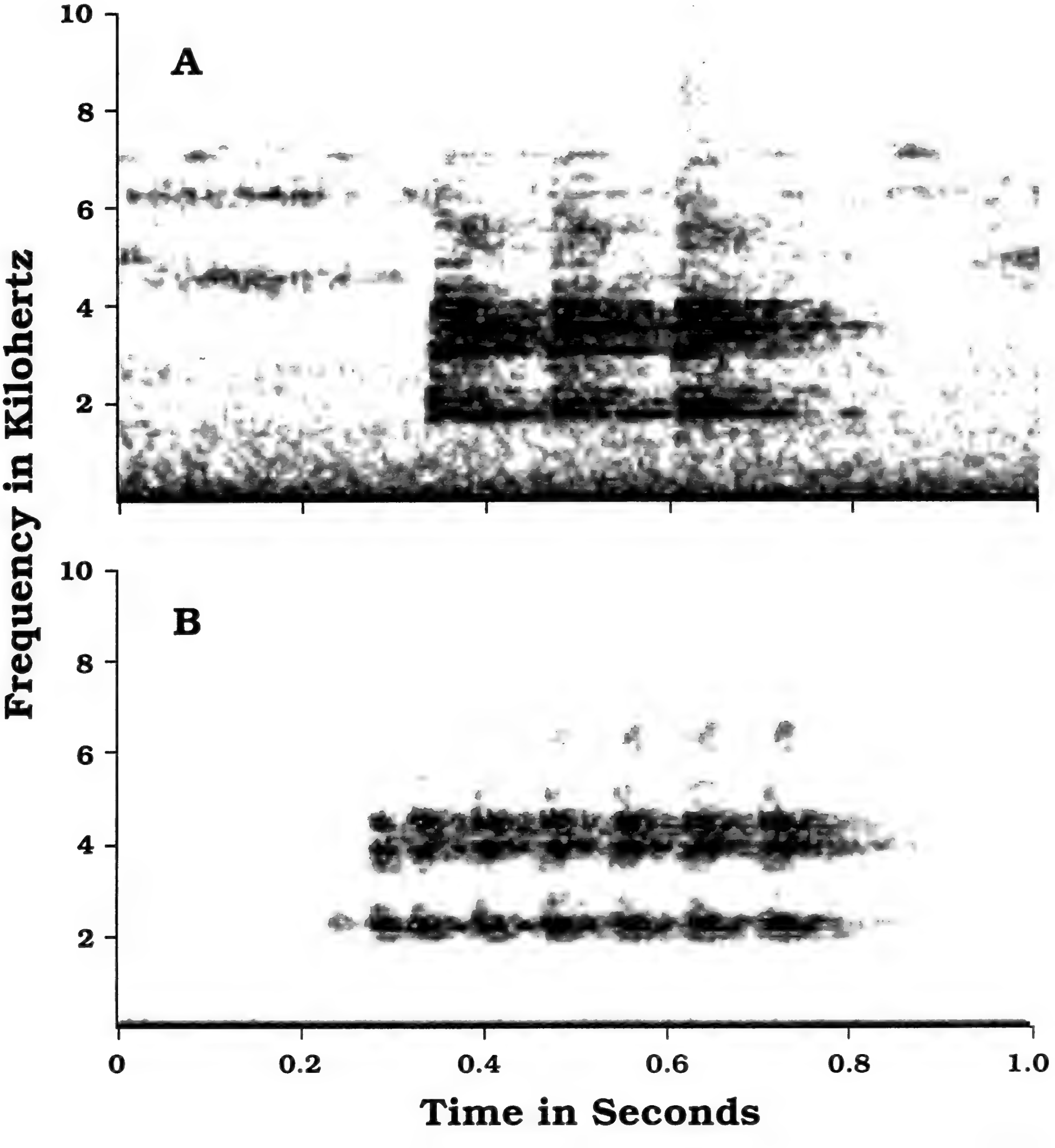

Fig. 1. A. Advertisement call of *Eleutherodactylus fenestratus,* USNM Tape 206, Cut 2. B. Advertisement call of Chapada dos Guimarães form, USNM Tape 320, Cut 3.

second harmonic; additional harmonics are present, but weak. (Fig. 1b).

There is some variation between individual male vocalizations from the same locality. The variation observed between the recordings from Tambopata might be accounted for by differences of temperature of calling males, at least in part. As a general rule for frogs, increases in temperature result in decreased call and note duration and increased note repetition rate (Schneider et al. 1984; Duellman & Trueb 1986). The three degree difference of ambient temperature between the two recordings of the Peruvian specimens is in the predicted direction for call and note duration and note repetition rate. Note, however, that the recordings from Chapada dos Guimerães were recorded at lower temperatures than those of Peru, yet these Brazilian calls had

Table 1.—Advertisement call data for four *Eleutherodactylus* specimens from Tambopata, Peru and Chapada dos Guimarães, Brazil.

Geographic area USNM Tape and Cut	Peru 206, 2	Peru 266, 19	Brazil 320, 2	Brazil 320, 3
Call duration (sec)	0.21–0.36	0.16–0.20	0.29	0.53
Number of notes/call	2–3	2	5	8
Note duration (sec)	0.06–0.09	0.05–0.08	0.04	0.05
(Mean) note repetition rate per sec	7.6	9.1	14.7	13.7
Fundamental frequency range	1636–2411	1464–2497	1894–2239	1808–2497
Peak fundamental frequency	1720	2067	2067	2153
Dominant frequency range	2842–4392	2842–4220	3014–4220	3273–4737
Peak dominant frequency	3531	3617	3692	3875

shorter note durations and higher note repetition rates than the Peruvian calls, indicating that temperature differences do not explain the differences between the Brazilian and Peruvian calls.

The calls from Brazil and Peru do not differ in terms of carrier frequencies; they are broadcasting in the same frequency band. The calls differ markedly in terms of temporal packaging (Table 1), such as number of notes per call, individual note duration, and note repetition rate. Penna (1997) among others, has experimentally demonstrated that the kinds of temporal differences found between the Tambopata and Chapada dos Guimarães frogs are recognized as species differences by frogs.

Unfortunately, to date, there are no recordings of what we consider to be Amazonian *Eleutherodactylus fenestratus* from the hylaea of northern Mato Grosso. In fact, the only other published recordings for *E. fenestratus* are from Amazonian Bolivia (Marquez et al. 1995) and are very similar to the recordings from Tambopata. Ronald I. Crombie made three recordings in Rondônia, Brazil in which a single call of an *E. fenestratus* is in the background. In two of them (USNM Tape 55, Cut 5 and USNM Tape 56, Cut 5, both from Alto Paraiso), the call sounds as though it consists of two notes, but can not be confirmed on an audiospectrogram due to the relative weakness of the call and strength of the background noise. The call on USNM Tape 56, Cut 8 from Santa Cruz da Serra is a bit stronger and the audiospectrogram indicates it is comprised of two notes at a dominant broadcast frequency of 3300 Hz. The calls from Rondônia, as expected, match the calls from Tambopata rather than the calls from Chapada dos Guimarães.

The advertisement call evidence is consistent with recognizing the Chapada dos Guimarães form as a species distinct from *Eleutherodacytlus fenestratus.*

Morphology.—There are two available names for *Eleutherodactylus* from Mato Grosso that potentially could apply to the Chapada dos Guimarães form. There are also a number of *Eleutherodactylus fenestratus*-like specimens from Mato Grosso. The purpose of this section is to compare the Chapada dos Guimarães form with these specimens to determine whether the Chapada dos Guimarães form occurs more broadly within the State of Mato Grosso and to determine whether there is an available name for it.

The materials for comparison comprise the following (Fig. 2 for Mato Grosso localities; Appendix 1 for specimen lists): the 2 types of *Telatrema heterodactylum* Miranda-Ribeiro, 1937; the 3 type specimens of *Eleutherodactylus crepitans* Bokermann, 1965; 11 specimens from Chapada dos Guimarães; 2 specimens from Fazenda Santa Edwiges; 1 specimen from Jacubim; 2 specimens from Barra do Tapirapés; and specimens considered to be *E. fenestratus*; 3 specimens from São Jose do Rio Claro; 8 specimens from Apiacás, 48 specimens

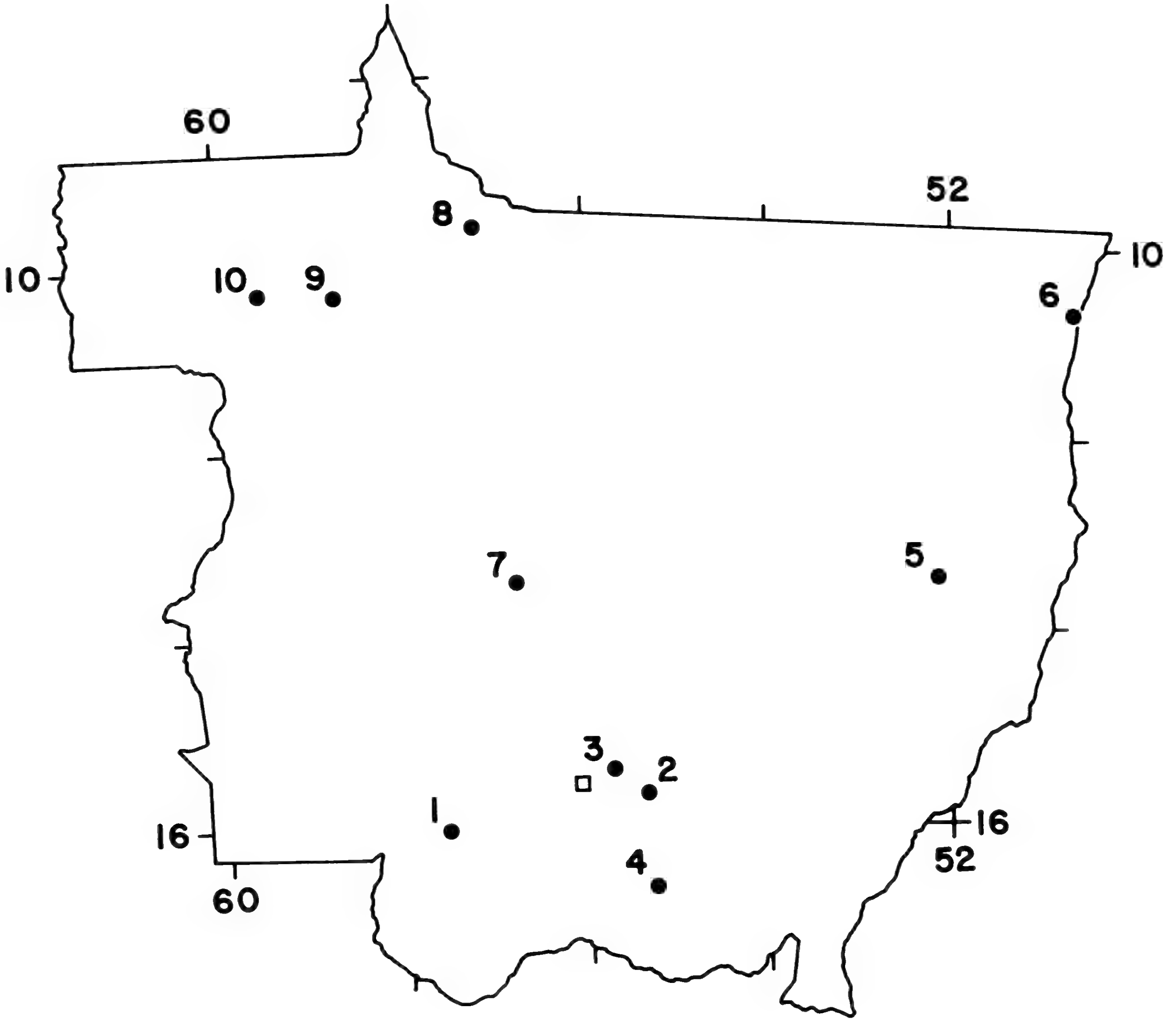

Fig. 2. Outline map of the State of Mato Grosso. See text for key to locality numbers. Open square is the city of Cuiabá.

from Juruena (measurement data taken for 10 females and 1 male), 1 specimen from Alto Juruena, 46 specimens from Aripuanã (measurement data taken for 10 males and females), and 28 specimens from Tambopata and Pakitza, Madre de Dios, Peru (the specimens from the nearby locality of Pakitza were added to those from Tambopata to bring the sample sizes up to at least 10 males and 10 females).

Patterns: The dorsal snout patterns demonstrate as much intra- as inter-population variation and are not discussed further. The other patterns analyzed demonstrate some levels of interpopulation variation (Tables 2–8). In some cases, the sample sizes are adequate to conclude that the variation is meaningful (e.g., the differences in loreal region pattern between the Mato Grosso populations of *Eleutherodactylus fenestratus* (Table 3, samples 7–10) and the Peruvian sample of *E. fenestratus*. In other cases, the differences are suggestive, but any conclusions are compromised by sample sizes. For example, there are two aspects of light mid-dorsal stripes that are impacted by small sample size. The first is that there is variation in the presence condition of the stripe. It may either be narrow or broad, and it may extend from the tip of the snout to the vent or from the interocular area to the vent. Because there were relatively few in-

Table 2.—Interorbital markings. Locality numbers refer to those in Fig. 2 (9a not mappable). A = Almost absent; B = Outlined only, not with expansion; C = Solid, not with expansion; D = Solid with single prominent posterior expansion; E = Solid with bifid prominent posterior expansion. Data are number of individuals demonstrating the various states (question mark indicates specimen faded, state uncertain).

Taxa	*E. heterodactylus*	*E. crepitans*	C. dos Guimarães	?	?	?	*E. fenestratus*					
Locality	1	2	3	4	5	6	7	8	9	9a	10	Peru
A												5
B								2	12		9	2
C	1[a]	3	11	1	1	?	3	6	9	1	11	9
D												6
E												6

[a] From illustration 2a (Miranda-Ribeiro 1937).

dividuals with light mid-dorsal stripes, the information had to be collapsed for comparison. Second, the sample size for the Chapada dos Guimarães form is too small to conclude that it lacks light mid-dorsal stripes, even though all 11 specimens examined lack them. There are three adequate samples of *E. fenestratus* to compare with the Chapada dos Guimarães form: Aripuanã, Juruena, and Peru. For Aripuanã, the probability of an individual having a mid-dorsal stripe is 0.35, thus the probability of not having a stripe is 0.65. If we use that probability to ask whether the Chapada dos Guimarães population could have the same occurrence of stripes, the answer is no: $0.65^{11} = P < 0.001$ (exact probability test). However, when the population data from Juruena and Peru are used, the answer is yes: for Juruena, the probability of not having a stripe is 0.91, for Peru 0.92, with $P = 0.35$ and 0.40 respectively. Thus, based on the low frequency of occurrence of mid-dorsal stripes in the Juruena and Peru samples, if the Chapada dos Guimarães form has mid-dorsal stripes at those same frequencies of occurrence, then the sample size is not adequate to have found individuals with that condition.

Morphological features: All but three individuals scored for tarsal fold variation had discernible tarsal folds (Table 9). It is likely that the three individuals thus scored actually have them but are preserved in such a manner that they are not discernible. The two individuals of *Eleutherodactylus crepitans* with discernible tarsal folds have a very different morphology from all other specimens examined (Table 9). The variation in toe fringe condition is continuous (Table 10). The fringed condition is weakly fringed, with noticeable basal toe webbing (the fringe is not as well-developed as in some species of *Leptodactylus,* for example). The variation in tubercles on the sole of the foot (Table 11) suggests that *E. crepitans* is distinctive (in contrast to completely distinct) from the other samples, and

Table 3.—Loreal region patterns. Locality numbers refer to those in Fig. 2 (Locality 9a not mappable). A = No pattern; B = Incomplete stripe in front of eye; C = Dark stripe from eye to nostril, entire loreal region may be dark. Data are number of individuals exhibiting various states. Pattern not discernible for specimen from locality 6.

Taxa	*E. heterodactylus*	*E. crepitans*	C. dos Guimarães	?	?	?	*E. fenestratus*					
Locality	1	2	3	4	5	6	7	8	9	9a	10	Peru
A												8
B	1	2	4		1				9	1	1	13
C		1	7	2			3	8	12		20	7

Table 4.—Supratympanic fold patterns. Locality numbers refer to those in Fig. 2 (9a not mappable). A = Fold not accentuated with dark brown band; B = Fold accentuated with interrupted dark brown band; C = Fold accentuated with solid dark brown band. Data are number of individuals demonstrating the various states (question mark indicates state uncertain due to fading or perspective of illustration).

Taxa	*E. heterodactylus*	*E. crepitans*	C. dos Guimarães	?	?	?	*E. fenestratus*					
Locality	1	2	3	4	5	6	7	8	9	9a	10	Peru
A	?[a]											2
B		3	2		1							12
C			9	2		?	3	8	21	1	21	14

[a] From illustration 2a (Miranda-Ribeiro 1937).

the variation in the Chapada dos Guimarães specimen tubercles is distinctive from the variation observed in the *E. fenestratus* samples.

Measurements: Male and female sizes vary among the samples (Table 12). Two points are worth noting, although additional samples are necessary to verify them statistically. There is no sexual size dimorphism in the *Eleutherodactylus crepitans* sample, whereas sexual size dimorphism is pronounced in all other samples that contain both sexes. The Chapada dos Guimarães form is smaller than the *Eleutherodactylus fenestratus* samples analyzed.

The results of multivariate discriminant function analyses for males and females (analyzed separately) agree in that the *Eleutherodactylus crepitans* specimens are clearly distinct from all other individuals analyzed (Fig. 3). The rest of the populations analyzed indicate that there is differentiation among them, but the degree of variation is consistent with both intra- and inter-specific variation based on similar studies in other groups of frogs.

Taxonomy

Telatrema heterodactylum *Miranda-Ribeiro, 1937.*—Alipio Miranda-Ribeiro described this species from "Matto-Grosso—Caceres, 2 exemplares colhidos na gruta dita 'Fazendinha' Comm. Rondon (1937: 67)." His son Paulo Miranda-Ribeiro designated specimen 106A in the collection of the Museu Nacional, Rio de Janeiro, as the lectotype (1955:411). The second specimen, the paralectotype, which also had the number 106 originally, was subsequently recatalogued as 5089.

Dr. P. E. Vanzolini (pers. comm.) was able to locate A. Miranda-Ribeiro's locality. Miranda-Ribeiro was a member of the Rondon Commission expedition and he collected the specimens in question himself. Caceres, as used by Miranda-Ribeiro, refers to the municipality, which at the time of the Rondon Commission expedition was very extensive. Vanzolini found in the Rondon Commission itinerary that Miranda-Ribeiro travelled to "Fazendinha" and returned to Caceres in the same day and that "Fazendinha" was near a place called Pirizal. Van-

Table 5.—Mid-dorsal stripe patterns. Locality numbers refer to those in Fig. 2 (9a not mappable). A = Absent; B = Present. Data are number of individuals demonstrating the states.

Taxa	*E. heterodactylus*	*E. crepitans*	C. dos Guimarães	?	?	?	*E. fenestratus*					
Locality	1	2	3	4	5	6	7	8	9	9a	10	Peru
A	1	3	11	2	1	2	3	8	44	1	34	26
B									4		12	2

Table 6.—Dorsal patterns. Locality numbers refer to those in Fig. 2 (9a not mappable). A = Indistinct or uniform; B = Dark symmetrical spots; C = Dark chevron in medial scapular region followed by dark blotches posteriorly; D = Dark W-shaped mark in medial scapular region followed by dark blotches posteriorly; E = Extended dark W-shaped pattern (additional strophes to next in series from inverted V to W) in medial scapular region followed by dark blotches posteriorly. Data are number of individuals demonstrating the various states (question mark indicates uncertain condition due to fading).

Taxa	*E. heterodactylus*	*E. crepitans*	C. dos Guimarães	?	?	?	*E. fenestratus*					
Locality	1	2	3	4	5	6	7	8	9	9a	10	Peru
A			2		1	?	1	3	7	1	9	13
B				2				1	3		4	
C	1[a]							4	2		2	
D		1	9				2		9		6	15
E		2										

[a] From illustration 2a, b (Miranda-Ribeiro 1937).

zolini located a "Fazendinha" that not only meets these conditions, but is in an area known to have sandstone caves (grutas = caves) at 16°00′S, 57°36′W (Fig. 2, Locality 1).

Lynch & Duellman (1997:225) recognized *Eleutherodactylus heterodactylus* (Miranda-Ribeiro, 1937) as a distinct species and included it in the *Eleutherodactylus binotatus* species-group. As Lynch and Duellman did not examine the types, we offer the following observations.

Both types are faded such that most features of any color patterns are no longer discernible. The lectotype is in poor condition, the paralectotype is in worse condition. The paralectotype is very brittle and fragile and disintegrates more each time it is handled. The lectotype is the (noticeably) larger of the two, and the only specimen measured for purposes of this paper. WRH recorded the measurements (in mm) of the lectotype as: SVL 24.6 (contrasted to Miranda-Ribeiro's measurement of 27); head length 8.6; head width 8.5; eye–nostril distance 3.5; eye–eye distance 5.1; greatest tympanum diameter 2.4; thigh 13.9; shank 14.1; foot 12.0; width of 3rd finger disk 1.4; width of 4th toe disk 0.7. The lectotype has slits in the floor of the mouth, but they appear to be cuts, not vocal slits. The sex of the lectotype can not be determined with certainty without dissection, which given the poor condition of the specimen was considered inappropriate.

The following support recognition of *Telatrema heterodactylum* as a distinct and valid species of *Eleutherodactylus,* confirming Lynch & Duellmans' (1997) assessment.

The disks on fingers 3 and 4 are very large, much larger than the disk on the fourth toe, and the shape is ovate (Fig. 4a). The disks on fingers 3 and 4 of the other *Eleutherodactylus* examined are expanded, but either the same size or just larger than

Table 7.—Posterior face of thigh patterns. Locality numbers refer to those in Fig. 2 (9a not mappable). A = Uniform; B = Finely mottled around vent, rest uniform; C = Finely mottled; D = Mottled. Data are number of individuals demonstrating the various states.

Taxa	*E. heterodactylus*	*E. crepitans*	C. dos Guimarães	?	?	?	*E. fenestratus*					
Locality	1	2	3	4	5	6	7	8	9	9a	10	Peru
A	2		7	2			3	7	18		20	5
B		3	3					1	3	1	1	8
C			1									15
D					1	1						

Table 8.—Belly patterns. Locality numbers refer to those in Fig. 2 (9a not mappable). A = Almost immaculate; B = Noticeably flecked or mottled. Data are number of individuals demonstrating the states. Specimen from locality 6 too faded to score.

Taxa	*E. heterodactylus*	*E. crepitans*	C. dos Guimarães	?	?	?	*E. fenestratus*					
Locality	1	2	3	4	5	6	7	8	9	9a	10	Peru
A	1	3	10	2	1			6	10		11	28
B			1				3	2	11	1	10	

the disks on toe 4 and they are broadly triangular in shape (Fig. 4b, c).

The type illustrations (most likely that of the lectotype, Miranda-Ribeiro 1937, Fig. 2a–b) show a pair of ill-defined light longitudinal stripes from behind the eye to the sacrum. This feature is not seen in any of the other *Eleutherodactylus* examined for this study.

The type locality is characterized by a very open vegetation formation lacking gallery forests. *Eleutherodactylus fenestratus* is a forest denizen and the Chapada dos Guimarães form inhabits well-developed gallery forests. *Eleutherodactylus crepitans* also occurs in open habitats, but is morphologically very distinct from *E. heterodactylus.*

One other morphological feature will require fresh material to evaluate. There is no indication of any tarsal fold or other tarsal decoration on either the lectotype or paralectotype, suggesting that, if in fact the tarsus lacks a fold, that would be another feature distinguishing the species from all other Mato Grosso *Eleutherodactylus.*

Eleutherodactylus heterodactylus (Miranda-Ribeiro 1937) is thus far known only from the original two specimens collected by Miranda-Ribeiro from "Fazendinha." All other members of the *Eleutherodactylus binotatus* group, to which Lynch & Duellman (1997) assigned *E. heterodactylus,* occur in eastern Brazil, primarily in the Atlantic Forest Morphoclimatic Domain. Inclusion of *E. heterodactylus* in this group does not make zoogeographic sense.

Status of Eleutherodactylus crepitans *Bokermann, 1965.*—Werner C. A. Bokermann described the species based on three specimens from São Vicente, Mato Grosso. The holotype and allotype are now in the collections of the Museu de Zoologia, Universidade de São Paulo and the other paratype is in the Museu Nacional, Rio de Janeiro.

John Lynch (1980:8) synonymized *Eleutherodactylus crepitans* Bokermann, 1965 with *E. fenestratus* (Steindachner 1864). Lynch did not examine the specimens of *E. crepitans* (1980:6). Lynch argued that because Bokermann was unaware

Table 9.—Tarsal fold states. Locality numbers refer to those in Fig. 2 (9a not mappable). A = Absent; B = Short, oblique, lying more than length of inner metatarsal tubercle from inner metatarsal tubercle; C = Moderately short, less than ½ length of tarsus, lying less than length of inner metatarsal tubercle from inner metatarsal tubercle; D = Long, greater than ½ length of tarsus, lying less than length of inner metatarsal tubercle from inner metatarsal tubercle. Data are number of individuals demonstrating the various states. Data not taken for one desiccated individual from locality 10.

Taxa	*E. heterodactylus*	*E. crepitans*	C. dos Guimarães	?	?	?	*E. fenestratus*					
Locality	1	2	3	4	5	6	7	8	9	9a	10	Peru
A	1	1									1	
B		2										
C			10	2	1	1	3	8	21	1	19	28
D			1			1						

Table 10.—Toe fringe states. Locality numbers refer to those in Fig. 2 (9a not mappable). A = Toes free; B = Toes with lateral ridges; C = Toes with modest lateral fringes. Data are number of individuals demonstrating the states.

Taxa	*E. heterodactylus*	*E. crepitans*	C. dos Guimarães	?	?	?	*E. fenestratus*					
Locality	1	2	3	4	5	6	7	8	9	9a	10	Peru
A	1	3							1		5	5
B			3					3	8		6	17
C			8	2	1	2	3	5	12	1	10	6

that *E. fenestratus* was a valid species, Bokermann compared his new species with inappropriate species from Ecuador, from which they were very distinct. However, had Lynch examined the type material of *E. crepitans,* he would have found that they differ from *E. fenestratus* as well.

The following argue for recognizing *Eleutherodactylus crepitans* as a valid species.

Eleutherodactylus crepitans has short, oblique tarsal folds, separated from the inner metatarsal tubercle by a distance greater than the length of the fold. *Eleutherodactylus heterodactylus* apparently lacks tarsal folds. *Eleutherodactylus fenestratus* and the Chapada dos Guimarães form have longer (but still relatively short) tarsal folds, parallel to the long axis of the tarsus, separated by a short distance (less than length of the fold) from the inner metatarsal tubercle.

Eleutherodactylus crepitans does not have marked sexual dimorphism in size. Both *Eleutherodactylus fenestratus* and the Chapada dos Guimarães form show marked sexual size dimorphism.

The overall body shape of *Eleutherodacytlus crepitans* differs markedly from that of *E. fenestratus* and the Chapada dos Guimarães form (Fig. 3).

Bokermann (1965:264) made a point of stating that the specimens of *Eleutherodactylus crepitans* were obtained in grass-shrub vegetation in the middle of large blocks of granite from such a dry habitat that he would never have expected to find frogs there. The immediate vicinity of São Vicente does have a granitic intrusion of rather small extent and is the only such granitic habitat in Mato Grosso (Brasil 1982). It would not be surprising if *E. crepitans* is limited to this distinctive habitat.

Bokermann (1965:264) indicated that males called at night from sandy hiding places among rocks. He described the call as consisting of two notes in sequence, like a short and coarse click, repeated many times but irregularly (translation by P. E. Vanzolini). The two note call of *Eleutherodactylus crepitans* is more similar to *Eleutherodactylus fenestratus* than the Chapada dos Guimarães form, but the frequent calling of *E. crepitans* is different from the very infrequent calls of both *E. fenestratus* and the Chapada dos Guimarães form.

Questionable status specimens.—The

Table 11.—Maximum number of tubercles on sole of foot. Locality numbers refer to those in Fig. 2 (9a not mappable). Data are number of individuals demonstrating the states.

Taxa	*E. heterodactylus*	*E. crepitans*	C. dos Guimarães	?	?	?	*E. fenestratus*					
Locality	1	2	3	4	5	6	7	8	9	9a	10	Peru
0			2								1	
1			8	2	1	2		5	9		9	23
2			1				1	2	9		9	5
3	1	1					2	1	3	1	2	
4		2										

Table 12.—Adult size. Locality numbers refer to those in Fig. 2 (9a not mappable). Data are SVL ranges in mm.

Taxa	*E. heterodactylus*	*E. crepitans*	C. dos Guimarães	?	?	?	*E. fenestratus*					
Locality	1	2	3	4	5	6	7	8	9	9a	10	Peru
Females		30	34–36			34	38–41		37–40	42	37–44	40–52
Males		28–29	22–27		30				30		26–32	27–34
Largest juveniles	25			30				29				

name *Hylodes gollmeri bisignata* Werner, 1899, which based on geography should be considered as an available name for the frogs considered in this paper, and specimens of *Eleutherodactylus* from three localities in Mato Grosso can not be unequivocally assigned to either *Eleutherodactylus crepitans, fenestratus, heterodactylus,* or the Chapada dos Guimarães form. Advertisement calls are not available at present for any of the specimens involved. At this time, they are best left as indeterminate.

Werner (1899) gave a brief description of *Hylodes gollmeri bisignata* without locality information in the type description. Häupl & Tiedemann (1978) indicated that the holotype, NMW 16502, in the Naturhistorischen Museums Wien collection was from Chaco, Bolivia. Lynch & Duellman (1997) considered *bisignatus* to be a synonym of *Eleutherodactylus fenestratus.* Based on the fact that the Chaco and Amazonian hylaea frog faunas are virtually distinct from each other at the species level, the validity of *E. bisignatus* should be reconsidered. The original description is too brief to be of help in evaluating this suggestion. Dr. Lynch examined the type of *H. g. bisignata,* but his original notes are not in the appropriate folder in his archives (pers. comm.). The Naturhistorisches Museum Wien now has a policy of not loaning types, precluding our examination of the type for this paper. We suspect that *bisignatus* is a species of *Eleutherodactylus* distinct from *E. fenestratus.* If it is the same as any species that occurs in Mato Grosso, it might be conspecific with *E. heterodactylus,* based on most similar (but still quite different) habitat occurrences.

The two specimens from the Panatanal locality of Fazenda do Santa Edwiges (Fig. 2, Locality 4) could either be the same as the Chapada dos Guimarães form or a distinct species. The smaller specimen (MZUSP 71103) has a tarsal fold like that of the Chapada dos Guimarães form, but the larger specimen (MZUSP 71104, which looks like it died before it was preserved) appears to have a much longer tarsal fold.

The single specimen from Jacubim (MZUSP 4277) has completely mottled thighs with a large pattern, such that the white blotches almost cover the same total area as the darker ground hue. The thigh pattern differs markedly from other specimens discussed in this paper, but is closer to that of specimens identified as *Eleutherodactylus* cf *peruvianus* (e.g., MZUSP 80854, 80856–80857, 80859, 80863) from the Amazon forest locality of Apiacás. Jacubim, however, is in an area of Cerrado-seasonal forest contact (Fig. 2, Locality 5).

The two specimens from Barra do Tapirapés are very faded and their proper taxonomic allocation may never be ascertained until fresh specimens from the locality are available. The fading extends to the posterior surfaces of the thighs, but it does appear that the thighs are mottled in a similar fashion to the pattern observed in MZUSP 4277 from Jacubim, with which they may be conspecific.

Status of the Chapada dos Guirarães form.—As documented above, the Chapada dos Guimarães *Eleutherodactylus* represents a distinct species from all other known *Eleutherodactylus,* which we describe as:

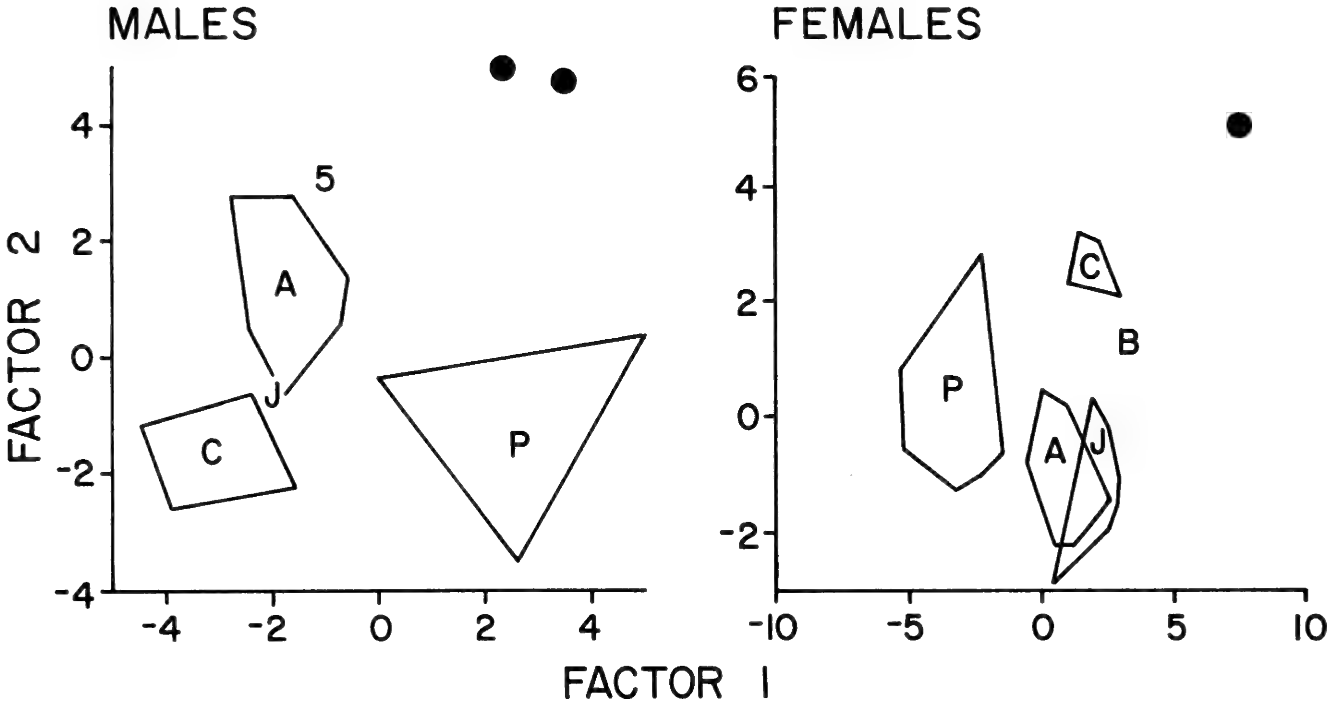

Fig. 3. Discriminant function analysis results for males and females. Minimum polygons contain all individuals for sample sizes >3. Dots = *Eleutherodactylus crepitans*; A = sample from Aripuanã, Mato Grosso; B = individual from Barra do Tapirapés, Mato Grosso; C = sample from Chapada dos Guimarães, Mato Grosso; J = individual (male) and sample (females) from Juruena, Mato Grosso; P = sample from Peru; 5 = individual from Jacubim, Mato Grosso.

Eleutherodactylus dundeei,
new species
Figs. 1b, 5

Holotype.—MZUSP 79834, adult male from Brazil: Mato Grosso; Chapada dos Guimarães, Veu da Noiva, Rio Coxipozinho, approximately 15°25′S, 55°47′W. Collected by Miriam H. Heyer, W. Ronald Heyer, and Liliam Patricia Pinto on 25 Sep 1996.

Paratopotypes.—MZUSP 79835–79837 (1 female, 2 males), same data as holotype.

Paratypes.—All from Brazil: Mato Grosso; Chapada dos Guimarães; MNRJ 19785 (female), collected by Ermínia (UFF) on 24 Oct 1987; MZUSP 76237 (juvenile), an originally unnumbered specimen from the Werner C. A. Bokermann collection collected by A. Sebben and A. Schwartz on 15 Jun 1988; MZUSP 85614 (male), originally WCAB 15546 collected by M. Alvarenga, F. M. Oliveira, and Werner C. A. Bokermann from 15–25 Nov 1963; USNM 507897–507898 (female, male), Casa de Pedra, collected by Miriam H. Heyer, W. Ronald Heyer, Liliam Patricia Pinto on 28 Sep 1996; USNM 507899 (male, call voucher for Fig. 1b), Estancia Monarca, collected by Miriam H. Heyer, W. Ronald Heyer, Liliam Patricia Pinto on 30 Sep 1996; USNM 507900 (female), Escola Evangelica de Buriti, collected by Miriam H. Heyer, W. Ronald Heyer, Liliam Patricia Pinto on 1 Oct 1996.

Diagnostic definition (scheme established by Lynch, e.g., 1979, of numbered character states followed here for ease of comparison).—Skin of upper surfaces finely

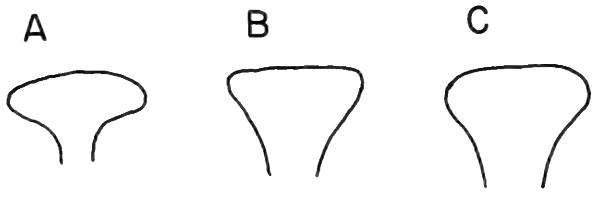

Fig. 4. Diagrammatic outlines of shape of third finger disk based on free-hand sketches. A. Holotype of *Telatrema heterodactylum,* actual width of disk 1.4 mm. B. Holotype of *Eleutherodactylus crepitans,* actual width 0.9 mm. C. Chapada dos Guimarães form, actual width 1.3 mm (based on USNM 507897).

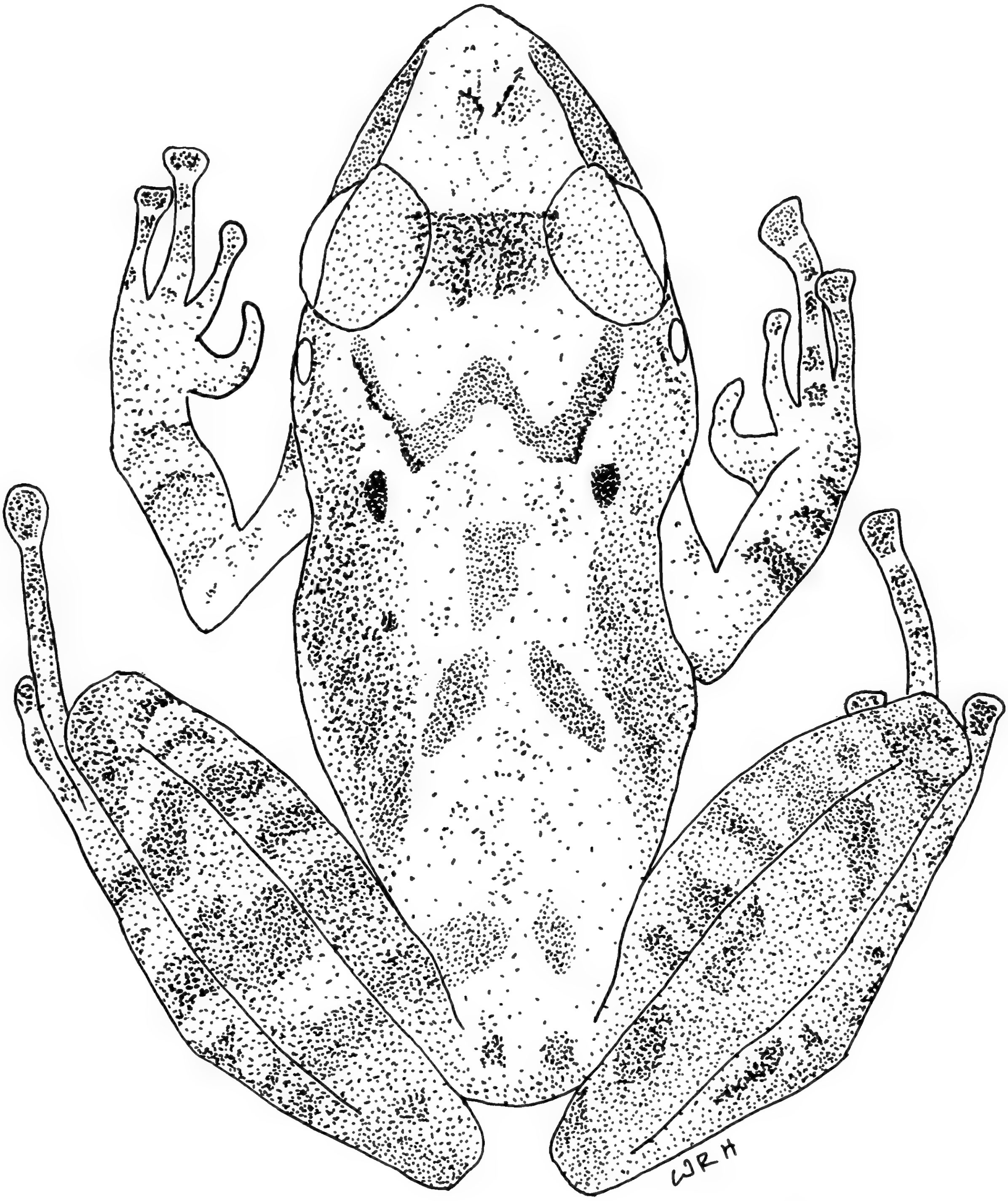

Fig. 5. Dorsal view of paratype of *Eleutherodactylus dundeei,* new species, USNM 507899. This specimen has the most contrasting pattern among the type series. Other specimens have similar, but fainter markings.

pebbled with few to many scattered white fleshy tubercles, tubercles denser posteriorly, skin of throat, chest, and anteriormost belly smooth, rest of belly weakly areolate; tympanum distinct, its horizontal diameter about $\frac{1}{2}$–$\frac{3}{5}$ eye opening diameter; snout subelliptical in dorsal view, rounded in profile; upper eyelid width equal to or (usually) slightly smaller than interorbital distance, with same fine pebbling of back with scattered, low, flattened, light tubercles; no cranial crests; vomerine teeth in two small patches well posterior to choanae, separated from each other by about the width of a single tooth patch; males with vocal slits and single subgular vocal sac, either noticeably expanded and wrinkled in preservation or not; male nuptial pads of two weak light glandular patches; first finger about same size or just longer than second; fingers bearing disks (largest on III and IV); largest disks broader than long; fingers free or with weak lateral keels; 2–7 light spots indicating weakly developed ulnar tubercles (tubercles themselves visible in only some individuals); short tarsal fold, about ⅓ length of tarsus, otherwise tarsus smooth; heel smooth to granular, lacking tubercle(s); 2 metatarsal tubercles, inner oval, 2–3 times size of outer; 0–2 fleshy plantar tubercles; toes free or (usually) bearing weakly to well developed lateral keels; individuals with well-developed keels with basal toe webbing; predominantly brown frog, no flash colors; posterior surfaces of thighs flesh color-purplish in life, tan/brown in preservative; adults small, males 22–27 mm, females 34–36 mm SVL.

Eleutherodactylus dundeei is most similar to and most likely to be confused with *Eleutherodactylus fenestratus. Eleutherodactylus dundeei* is smaller (males 22–27 mm, females 34–36 mm SVL) than *E. fenestratus* (males 26–34 mm, females 37–52 mm SVL). The belly of *E. fenestratus* is either entirely smooth; or weakly areolate only on the lateralmost portions, but not areolate posteriorly; the belly of *E. dundeei* is weakly areolate at least posteriorly. Male *E. dundeei* have two weakly developed light glandular nuptial asperities on each thumb; male *E. fenestratus* have a single, better developed light glandular nuptial asperity on each thumb.

Description of holotype.—Snout shape subelliptical in dorsal outline, rounded in profile; canthus rostralis sharply rounded; lip weakly flared; upper eyelid width about equal interocular distance; no external indications of cranial crests; tympanum distinct, horizontal diameter including annulus about ½ eye opening diameter, horizontal diameter < vertical diameter; vomerine teeth in two small patches, well posterior to rounded choanae, separated from each other by about width of a single tooth patch; vocal slits present, elongate; vocal sac single, subgular, slightly expanded externally in preservation; finger lengths I just >II<IV<III (left finger IV mostly missing); finger tips on fingers I and II slightly expanded, small, round, lacking circumferential grooves, fingers III and IV with expanded disks, triangular, broader than long, with circumferential groove and upper surface weakly to noticeably notched; fingers lacking noticeable lateral keels; no finger webbing; palmar tubercle large, ovate-heart-shaped, larger than proximate ovoid thenar tubercle, one well-developed supernumerary palmar tubercle associated with each digit; subarticular tubercles distinct, rounded, single, each thumb with 2 weakly developed but distinct patches of light glandular nuptial excrences; outer ulnar region with a series of 6–7 light spots, apparently with low tubercles in life, but only one weakly visible on each arm; supratympanic fold distinct; no other distinct glands or folds on body; upper eyelid weakly pebbled with several light tubercles, rest of back texture weakly pebbled with scattered light fleshy tubercles; throat smooth, discoidal belly fold distinct, chest and adjoining belly to about mid-belly smooth, sides of and posterior belly weakly areolate, ventro-posterior surfaces of thighs areolate, rest of ventral limb surfaces smooth; toe lengths I<II≈III<V<IV (condition B as used in Lynch & Duellman 1997, appendix III); disks on toes I and V small, round, disks on toes II, III, IV increasing in size, largest disks triangularly ovate, broader than long, upper surfaces emarginate or weakly notched; sides of toes keeled, strongest on inner sides of toes II, III, IV, forming basal web, not encompassing the basal subarticular tubercles, best developed between toes II, III, IV; outer round metatarsal tubercle about ¼ size of ovate inner metatarsal tubercle; tarsal fold distinct, short, about ¼ length of tarsus, separated from inner metatarsal tubercle by a distance of about ½ length of tarsal fold, rest of outer tarsus smooth; heel smooth, lacking tubercle(s) or calcar; plantar surface with one prominent

fleshy tubercle; subarticular tubercles moderately developed, weakly pungent.

Coloration in alcohol: A tan frog with brown markings. Tip of snout lightest, expanding into somewhat darker but light triangle bounded by canthus rostralis and dark interorbital mark, with a few brown dots and lines. Dark canthal stripe in front of eye only extending about ¼ distance to nostril. Loreal region almost uniform brown. Upper lip indistinctly barred. Supratympanic fold dark brown. Faint interorbital bar, defined by straight solid brown line anteriorly, very weakly defined posteriorly as a shallow U with a few dark dots in the interorbital mark. A faint dark W-shaped mark in the pre-scapular area followed by a median, faint, inverted Y-shaped mark between scapular and sacral region, followed by two median irregular sacral chevrons. Noticeably dark pair of lateral spots behind eyes in scapular region. Upper limbs tan with irregular darker cross bands. Series of 6–7 light spots on outer ulnar region. Throat speckled with melanophores. Chest and belly light, almost immaculate, but with a very few scattered melanophores. Posterior surfaces of thighs with very fine mottle pattern on area just around vent, otherwise uniform tan. Outer tarsus and sole of foot dark brown.

Measurements of holotype.—SVL 23.6 mm, head length 9.6 mm, head width 7.9 mm, eye opening diameter 3.0 mm, eye–nostril distance 3.0 mm, eye–eye distance 4.9 mm, horizontal tympanum diameter 1.8 mm, vertical tympanum diameter 1.9 mm, thigh length 11.6 mm, shank length 13.3 mm, foot length 11.7 mm, width of 3rd finger disk 1.0 mm, width of 4th toe disk 0.7 mm.

Variation.—Most details of variation have been described in the preceding sections. Additional measurement variations are (broken down by sex only when range of one not subsumed in other): head length 39–42% SVL; head width 33–38% SVL; eye–nostril distance 12–14% SVL; eye–eye distance 20–22% SVL for males, 18–19% for females; tympanum diameter 7–9% SVL; thigh length 48–53% SVL; shank length 52–57% SVL; foot length 47–54% SVL for males, 46–53% for females; width of 3rd finger disk 3–4% SVL; width of 4th toe disk 3–4% SVL.

Color in life.—Iris bright bronze above, dull bronze below; posterior face of thigh flesh color-purplish; belly white with yellow wash; no flash colors (based on USNM 507897–507898).

Advertisement call.—Described in previous section (Fig. 1b).

Etymology.—Named for Dr. Harold A. Dundee for his personal, financial, and scientific contributions to the field of herpetology.

Ecological notes.—Data are available for eight individuals. Five of them were collected in the late morning on dead leaves or under 5 cm diameter rocks on the ground, four of these 3–6 m from a river bank in rainforest-like gallery forest (MZUSP 79834–79837), one of these on dead leaves on the ground on the bank of a tree-shaded pond (USNM 507900). Two individuals were taken shortly after dark in cerrado gallery forest 2 m from a 2 m wide stream either on the surface of the soil (USNM 507897) or on a 0.3 m diameter log (USNM 507898). The call voucher (USNM 507899) was taken at night from secondary cerrado vegetation on a leaf of a herbaceous plant, less than 1 m above ground.

Distribution.—All known specimens have been collected from within 25 km of the town of Chapada dos Guimarães in the limited region identified as having mesophilic seasonal forest vegetation cover in the Cartograma de Vegetação do Estado de Mato Grosso, produced by the Consórcio Nacional de Engenheiros Consultores S.A., published by the Governo do Estado de Mato Grosso (Fig. 6). There are other islands of similar vegetation cover in the same region (Fig. 6) which might be expected to contain *Eleutherodactylus dundeei.* We predict that either *E. dundeei* is restricted to the known Chapada dos Gui-

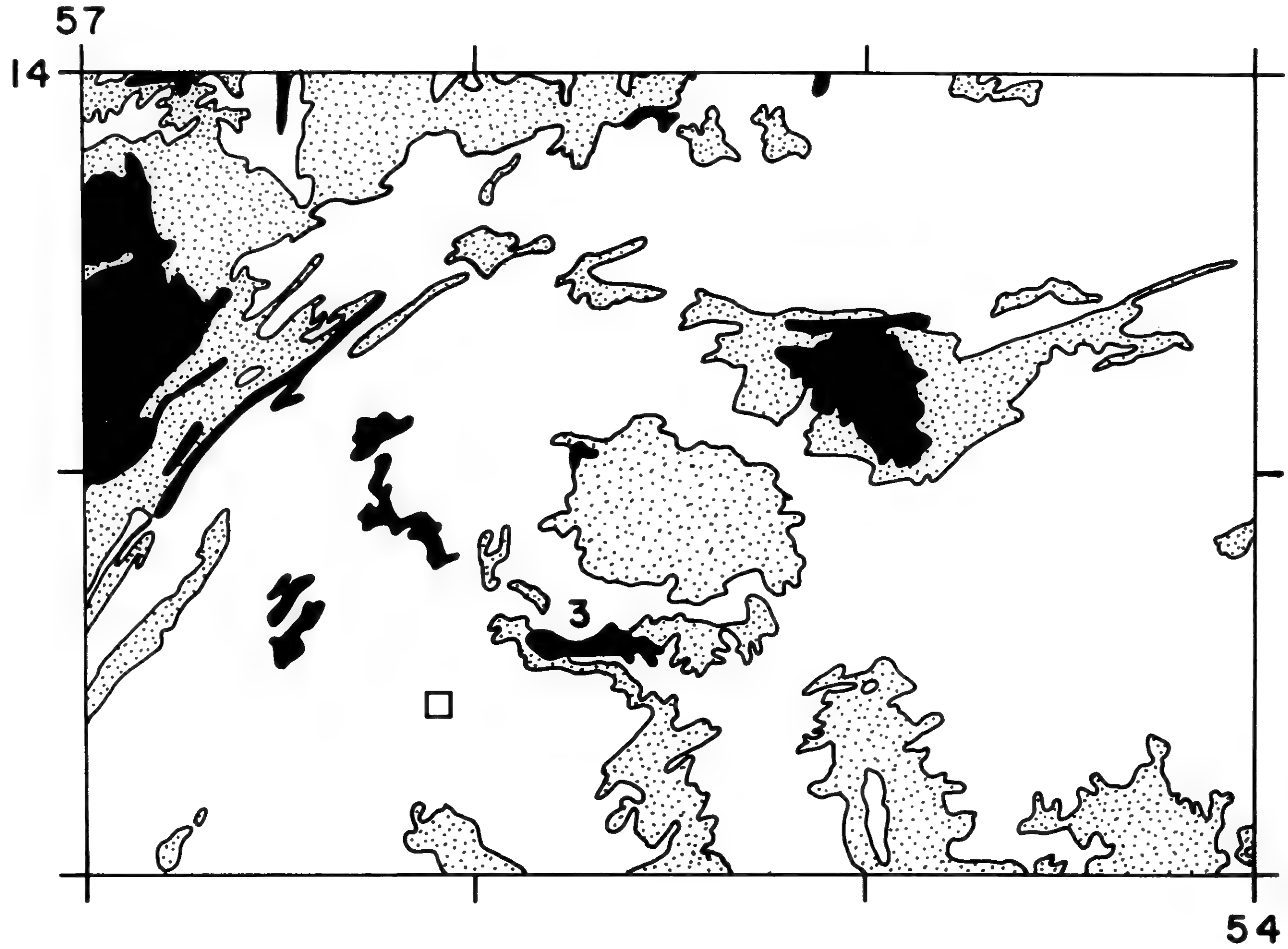

Fig. 6. Major vegetation types in portion of the State of Mato Grosso surrounding Chapada dos Guimarães. Black areas are mesophilic seasonal forests. Stippled areas are dense cerrado (cerradão) and forest/cerrado contact regions. Rest of region is covered by various forms of cerrado vegetation (except cerradão). Open square is the city of Cuiabá.

Eleutherodactylus dundeei is thus far only known from the mesophilic seasonal forest block identified as 3 on the map, but other nearby blocks should be explored for the species. Map redrawn from "Cartograma de Vegetação do Estado do Mato Grosso," produced by Consórcio Nacional de Engenheiros Consultores S.A.

marães vegetation type block or to it and one or more of the additional habitat islands identified in Fig. 6.

Discussion

Eleutherodactylus fenestratus, with the removal of *Eleutherodactylus crepitans* and *dundeei,* has an Amazonian rainforest distribution (assuming *Eleutherodactylus bisignatus* is not a synonym of *E. fenestratus*). There has not been an adequate study of variation for *E. fenestratus.* The limited data we analyzed indicate that there is at least interpopulational variation in *E. fenestratus.* Analyzing variation throughout the entire range of the species would be an obvious next step to understand the significance of the variation we found.

Chapada dos Guimarães has a very interesting frog fauna from a zoogeographical perspective. The landscape surrounding the Chapada is cerrado. There are expected cerrado frog species at Chapada dos Guimarães, such as *Bufo paracnemis, Scinax fuscovarius, Leptodactylus labyrinthicus,* and *Physalaemus nattereri.* There are also Chaco and Amazonian elements represented. For example, the Chaco species *Leptodactylus chaquensis* was collected syntopically with the Amazonian species *Leptodactylus mystaceus* in 1996. Finally, there are at least two species thus far known only from Chapada dos Guimarães, *Phyllomedusa cen-*

tralis Bokermann, 1965 and *Eleutherodactylus dundeei.* Obviously, the frog fauna of Chapada dos Guimarães represents a rich and complicated history, worthy of much more detailed study. There is actually a fair amount of information available for frogs from Chapada dos Guimarães to base such a study upon. Herbert Huntingdon Smith collected materials reported on by E. D. Cope (1887) and housed at the Academy of Natural Sciences in Philadelphia. At least one of the species reported, *Leptodactylus petersii,* has not been collected since from Chapada dos Guimarães (Heyer 1994:79, Cope's *Leptodactylus brevipes* = *L. petersii*). Boulenger (1903) listed nine species collected by the Percy Sladen Expedition to central Brazil. The species Boulenger listed as *Hylodes gollmeri* is probably the species we describe as *Eleutherodactylus dundeei.* All other species of Boulenger's list are plausible (with taxonomic adjustments) except for *Ceratophrys cristiceps,* which should be re-examined. Werner C. A. Bokermann and colleagues made collections which now (for the most part) are at MZUSP. MZUSP also has materials collected by Drs. Rita Kloss and Francisca C. do Val. Adão Cardoso also collected at Chapada dos Guimarães, and those specimens are housed at the Universidade Estadual de São Paulo in Campinas. As Chapada dos Guimarães is now a tourist attraction, it is likely that there are other incidental collections waiting study in various collections as well.

Acknowledgments

PRODEAGRO and CENEC made the fieldwork possible during which the recordings of *Eleutherodactylus dundeei* were obtained. Without these recordings, this paper would not have been initiated. Drs. John D. Lynch and P. E. Vanzolini critically reviewed the manuscript. AMM thanks the National Museum of Natural History for the opportunity to participate in the 1997 Research Training Program. WRH thanks Dr. P. E. Vanzolini and the Museu de Zoologia da Universidade de São Paulo for characteristic help and access to the collections. Dr. Ulisses Caramaschi facilitated examination of specimens in the collections of the Museu Nacional, Rio de Janeiro. WRH's research for this paper was supported by the Neotropical Lowlands Research Program, National Museum of Natural History, Dr. Richard P. Vari, Principal Investigator.

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Appendix 1
Specimens examined

Eleutherodactylus crepitans.—Brazil: Mato Grosso; São Vicente, 15°38′S, 55°23′W, MNRJ 3985 (paratype), MZUSP 73671 (allotype), 85628 (holotype).

Eleutherodactylus dundeei.—See species account.

Eleutherodactylus fenestratus.—Brazil: Mato Grosso; [Alto Juruena—see preceding Juruena], Apiacás, 09°34′S, 57°23′W, MZUSP 80851–80853, 80855, 80858, 80860–80862; Aripuanã, 10°24′S, 59°19′W, MZUSP 80643–80648, 80652–80654, 86410; Alto Juruena (locality is the upper Rio Juruena and cannot be assigned specific coordinates), MZUSP 85540; Juruena, 10°18′S, 58°32′W, MZUSP 86153–86200; São José do Rio Claro, 13°26′S, 56°44′W, MZUSP 86358–86360.

Peru: Madre de Dios; Pakitza, 11°58′S, 71°14′W, USNM 333014, 342618–342622, 342851–342853, 345172; Tambopata, 12°50′S, 69°17′W, USNM 222268, 247298–247304, 247630–247631, 268941–268944, 314901, 332438–332439, 342993.

Eleutherodactylus heterodactylus.—Brazil: Mato Grosso; Fazendinha, near Pirizal, 16°00′S, 57°36′W, MNRJ 106 (lectotype), 5089 (paralectotype).

Eleutherodactylus sp.—Brazil: Mato Grosso, Barra do Tapirapés, 10°39′S, 50°36′W, MZUSP 85645–85646; Jacubim, 13°20′S, 52°09′W, MZUSP 4277; Fazenda Santa Edwiges, 16°38′S, 55°11′W, MZUSP 71103–71104.

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A new genus and species of frog from Bahia, Brazil (Amphibia: Anura: Leptodactylidae) with comments on the zoogeography of the Brazilian campos rupestres

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Abstract.—A new genus and species of frog, *Rupirana cardosoi,* is described from the northern Espinhaço Range in the State of Bahia, Brazil. The new genus shares most character states with the genus *Thoropa,* but cladistic analysis of morphological data indicates that most of these shared features are primitive states. The cladistic analysis indicates that *Rupirana* and *Thoropa* do not have a close sister-group relationship with each other. *Rupirana cardosoi* is another addition to the many species endemic to the campos rupestres of the Espinhaço Range. The amphibians of the campos rupestres show a much stronger biogeographical affinity with the Atlantic Forest biota than other groups studied; these other groups show a much stronger affinity with the biota of the diagonal of open formations running from northeast Brazil (caatingas-cerrados) to Argentina and Paraguay (Gran Chaco).

Several years ago, Dr. Miguel T. Rodrigues brought my attention to a series of unusual frogs he had collected at two localities in the State of Bahia, Brazil, asking me if I knew what they were. I did not. Drs. Rodrigues and P. E. Vanzolini kindly put the specimens at my disposal for further study, but for various reasons, detailed study was delayed. Shortly after I had examined aspects of the myology and skeleton of the taxon, I had occasion to evaluate some of the problematical specimens of the Werner C. A. Bokermann collection as they were being catalogued into the Museu de Zoologia da Universidade de São Paulo collection. I found a series of the same taxon from a third locality in Bahia. All known localities are in the distinctive campos rupestres formation of Brazil. The purpose of this paper is to demonstrate that the new frog differs from all other known leptodactylid genera, provide a description for it, and briefly comment on its relationships and zoogeography.

Methods and Materials

One male (MZUSP 65204) was superficially dissected to obtain myological information on jaw, hyoid, and thigh musculature for the characters used in a previous study of leptodactylid relationships (Heyer 1975). A second female specimen (MZUSP 68959) was cleared-and-stained using the double-staining technique for cartilage and bone (Dingerkus & Uhler 1977) to evaluate osteological features.

For the species description, measurement data were taken with a dial calipers to the nearest 0.1 mm following the definitions in Heyer et al. (1990).

Relationships were analyzed with PAUP 3.1 (Swofford 1993).

Comparison with Leptodactylid Genera

Lynch (1971) still provides the most complete data set for leptodactylid genera, providing a baseline for comparison with subsequent studies. He recognized four New World subfamilies of the family Lep-

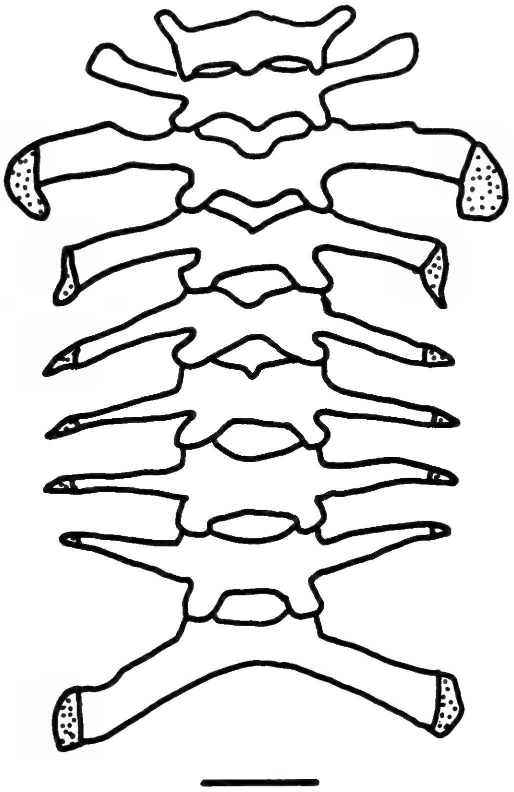

Fig. 1. Vertebral column of *Rupirana cardosoi,* MZUSP 68959. Cartilage stippled. Scale line = 2 mm.

todactylidae: Ceratophryinae; Elosiinae; Leptodactylinae, and Telmatobiinae. The Australian and African leptodactyloids Lynch treated as subfamilies of the family Leptodactylidae are now recognized as the separate families Myobatrachidae and Heleophrynidae, respectively (Frost 1985; Duellman & Trueb 1986).

The Bahia frog is not a member of the subfamilies Ceratophryinae, Elosiinae, or Leptodactylinae as defined by Lynch (1971). Rather than document this statement with a comparison of all states Lynch used, only a single character is used as an example. Ceratophryinae members have widely expanded transverse processes of the anterior presacral vertebrae; the Bahia frog does not (Fig. 1). Elosiinae species have a pair of dermal, scute-like glandular pads on the dorsal surface of each digital disk; the Bahia form lacks digital disks. Leptodactylinae genera have a bony sternal style; the sternum is a cartilaginous plate in the Bahia frog (Fig. 2).

Lynch (1971:112–113) listed nine characters defining the subfamily Telmatobiinae (character numbers are those used by Lynch): (1) sternum cartilaginous; (2) vertebral shield lacking; (3) transverse processes of the anterior presacral vertebrae not widely expanded; (9) when present, maxillary teeth blunt and pedicellate; (35) mandible lacking odontoids; (39, the 38 is a typographical error on p. 113) *m. petrohyoideus anterior* and *m. sternohyoideus* insert on the lateral edge of hyoid plate; (48) eggs laid in water, in terrestrial situations, or in bromeliads. The egg deposition site is unknown for the Bahia frog; it agrees in the rest of the character states listed for the subfamily.

Lynch (1971) defined five tribes of Telmatobiinae and one genus he was unable to assign to any of these tribes: Alsodini; Eleutherodactylini; Grypiscini; Odontophrynini; Telmatobiini; and the genus *Scythrophrys.*

The Bahia frog cannot be assigned to the Eleutherodactylini, Grypiscini, Odontophrynini, Telmatobiini, or *Scythrophrys.* Again, for sake of brevity, only examples are used to document this statement. Members of the Eleutherodactylini have rounded sacral diapophyses and males lack cornified nuptial asperities; the Bahia frog has flattened sacral diapophyses and the males have cornified nuptial asperities. In species of the Grypiscini, the frontoparietal fontanelle is not exposed; in the Bahia frog it is (Fig. 3). Members of the Odontophrynini have short transverse processes of the posterior presacral vertebrae; the Bahia frog has long processes (Fig. 1). Members of the Telmatobiini have cervical cotyles that are narrowly separated with two distinct articular surfaces (Lynch's type II, 1971:54); the Bahia frog has widely spaced cervical cotyles with two distinct articular surfaces (Fig. 4, Lynch's type I, 1971:53). *Scythrophrys* has rounded sacral diapophyses and a concealed tympanum; the Bahia frog has flattened sacral diapophyses and an exposed, well-developed tympanum.

Lynch (1971:123–124) defined the Tribe

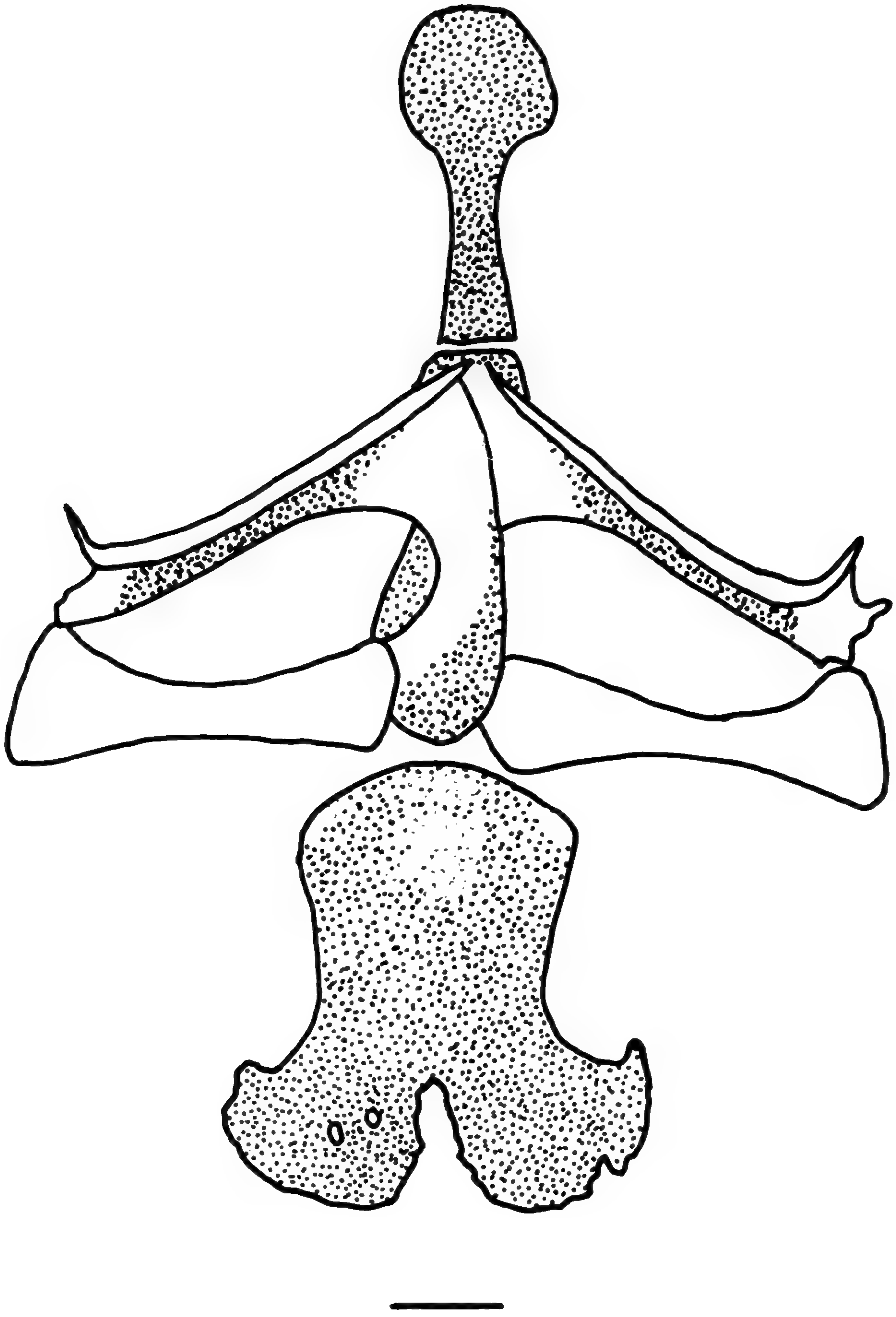

Fig. 2. Ventral portion of pectoral girdle of *Rupirana cardosoi,* MZUSP 68959. Cartilage stippled. Scale line = 1 mm.

Alsodini based on 16 characters (numbers are those of Lynch): (3) transverse processes of posterior presacral vertebrae long; (4) cervical cotylar arrangements type I or II; (5) cervical and second vertebrae not fused; (6) cranial bones not involved in dermostosis; (7) omosternum present, moderately large; (8) sacral diapophyses somewhat enlarged; (9) maxillary teeth blunt, pedicellate; (12) facial lobe of maxilla deep, not exostosed; (17) nasals not in contact with frontoparietals; (18) frontoparietal fontanelle exposed, moderate-sized; (19) frontoparietal not fused with proötic; (21) temporal arcade lacking; (37) alary processes of hyoid plate on narrow stalks; (42) male with cornified nuptial asperities on thumb; (45) outer metatarsal tubercle present, inner metatarsal tubercle normal; (46) larvae with median vent. Larvae are unknown for the Bahia frog. In all other characters, except (8), the Bahia frog matches exactly the def-

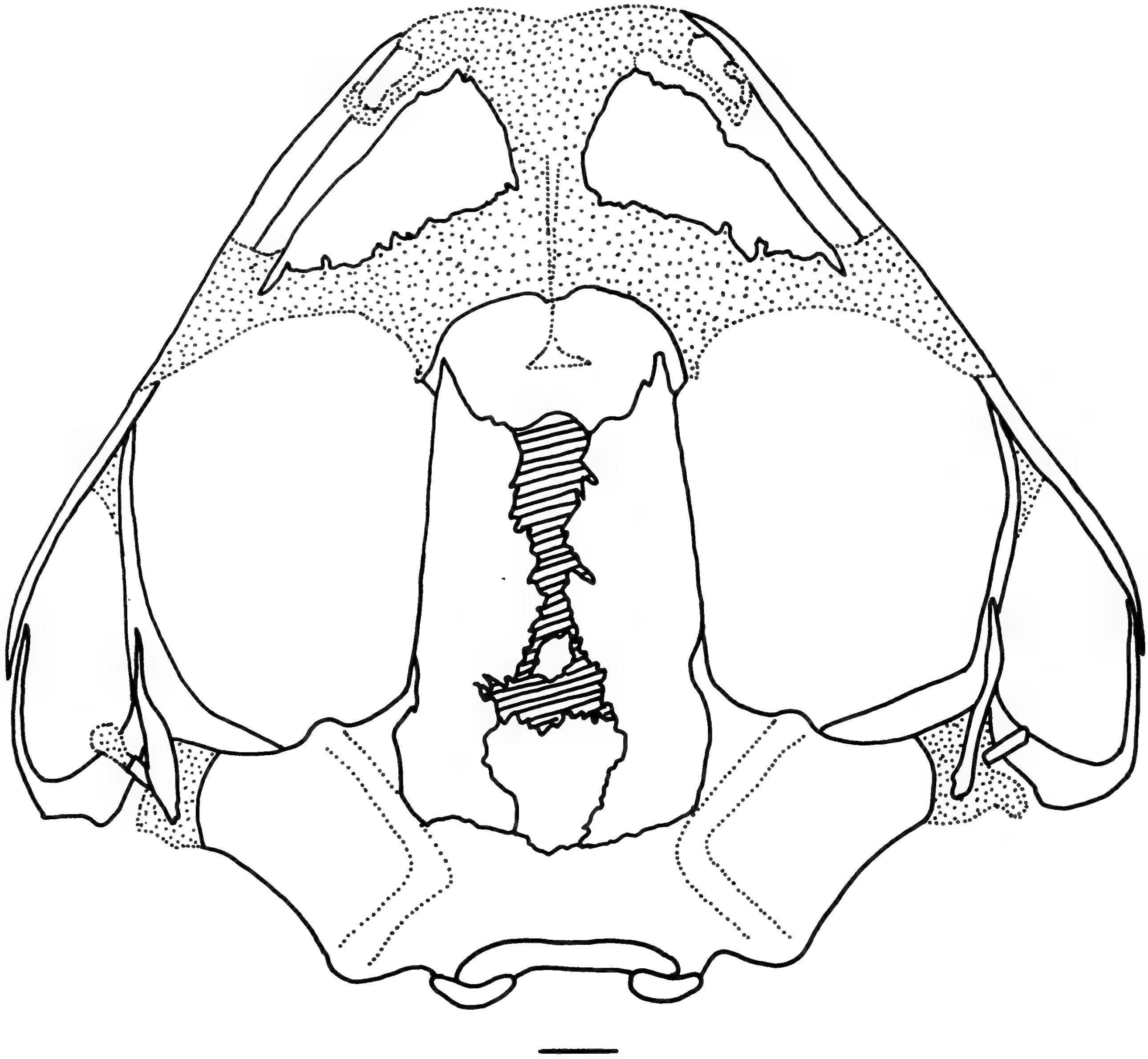

Fig. 3. Dorsal view of skull of *Rupirana cardosoi,* MZUSP 68959. Cartilage stippled. Frontoparietal fontanelle hatched. Scale line = 1 mm.

inition of the subfamily. In the Bahia frog, the sacral diapophyses are flattened (not rounded), but they are not really enlarged (Fig. 1). However, the differences involved in the shape of the sacral diapophyses are minor and alone do not argue for a distinct tribe status for the Bahia frog.

Lynch (1971) included four genera in his concept of Alsodini: *Batrachyla, Eupsophus, Hylorina,* and *Thoropa* (in 1978 he restricted the Tribe Batrachylini to the genera *Batrachyla* and *Thoropa*). Of these, the Bahia frog is most similar to *Thoropa. Eupsophus* and *Hylorina* have the type II cervical cotylar arrangement; the Bahia frog has type I. The maxillary arch of *Batrachyla* is incomplete and the quadratojugal is absent; the maxillary arch of the Bahia frog is complete (Figs. 3–4).

Lynch (1971:129–130) defined the genus *Thoropa* by 31 characters (following his numbers): (4) cervical cotylar arrangement type I; (10) alary processes of premaxillae directed dorsally and slightly anteriorly, relatively narrow at base; (11) palatal shelf of premaxilla very narrow with elongate palatal process present [I could not find where Lynch defined what a palatal process of the maxilla was and I do not find such a structure for either *Thoropa* or the Bahia frog];

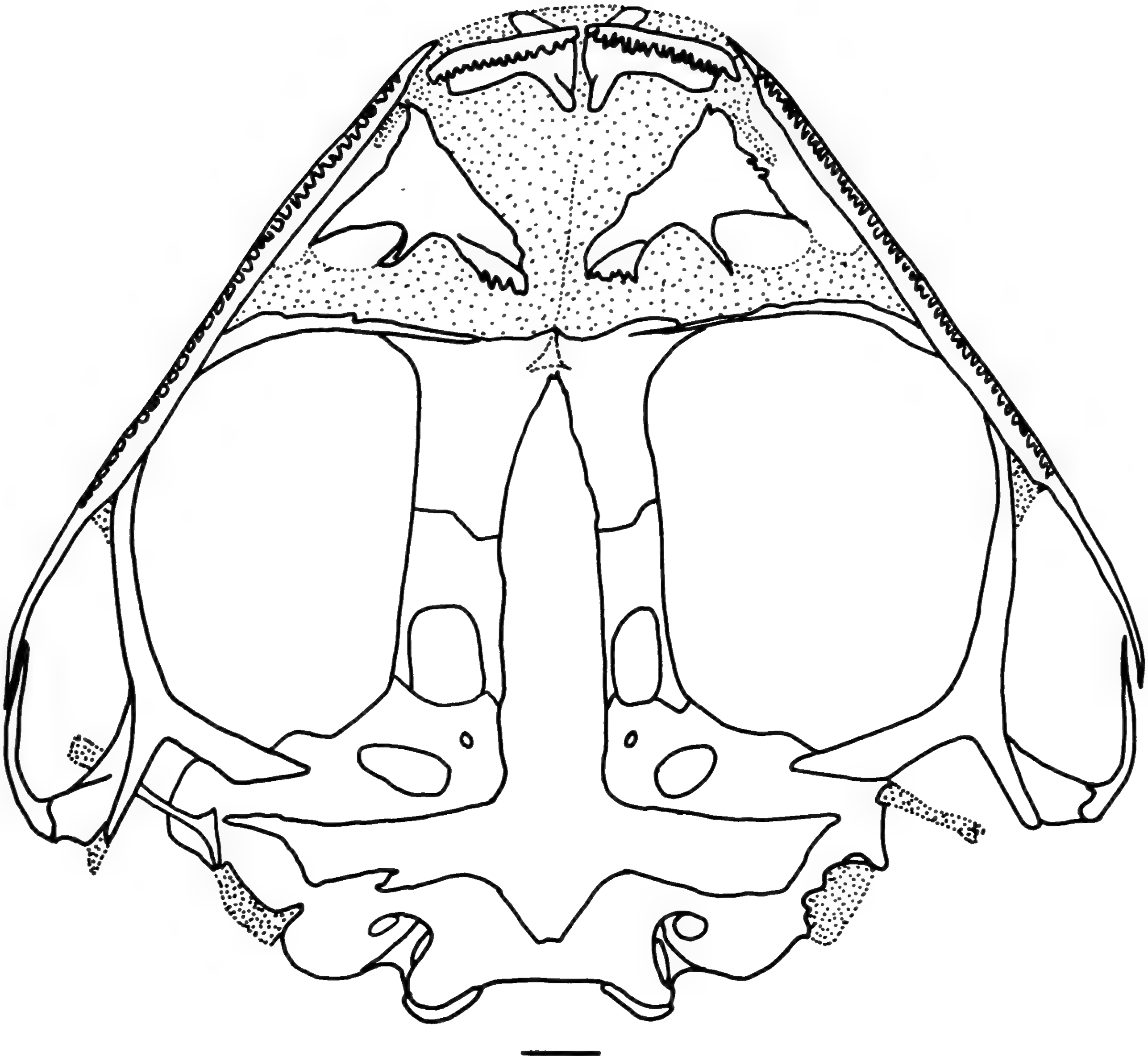

Fig. 4. Ventral view of skull of *Rupirana cardosoi,* MZUSP 68959. Cartilage stippled. Scale line = 1 mm.

(14) maxillary arch complete, quadratojugal present; (15) nasals relatively large with moderately long maxillary processes, separated medially; (16) nasals not in contact with maxillae or pterygoids; (22) epiotic eminences relatively long and narrow or short and stocky, carotid artery passes dorsal to skull bones; (24) zygomatic ramus of squamosal relatively short; (25) otic ramus of squamosal moderately long, no otic plate; (26) squamosal-maxillary angle 50–70°; (27) columella present; (28) prevomers relatively small, entire, separated medially, toothed; (29) palatine long and narrow, expanded laterally, separated medially; (30) sphenethmoid entire, extending anteriorly to posterior edge of nasals or not reaching nasals; (31) anterior ramus of parasphenoid broad, keeled medially, extending anteriorly to prevomers; (32) parasphenoid alae oriented at right angles to anterior ramus of parasphenoid, relatively short, not overlapped laterally by median ramus of pterygoids; (33) pterygoids large, anterior rami in long contact with maxillae, not reaching palatines; (34) occipital condyles large or small, not stalked, moderately to widely separated medially; (36) terminal phalanges T-shaped; (40) *m. depressor mandibulae* in two slips; (41) pupil horizontal; (42) males with median subgular vocal sac; (43) body lacking glands; (44) tongue large, oval, pos-

terior edge free; (45) toes lacking webbing, bearing lateral fringes, digital tips bulbous, somewhat dilated, first finger shorter than second; (46) larvae with 2/3 tooth rows, labial papillae broadly interrupted anteriorly; (48) eggs large, few in number, laid in lotic situations; (49) males 19–78, females 24–70 mm SVL; (50) tympanum visible externally; (51) tadpoles with greatly flattened and attenuate bodies and tails.

There is no egg placement or larval information for the Bahia frog.

Several features require further comment. The Bahia frog does not have a medial keel of the parasphenoid, nor does the parasphenoid extend anteriorly to the vomers (Fig. 4), as stated for character 31 in *Thoropa.* However, Lynch's Fig. 86 (1971:130) does not show the conditions he described. In re-examining the material used by Lynch, I find that in *Thoropa miliaris* (KU 92855), the parasphenoid has a weak medial keel and does extend to the vomers, but in both *T. lutzi* (KU 92908), and *T. petropolitana* (KU 92862), the parasphenoid lacks a median keel and extends far short of the vomers (as in the Bahia frog). For character 32, in the Bahia frog the parasphenoid is overlapped by the median rami of the pterygoids, contrasting with Lynch's statement for *Thoropa.* However, Lynch's Fig. 86 (1971:130) shows overlap, which I also find in *T. lutzi* (KU 92908), *T. miliaris* (KU 92855), and *T. petropolitana* (KU 92862). The terminal phalanges of the Bahia frog, character 36, are not distinctly T-shaped as in *Thoropa,* but either expanded or weakly T-shaped (Fig. 5). Although the shape of the terminal phalanges in the Bahia frog differs from the distinct T-shaped condition in *Thoropa,* this condition could be interpreted as part of a morphological continuum in degree of expansion of the terminal phalanges. The depressor mandibulae muscle, character 40, of the Bahia frog is the DFSQat condition (three slips, the third a small slip originating from the tympanic annulus), contrasting with the DFSQ state listed for *Thoropa* by Lynch. I find both the two and three slip conditions in *Thoropa,* however (*T. miliaris,* DFSQ [USNM 97765]; *T. petropolitana,* DFSQat [USNM 164135]).

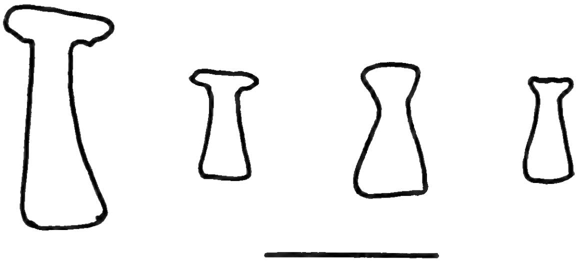

Fig. 5. Terminal finger phalanges. Left to right, *Thoropa lutzi,* from cleared-and-stained specimen KU 92908, third finger; *Thoropa petropolitana,* from cleared-and-stained specimen KU 92862, third finger; *Rupirana cardosoi,* from cleared-and-stained specimen MZUSP 68959, third finger; *Rupirana cardosoi,* from partially dissected wet specimen MZUSP 76035, fourth finger. Scale line = 1 mm.

There have been two additional species of *Thoropa* described since Lynch's (1971) publication (*T. megatympanum, T. saxatilis*) which require modification of character 45 in that genus. *Thoropa lutzi* and *T. petropolitana* have weak lateral toe ridges that are less well-developed than in the Bahia frog. *Thoropa miliaris* has weak ridges, similar to the condition of the Bahia species. The toe ridges of *T. megatympanum* are even weaker than those of *T. lutzi* and *T. petropolitana. Thoropa saxatilis* lacks any toe ridge or fringe. The digital tips of the Bahia frog are narrow, not dilated. In both *T. lutzi* and *T. saxatilis,* the digit tips are dilated and the finger tips are more dilated than the toe tips. In *T. miliaris,* the digital tips are bulbous and somewhat dilated (Lynch's description), and there is no size difference between the finger and toe tips. In both *T. megatympanum* and *T. petropolitana,* the tips of the digits are slightly dilated but not particularly bulbous and the finger and toe tips are equal sized. The first finger is the same length as the second in the Bahia species, the same condition that I find in *T. miliaris* (contra Lynch). The first finger is shorter than the second in *T. lutzi, T. petropolitana,* and *T. saxatilis.* In *T. megatympanum,* the first finger is either just shorter than the second or the first and second are of equal length.

Summarizing thus far, the Bahia frog is most similar to species in the genus *Thoropa,* but differs consistently by two characters used by Lynch (1971): shape of the terminal phalanges (but see discussion of character 36 above) and dilation of digit tips.

In a preliminary analysis of relationships of leptodactylid genera, I (Heyer 1975) came to quite a different conclusion from Lynch (1971) regarding the relationships of *Thoropa.* I did not recognize formal taxonomic groupings such as subfamilies and tribes, but used informal grouping names, which are equivalent in scope to Lynch's subfamilies. Specifically, my concept of a grypiscine clade combined the content of Lynch's Grypiscinae plus Elosiinae with the genera *Paratelmatobius* and *Thoropa.* The reasons for this very different viewpoint are due to two factors: although Lynch and I analyzed most of the same characters, there were some differences; and I attempted a phylogenetic analysis, whereas Lynch's analysis was phenetic.

I analyzed 37 characters. For the states that I listed for *Thoropa* (1975, table B, p. 51), the following differ from the conditions found in the Bahia species. Character 5, state B, disks on toes (see discussion of Lynch's character 45 above). Character 6, state A, no tarsal fold, flap, or tubercle. The Bahia frog has a tarsal fold, however, reexamination of *T. miliaris* indicates that specimens have weak tarsal folds as do specimens of *T. saxatilis.* Character 9, state D, toes with lateral fringe (see discussion of Lynch's character 45 above). Character 12, state B, depressor mandibulae origin from dorsal fascia, squamosal, and otic region only (see discussion of Lynch's character 40 above). Character 16, state B, omohyoideus insertion on hyoid body and fascia between posteromedial and posterolateral processes. In the Bahia species, the omohyoideus inserts only on the hyoid plate. Character 17, state B, iliacus externus extends ½–¾ anterior on ilium. In the Bahia species, the extension is >¾, about 90%. Character 20, state B, adductor longus poorly developed, inserting on adductor magnus, covered by sartorius. In the Bahia frog, the adductor longus is well-developed, inserting on the knee. Character 30, state C, anterior process of hyale absent. In re-examining material, I found that the process is clearly absent in *T. miliaris* (USNM 97765). In *T. petropolitana* (USNM 164135), there is a medial, but not an anterior swelling of the hyale at its most anterior extent, contrasting markedly with the well-developed anterior process found in the Bahia species (Fig. 6). Character 34, state A, sacral diapophyses expanded. In the Bahia frog, the sacral diapophyses are flattened, but not expanded (Fig. 1). In reexamining the two *Thoropa* species that are similar in size to the Bahia species (*T. lutzi,* KU 92908, *T. petropolitana,* KU (92862), the sacral diapophyses are flat, as in the Bahia species, and differ slightly from the Bahia species in being expanded. Character 35, state B, terminal phalanges T-shaped is the same as Lynch's character 36 (see discussion above).

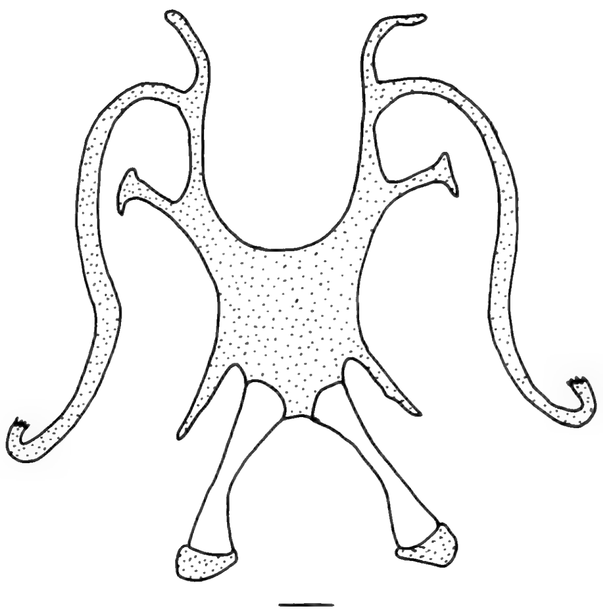

Fig. 6. Hyoid apparatus of *Rupirana cardosoi,* MZUSP 68959. Cartilage stippled. Scale line = 1 mm.

The Bahia species clearly shares most features of all known leptodactylid genera with the genus *Thoropa.* The question is whether the definition of *Thoropa* should be expanded to include the Bahia species, or whether the Bahia frog should be treated as a genus distinct from *Thoropa.*

The Bahia species differs from all known *Thoropa* in seven characters (of the characters examined for this study). For two of these, the definition of the genus *Thoropa* would only have to be slightly modified to incorporate the Bahia frog: degree of expansion of the flattened sacral diapophyses and shape of the terminal phalanges. The other five characters would require a more drastic redefinition of *Thoropa:* toe disks; insertion of the omohyoideus muscle; length of the iliacus externus muscle; development of the adductor longus muscle; anterior process of the hyale. These latter five characters demonstrate different conditions involving toe, hyoid, and thigh morphologies. These kinds of differences are consistent with the Bahia species being on a separate evolutionary track from *Thoropa.* Thus, if the Bahia form were described as a species of *Thoropa,* evolutionary relationships would be obscured (also see section on relationships, below). Therefore, in order to emphasize the evolutionary distinctiveness of the Bahia species, it is described as:

Rupirana, new genus
Figs. 1–6

Type-species.—*Rupirana cardosoi,* new species.

Diagnosis.—The only leptodactylid genera that share the combination of sternum cartilaginous, widely spaced cervical cotyles with two distinct articular surfaces, long transverse processes of posterior presacral vertebrae, flattened sacral diapophyses, and an exposed frontoparietal fontanelle are *Batrachyla, Thoropa,* and *Rupirana. Batrachyla* has an incomplete maxillary arch; in *Rupirana* the maxillary arch is complete. *Thoropa* has well-developed T-shaped terminal phalanges, dilated digit tips, and lacks an anterior process of the hyale; *Rupirana* does not have well-developed T-shaped terminal phalanges, has narrow digital tips, and has an anterior process of the hyale.

Definition.—Pupil horizontal; tympanum distinct; vocal sac single, subgular, slightly expanded externally; male thumb with one extensive and one small patch of keratinized sandpaper-like asperities; body without well-defined glands; digital tips narrow, not dilated; tarsus with a tarsal fold; outer metatarsal tubercle small; inner metatarsal tubercle large, ovoid, not cornified; toes with lateral fringes, joined at base of toes.

Adductor mandibularis muscle condition adductor mandibulae posterior subexternus only; depressor mandibulae condition DFSQat; geniohyoideus muscle contiguous medially; anterior petrohyoideus insertion on lateral edge of alary process and hyoid plate; sternohyoideus muscle insertion entirely near edge of hyoid body; omohyoideus muscle insertion entirely on hyoid plate; iliacus externus muscle extending almost to anterior tip of ilium; tensor fasciae latae muscle insertion posterior to iliacus externus muscle on iliac bone; interior and exterior portions of semitendinosus muscle uniting in a common distal tendon distally, exterior portion larger than interior; adductor longus muscle about same size and shape as sartorius muscle, inserting on knee and adductor magnus.

Quadratojugal present, contacting maxilla; frontoparietals not meeting medially, exposing moderate-sized fontanelle; vomerine teeth present; occipital condyles widely separated; anterior process of hyale present; alary processes of hyale on narrow stalks; posterior sternum a cartilaginous plate, terminally expanded and bifid; last presacral vertebra just narrower than sacrum; sacral diapophyses flattened, not noticeably expanded; dorsal crest of ilium present; terminal phalanges barely expanded, not or weakly T-shaped.

Etymology.—From the Latin *rupes,* rock, and *rana,* frog. The gender is feminine. The

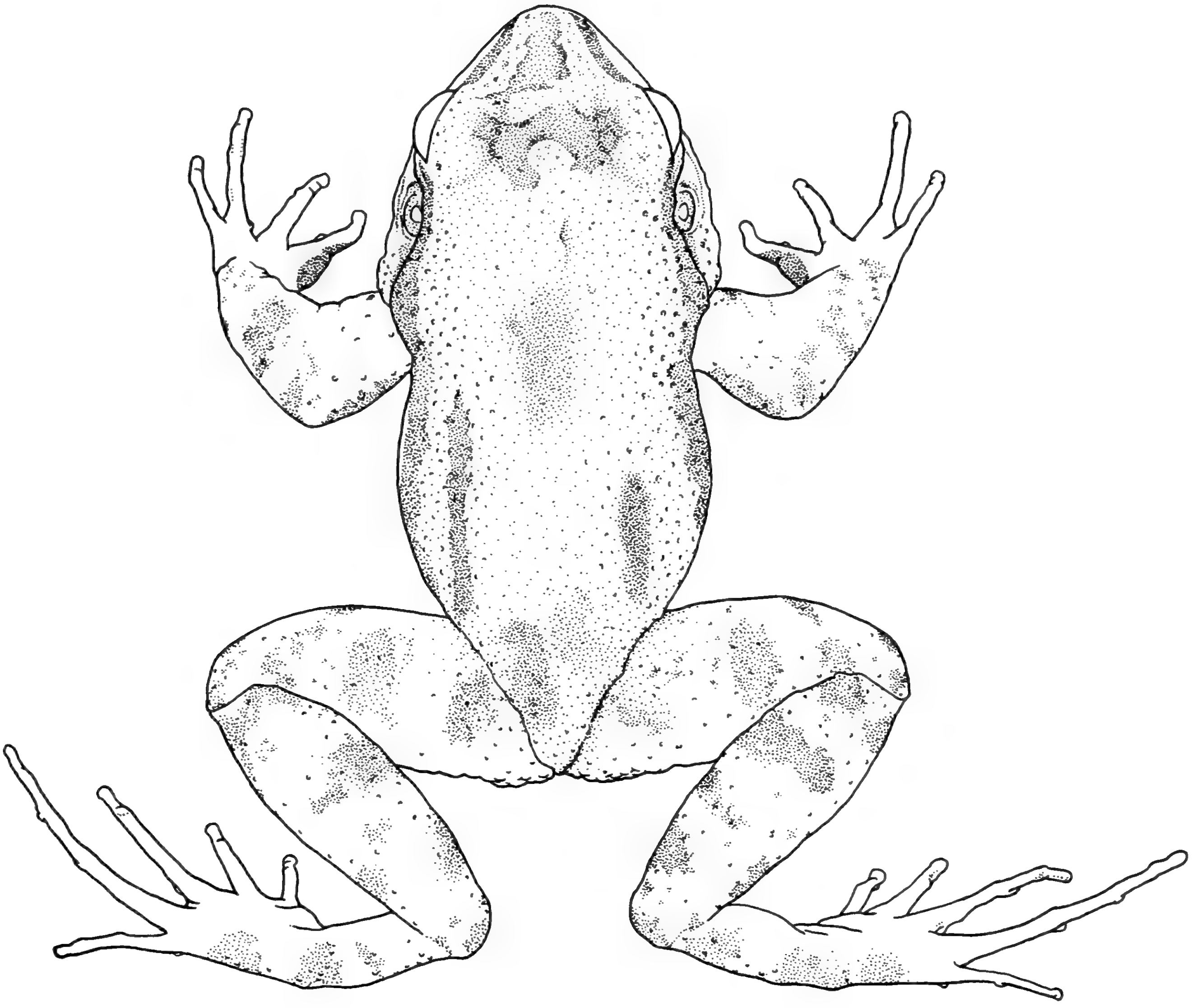

Fig. 7. Dorsal view of male paratype of *Rupirana cardosoi,* MZUSP 76032.

name is to highlight the association of this genus with the campos rupestres of Brazil.

Content.—Monotypic.

Rupirana cardosoi, new species
Figs. 7–8

Holotype.—MZUSP 65203, adult male, 27 Sep 1987, Mucujê, Bahia, Brazil, 13°00′S, 41°23′W, Miguel T. Rodrigrues.

Paratopotypes.—MZUSP 65202 (adult male), 65204 (adult male), 65205 (juvenile), same data as holotype; MZUSP 68959 (cleared and stained adult female), 68960 (juvenile), 2 Oct 1990, Miguel T. Rodrigues.

Paratypes.—MZUSP 68961–68962 (adult females), Morro do Chapeu, Bahia, Brazil, 3 Oct 1990, 11°33′S, 41°09′W, Miguel T. Rodrigues; MZUSP 76017–76018 (adult males), 76023–76030 (adult males), 76031 (adult female), 76032–76034 (adult males), 76035 (adult female, skull removed), 76036 (adult male), 76037 (juvenile male), 76038–76040 (adult males), USNM 519755–519757 (adult males), 519758 (adult female), Andaraí, Bahia, Brazil, 12°48′S, 41°20′W, 19–22 Nov 1968, Werner C. A. Bokermann, Francisco M. Oliveira, and B. D. Silva.

Diagnosis.—As for genus.

Description of holotype.—Snout round in profile and from above; nostrils anterolateral, near tip of snout; canthus rostralis indistinct; loreal obtuse; tympanum distinct,

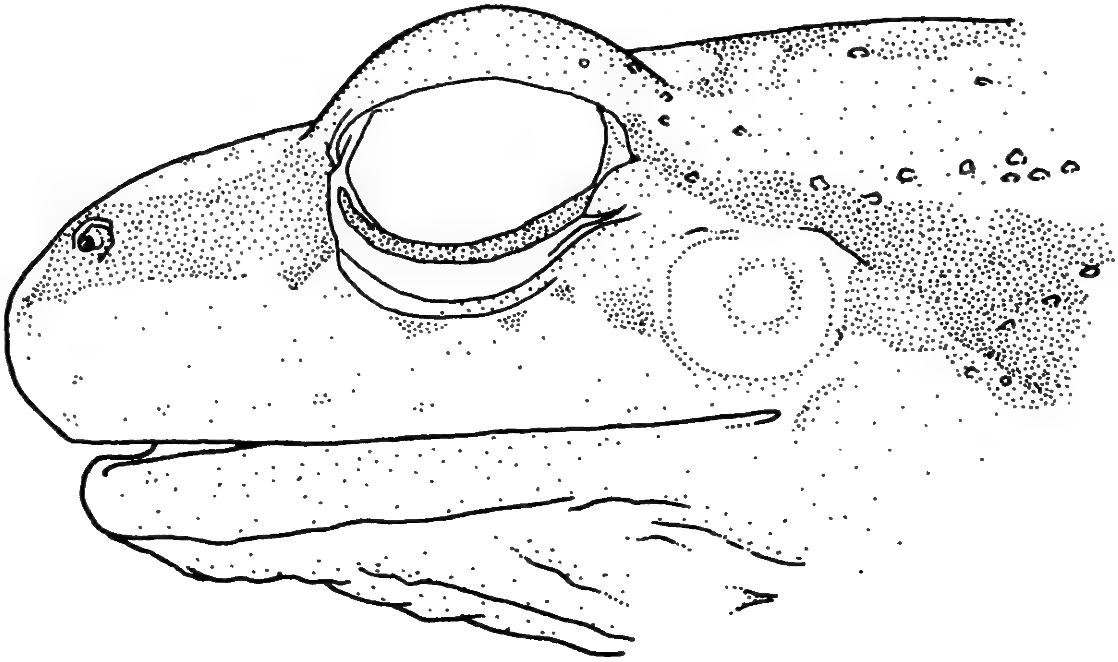

Fig. 8. Profile of head of holotype of *Rupirana cardosoi,* MZUSP 65203.

rounded, about ½ diameter of eye; supratympanic fold distinct from behind eye to shoulder, bordering tympanum dorsally; tongue elongate, triangular, with slight emargination on anterior edge; vomerine teeth in two small transverse patches in line with posterior borders of small, round choanae, vomerine tooth patches separated from each other by about width of single tooth patch; vocal slits elongate; vocal sac single, subgular, indicated externally by lateral skin folds/wrinkles; finger lengths I≈II≈IV<III; fingers free of web, very slight lateral ridges; tips of fingers rounded, not expanded; palmar tubercle ovoid, just smaller than ovoid thenar tubercle; subarticular tubercles moderately developed, slightly pungent; no supernumerary tubercles; accessory palmar tubercles present, two in line with each digit; thumb with extensive keratinized sandpaper-appearing asperity from penultimate phalanx to base of thumb, a second ovoid patch on inner half of thenar tubercle; forearm slightly hypertrophied; dorsum, including upper eyelid, smooth with many scattered large white tubercles; body lacking any obvious glands; venter smooth except for areolate posteroventral thigh surfaces; belly disk weakly indicated; toe lengths I<II<V<III<IV; tips of toes rounded, not expanded; toes with weak lateral ridges expanded into weak fringes at base of inner sides of toes II and III resulting in trace of strap-shaped basal web between toes I, II, and III; inner metatarsal tubercle small, round, about ⅓ size of small, ovoid outer metatarsal tubercle; distinct but relatively weak tarsal fold extending about ½ length of tarsus; sole of foot smooth; subarticular tubercles moderate, pungent.

SVL 27.3 mm; head length 9.8 mm, head width 10.3 mm; horizontal diameter of tympanum 2.1 mm, including annulus; distance from eye to posterior edge of naris 2.8 mm; internarial distance 2.5 mm; thigh length 12.5 mm; shank length 13.4 mm; foot length 14.3 mm.

In preservative, dorsal body brown with darker brown markings, upper limbs tan with brown markings; upper snout with a few irregular darker blotches and dots; irregular interorbital bar connecting with lichenous network behind eyes, rest of dorsum with mostly elongate blotches and broad stripes; upper limbs weakly cross-banded; distinct broad dark brown canthal stripe extending more faintly from nostril to

Table 1.—Measurements (mm) of adult *Rupirana cardosoi* from three localities in Bahia, Brazil.

	SVL		HL		HW		TD		E-N		IN		Thigh		Shank		Foot	
	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
Andaraí																		
Males (*n* = 20)	27.8	31.2	10.4	11.9	10.7	12.1	2.0	2.6	2.6	3.3	2.6	3.0	12.9	14.5	13.0	15.1	13.9	16.5
Females (*n* = 2)	30.2	34.4	10.4	11.8	10.3	12.3	2.0	2.6	3.0	3.1	2.8	2.9	13.1	14.3	14.0	15.1	14.9	15.6
Morro do Chapeu																		
Females (*n* = 2)	32.3	32.9	10.5	12.0	12.4	12.6	2.0	2.4	2.8	2.9	2.7	3.0	14.3	14.3	15.3	15.3	15.0	15.6
Mucugê																		
Males (*n* = 3)	27.3	27.6	9.8	10.3	10.3	10.6	2.1	2.2	2.7	2.8	2.3	2.5	12.5	12.7	13.4	14.0	14.1	14.3
Female (*n* = 1)	30.3		11.8		11.8		2.4		3.5		NA		13.5		13.9		14.4	

tip of snout (Fig. 8); upper lip mostly uniform light tan; supratympanic fold dark brown, expanded into dark triangular blotch posteriorly followed by series of small dark spots on anterior half of otherwise light tan flanks; throat, chest, and belly light tan with lighter spots lacking melanophores; sole of foot brown; posterior surfaces of thighs uniform tan.

Variation.—Available data do not indicate any marked variation in measurements among sites, with a suggestion of slight sexual dimorphism in size (Table 1). Measurement variation of the entire sample of adults (male *n* = 23, female *n* = 5) is (means in parentheses): SVL 27.3–31.2 (29.6) mm for males, 30.2–34.4 (32.0) mm for females; % head length/SVL 34–40 (37.3) for males, 32–39 (35.0) for females; % head width/SVL 36–40 (37.9) for males, 34–39 (37.0) for females; % tympanum diameter/SVL 7–9 (7.7) for males, 6–8 (7.2) for females; % eye-nostril distance/SVL 9–11 (10.0) for males, 9–12 (9.8) for females; % internarial distance/SVL 8–10 (9.1) for males, 8–10 (8.8) for females; % thigh length/SVL 44–48 (45.7) for males, 42–44 (43.2) for females; % shank length/SVL 44–51 (48.2) for males, 44–47 (45.8) for females; % foot length/SVL 47–54 (51.0) for males, 45–49 (47.0) for females. The sample size for females is small, but it does appear as though the female legs are proportionately shorter than in males.

The most striking variation in addition to the male secondary sexual characteristics involving vocal slits, vocal sacs, thumb asperities, and forearm hypertrophy is the sexual variation in dorsal texture. In females, the dorsum is either smooth or with a weak shagreen, whereas the males have many, large, white tubercles scattered profusely over the back (Fig. 9). In the specimens from Morro do Chapeu and Mucujê, the male dorsal tubercles are largely limited to the upper eyelids and the back. The males from Andaraí have a much more extensive distribution of tubercles, including the snout, outer arms, dorsal thigh surfaces,

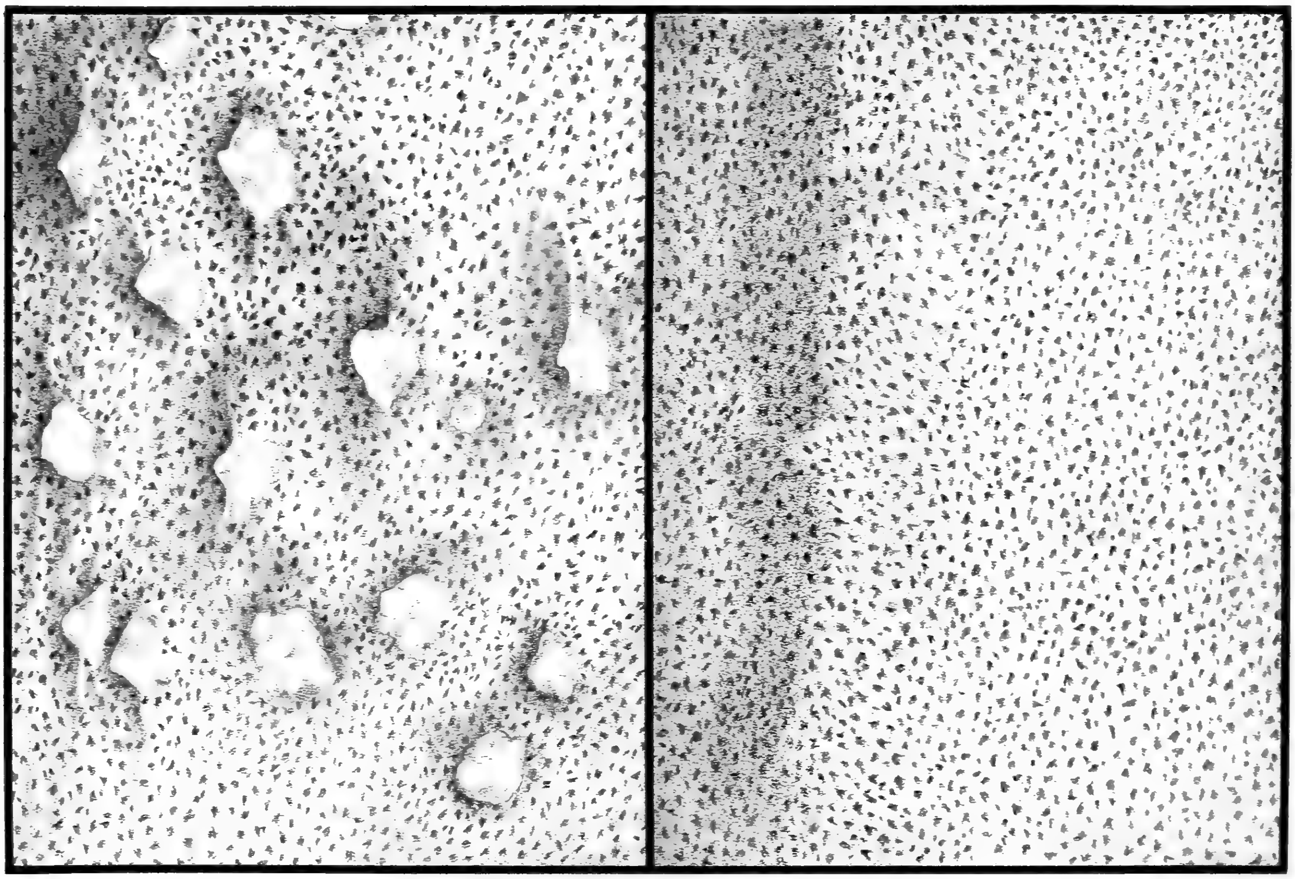

Fig. 9. Skin texture of male and female *Rupirana cardosoi.* Portions illustrated are at the transition from the dorsum to the flank above the arm insertion on the left side of the animal. Left illustration drawn from male specimen, MZUSP 76032, right illustration drawn from female specimen, MZUSP 76031.

dorsal shank surfaces, outer tarsus, and variably, the sole of the foot.

Other aspects of variation noted among the specimens (males and females, except as noted) include: tongue shape also ovoid or round; vomerine tooth placement between to just posterior to choanae, separated from each other by <½ distance of length of a single tooth patch; finger lengths also II just <IV just <I<III; some males with no external indication of a vocal sac; finger subarticular tubercles sometimes pungent; outer tarsus sometimes shagreened; tarsal fold occasionally extending ⅔ distance of tarsus; the inner metatarsal tubercle sometimes elevated; the sole of the foot sometimes with series of small, fleshy tubercles in line with digits; the dark supratympanic stripe sometimes extending continuously to mid-flank; front of tympanum sometimes bordered by dark brown spur extending from dark supratympanic stripe; dorsum relatively uniform to longitudinally striped; chin through the chest sometimes scattered uniformly with melanophores with anterior belly with mottled pattern and posterior belly lacking melanophores to the entire region from chin through belly lightly brown mottled.

MZUSP 76037, a 29.4 mm SVL specimen, is a juvenile male, although not the smallest male in the sample. The specimen does not have vocal slits, but it has a small thumb patch asperity (on the thumb only, not on the thenar tubercle) and no dorsal tubercles. MZUSP 76039, a 30.2 mm SVL male, has vocal slits that are in early development, but has fully developed nuptial pads and dorsal tubercles.

The cleared-and-stained female (MZUSP 68959) contained mature-appearing ova, of varying sizes up to about 1.5 mm diameter with melanophores on the animal pole.

Etymology.—Named in honor of Dr. Adão José Cardoso, a colleague whose tragic death is deeply felt both at a personal level and as a premature halt to his significant contributions to our understanding of the Neotropical amphibian fauna.

Distribution and habitat.—At present, *Rupirana cardosoi* is known from three localities in the northern portion of the Espinhaço Range in the State of Bahia, Brazil (Fig. 10).

Dr. Rodrigues kindly provided the following habitat information. MZUSP 65202–65205 were obtained during the day on the bank of a small stream with white sand and rocks. The stream crosses the city of Mucujê. The water of the stream was very clear but with a red-brown tint (as usual in the Espinhaço Range). The vegetation was typical of quartzitic campos rupestres: dominated by Velloziaceae, Euriocaullaceae, Xiridaceae and other endemics. There were many large and highly eroded quartzitic outcrops. MZUSP 68959–68960 were collected during the day at a similar stream habitat (2–3 m wide) less than 2 km from Mucujê. The general habitat was the same as for the Mucujê stream. Both of these sites were also visited at night, but no *Rupirana cardosoi* were found. MZUSP 68961–68962 were collected in a relictual patch of white sands on a large red rocky mountain not far from Morro de Chapeu. The frogs were on the margins of two small, drying ponds. The vegetation, dominated by Mellastomataceae on the sand, was typical for campos rupestres. Several specimens of the sand-adapted *Tropidurus cocorobensis* were also collected at the same time, around 1500 h.

Relationships

Rupirana shares the most character states with the genus *Thoropa,* as documented in the section, "Comparison with leptodactylid genera." The evaluation of character states in that section did not differentiate between shared primitive and shared derived states, however. If most of the states shared by *Rupirana* and *Thoropa* are shared primitive states, then there would be little support for a close sister-group relationship.

In order to undertake a first approximation of the relationships of *Rupirana* within leptodactylid frogs, the data assembled for an earlier study (Heyer 1975) are used as a basis for a cladistic analysis (Appendix 1). As indicated above, the relationships of *Thoropa* within the Leptodactylidae have been disputed by Lynch (1971, 1978) and me (Heyer 1975). In order to evaluate the relationships of *Rupirana* relative to *Thoropa,* the genus *Batrachyla* is included to evaluate Lynch's position that *Batrachyla* and *Thoropa* are sister-taxa (Lynch 1978), and the genera *Cycloramphus* and *Megaelosia* are included to evaluate my position that *Thoropa* is a member of a grypiscine clade (Heyer 1975). Three additional representatives of telmatobiine genera are included to provide structure to test the alternative hypotheses: *Eleutherodactylus, Eupsophus,* and *Hylorina.* Three genera are used as outgroups: *Ceratophrys* as a representative of the South American ceratophryine clade and a representative each of two subfamilies of the Australian Family Myobatrachidae, *Adelotus* and *Crinia.* In all cases except for *Eleutherodactylus,* the character states analyzed are for genera. As *Eleutherodactylus* is currently in the process of being broken into smaller monophyletic units, with the final configuration of this effort far from clear, data for a single species, *E. coqui,* are used for purposes of this analysis.

The data were analyzed with as much ordering of character states as unambiguous morphoseries would allow (Appendix 1).

Phyletic signal in the data set.—The strength of the phyletic signal in the data set is evaluated with two tests: the indirect g_1 statistic (Hillis 1991) and the more direct Permutation Tail-Probabilities (PTP) test (Faith and Cranston 1991).

Hillis (1991) explained the rationale for the g_1 statistic and provided probability levels for cases using 6, 7, or 8 taxa. As there is no graphable correlation between the

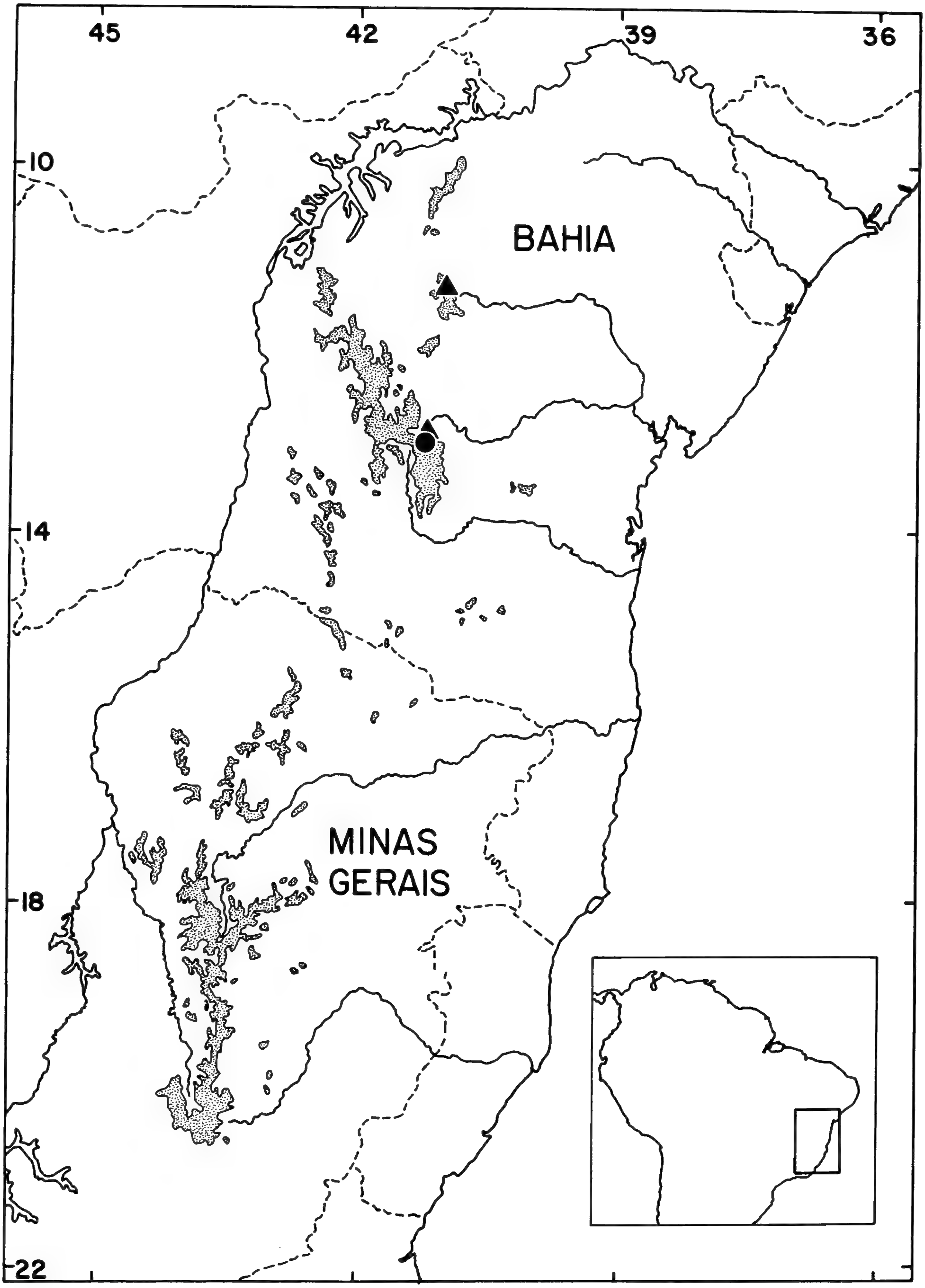

Fig. 10. The Espinhaço Range in the States of Bahia and Minas Gerais. Stippling indicates areas above 1000 m. Dot is the type locality of *Rupirana cardosoi*; triangles indicate the other two known localities for *R. cardosoi*. Map redrawn from Map 56, page 398 in Giuletti et al. 1997.

number of taxa and g_1 critical values, exhaustive PAUP analyses were run using 8 taxa with *Adelotus* or *Crinia* or *Ceratophrys* used as sole outgroup taxa and deleting *Hylorina.* The g_1 statistics for the 8 taxa are 0.31, 0.29, and 0.01 respectively when *Rupirana* is coded as not having T-shaped phalanges and 0.17, 0.39, and 0.08 respectively when *Rupirana* is coded as having T-shaped phalanges. The critical g_1 values for 8 taxa for P of 0.05 is -0.34 and P of 0.01 is -0.47. None of the g_1 statistic values obtained in the six analyses approaches those critical values. The distribution of trees is not skewed.

The PTP test was run with *Rupirana* coded as not having T-shaped phalanges. The P value is 0.06, which is not significant at the traditional 0.05 level, but indicative that there is likely some phylogenetic content in the data.

Clearly, the phyletic signal in this data set is not strong and the results must be interpreted extremely conservatively.

Cladistic relationships.—The results of PAUP analyses run on the entire data set with a branch-and-bound search or with the outgroup taxa run individually with exhaustive searches (using the data matrix in Appendix 1) all have the same outcome: multiple numbers of shortest trees, for which the strict consensus tree is an entirely unresolved polytomy. The branch-and-bound search of the entire data set yields 19 shortest trees of tree length 112, with a consistency index (CI) excluding uninformative characters of 0.52. The exhaustive search of the data set using *Adelotus* as the sole outgroup taxon gives 240 shortest trees of tree length 86, with a CI value excluding uninformative characters of 0.56. Similar results for *Crinia* as the outgroup are 45 trees of length of 91, CI = 0.54 and for *Ceratophrys* as the outgroup are 45 trees of length 89, CI = 0.56.

In case the coding of the shape of the terminal phalanges in *Rupirana* might be pivotal, exhaustive searches were also run using *Adelotus, Crinia,* and *Ceratophrys* individually as outgroup taxa with *Rupirana* coded as having T-shaped terminal phalanges. Again the analyses resulted in multiple shortest trees with the strict consensus tree of each being an entirely unresolved polytomy. The results for using *Adelotus* as the outgroup are 240 trees of shortest length 85, CI (excluding uninformative characters) = 0.57; for *Crinia,* 150 trees of shortest length 91, CI = 0.55; for *Ceratophrys,* 45 trees of shortest length 88, CI = 0.56.

These results certainly do not resolve any questions about the relationships of *Thoropa* within the Family Leptodactylidae. However, there is one result that is so consistent that a statement about relationships can be made: *Rupirana* and *Thoropa* do not share a close relationship. In fact, *Rupirana* and *Thoropa* never form a sister-group relationship in any trees, and *Thoropa* either demonstrates a basal relationship with all or most other taxa or (usually) forms a sister-group relationship with *Batrachyla* (e.g., 17 out of 19 trees in the trees based on the entire data set). This *Batrachyla-Thoropa* sister-group relationship, repeated in most, but not all trees, lends support for Lynch's proposal of relationships. However, the potential problem of long-branch attraction (Swofford et al. 1996:427) would have to be ruled out to support the *Batrachyla-Thoropa* relationship.

The results of the above analyses indicate that the similarities analyzed between *Rupirana* and *Thoropa* are due to shared primitive state conditions, not shared derived states, and that there is no close sister-group relationship between the two genera.

Zoogeography

The campos rupestres contain a notably endemic biota at the species level (for a botanical introduction, see Giuletti & Pirani 1988), including amphibians and at least some reptiles (e.g., Vanzolini 1982, Rodrigues 1988). As I have extremely limited experience with the campos rupestres, the following comments are very superficial.

Hopefully these comments will encourage an honest zoogeographical study of the amphibians of the campos rupestres, because I think the amphibians show a pattern that differs from those based on study of other groups.

The campos rupestres occur above 800–900 m and, as the common name indicates, are rocky places with poor soils (see Giuletti & Pirani 1988 and Giuletti et al. 1997 for better characterizations and maps). Plants have been the most throroughly studied campos rupestres group (Giuletti & Pirani 1988), otherwise, there has been little research on the distributions of other groups of organisms found in the campos rupestres with the exception of certain lizards (for *Tropidurus* see Rodrigues 1987, 1988, for other lizards see Vanzolini 1982). Most of the plant and lizard species found in the campos rupestres are either endemic to them or show their major central distributions on them. Species such as *Polychrus acutirostris* and *Tropidurus hispidus,* which occur in both the campos rupestres and more broadly beyond them, seem to be exceptional cases. Even though the endemicity at the species level is rather astounding, there are few endemic genera of plants (Giuletti & Pirani 1988). The affinities for the campos rupestres endemic species are primarily with cerrado and caatinga species (for plants and *Tropidurus*), and cerrados and caatingas likely served as the primary source of species which differentiated in the campos rupestres environment. Whereas the campos rupestres could be considered a part of the diagonal of open formations (caatingas-cerrados-Gran Chaco), first noticed by K. P. Schmidt (e.g., Schmidt & Inger 1951), the campos rupestres do not fit comfortably within the diagonal from a zoogeographic perspective. Another common affinity for both plants and *Tropidurus* is with the restingas (sand beaches) scattered along the east coast of Brazil. In this case, the restinga associated elements are thought to be derived from campos rupestres ancestors (Giuletti & Pirani 1988, Rodrigues 1988). The plants also show affinities that the campos rupestres lizards do not, i.e., with the mountain biotas of northern South America (stronger) and the Andes (weaker) (Giuletti & Pirani 1988, Harley 1988). There is a minor affinity with Atlantic Forest plants and lizards; the plant genus *Pleurostima* (Veloziaceae) occurs on the tops of some granitic outcrops in the Atlantic Forests, and the Atlantic Forest lizard genera *Enyalius, Placosoma,* and perhaps *Heterodactylus* have representatives in the campos rupestres.

Most of our knowledge of campos rupestres amphibians comes from the work of Werner C. A. Bokermann and Ivan Sazima, who published several papers describing new species of amphibians from the Serra do Cipó, southern Espinhaço Range, in the State of Minas Gerais. Many of the new species described from Serra do Cipó belong to well delineated species groups or genera for which the general distributions are known. For most of these, the Serra do Cipó endemics are related to Atlantic Forest groups from which they must have been derived. For example all species of the genera *Hylodes, Phasmahyla,* and *Thoropa* and the *Scinax catherinae* species group occur only in the Atlantic Forests except for disjunct endemic species at Serra do Cipó (*H. otavioi, P. jandaia, T. megatympanum,* and *S. machadoi*). Determining the faunistic origin of several other species from the Serra do Cipó is not as clear, but it would seem that the majority of them were derived from Atlantic Forest lineages and a smaller number from cerrado groups. Some of the non-endemic species that occur at Serra do Cipó are likely cerrado species, such as *Leptodactylus furnarius, L. jolyi,* and *Physalaemus cuvieri.* Some of the Serra do Cipó endemics may also have been derived from cerrado ancestors, for example *Leptodactylus camaquara, L. cunicularius, Physalaemus evangelistai* and *Proceratophrys cururu.* The frog fauna of the campos rupestres thus has a strong faunal element derived from Atlantic Forest ancestors and this pattern is different from that found in plants or lizards.

Remnants of the Atlantic Forest vegetation occur today in the Espinhaço Range (e.g., Pico das Almas, Harley 1995:20–24). The Atlantic Forests certainly were more extensive in the Espinhaço Range and continuous with the coastal forests during more mesic times. The campos rupestres, a very open formation habitat, would be expected to show biotic affinities with adjacent open formation habitats, as is true for plants and lizards. The campos rupestres would not be expected to show a primary affinity with the Atlantic Forest biota, as the basic adaptations for those two environments are profoundly different.

One aspect of anuran ecogeography could explain why many campos rupestres frogs were derived from the Atlantic Forest frog fauna rather than entirely from the cerrado/caatinga frog fauna. There are small streams (mostly seasonal at this stage of the interglacial) in the campos rupestres landscape. There are, as far as I know, no strictly stream-adapted frogs in the cerrados or caatingas, whereas many of the Atlantic Forest frogs are stream-adapted. Thus, the most probable source of stream frogs in the campos rupestres would come from the Atlantic Forests rather than the cerrados or caatingas. If, during periods of drier climates, the Atlantic Forests underwent gradual change, first contracting to gallery forests and then degrading to even more open vegetation, the stream frogs may have been able to adapt to the more open habitat conditions and occupy the campos rupestres.

In summary, from the available data, it would seem that the unique campos rupestres frog fauna has been derived from only two sources: Atlantic Forest (strongest); and cerrado/caatinga (the conclusion of Heyer 1988, that present data are inadequate to determine whether the caatingas harbor a frog fauna distinct from that of the cerrados is unfortunately still true).

The discovery of *Rupirana cardosoi* has one expected and one unusual zoogeographical consequence. The Espinhaço Range is comprised of a series of individual isolated mountains (Fig. 10), with many species narrowly endemic to single mountain systems within the entire Range (Giuletti & Pirani 1988). Finding a new species in the Chapada Diamantina, which is still poorly sampled for its frog fauna, is to be expected. What is unusual is that the new species also represents a new genus.

The fact that all but one of the endemic campos rupestres frogs are endemic only at the species level suggests that the differentiation of the campos rupestres biota occurred in a single episode and relatively recently in terms of geological time. Discovery of an endemic campos rupestres genus of frogs requires that the single episode of faunal differentiation requires emendment or explanation. There seem to be three most likely alternatives.

Rupirana is an endemic campos rupestres genus of frog. If this is true, that suggests that it had an earlier episode of differentiation than other campos rupestres endemic frogs. Although this alternative requires an additional episode of differentiation for frogs, this is not unusual for the rest of the campos rupestres biota, as there are endemic genera of campos rupestres plants (e.g., *Barbacenia* (Velloziaceae), *Morithamnus* (Compositae), *Pseudotrimezia* (Iridaceae), and *Raylea* (Sterculiaceae), Giuletti and Pirani 1988) and fishes (*Copionodon* and *Glaphryopoma* (Trichomycteridae), Pinna 1992).

Rupirana represents a sampling problem. It could be that *Rupirana* had or has a distribution with other species occurring in the Atlantic Forests (I think this more likely than in the cerrados/caatingas). If this is true, then either the Atlantic Forest species of the genus have become extinct and/or they are still extant but have not been found. The frog fauna of the northern Atlantic Forests is not well known and I would not be surprised if additional species of *Rupirana* were found there.

Recognition of *Rupirana* as a distinct genus is a taxonomic error. If this is the case, the new species does not require an historical zoogeographical explanation different from that for other campos rupestres endemic frogs.

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Appendix 1.— Character state descriptions and data matrix for phylogenetic analysis of selected genera of leptodactylid frogs.

Data from Heyer (1975) supplemented by taxa examined for this study as indicated in body of text.

Multistate characters ordered by criterion of morphoseries when reasonable. Character states not polarized.

Character 1. Pupil shape. State 0—round; State 1—horizontal.

Character 2. Tympanum visibility. State 0—external, visible; State 1—partially concealed; State 2—concealed. Character state order 0-1-2.

Character 3. Male thumb. State 0—no asperities; State 1—pad; State 2—spines. Character states not ordered.

Character 4. Body glands. State 0—none; State 1—paratoids; State 2—inguinals. Character states not ordered.

Character 5. Toe disks. State 0—none; State 1—disks but no grooves; State 2—disks with circumferential grooves; State 3—disks with dorsal scutes. Character states not ordered.

Character 6. Tarsal decoration. State 0—none; State 1—fold; State 2—flap. Character state order 0-1-2.

Character 7. Toe webbing. State 0—web; State 1—fringe; State 2—ridge; State 3—none. Character state order 0-1-2-3.

Character 8. Life history. State 0—tadpole with 2/3 denticle formula; State 1—tadpole with >2/3 denticle formula; State 2—tadpole with <2/3 denticle formula; State 3—direct development. Character states ordered in a triangular relationship with the following connections: 2-0-1; 2-3; 0-3; 1-3.

Character 9. Depressor mandibulae muscle. State 0—three slips (DFSQAT to dfsqat); State 1—two slips (DFSQ to dfsq); State 2—one slip (SQ). Character state order 0-1-2.

Character 10. Sternohyoideus muscle insertion. State 0—on lateral edge of hyoid plate; State 1—on lateral edge and midline of hyoid body; State 2—on midline of hyoid body. Character state order 0-1-2.

Character 11. Omohyoideus muscle insertion. State 0—muscle absent; State 1—insertion on hyoid body and fascia between posteromedial and posterolateral processes; State 2—insertion on hyoid body only; State 3—insertion on hyoid body adjacent to posteromedial process. Character states unordered.

Character 12. Iliacus externus muscle. State 0—extends <½ ilium length; State 1—extends ½–¾ ilium length; State 2—extends ¾–full length of ilium. Character state order 0-1-2.

Character 13. Tensor fasciae latae muscle insertion. State 0—posterior to anterior extent of iliacus externus muscle; State 1—at same level as anterior extent of iliacus externus muscle.

Character 14. Semitendinosus muscle. State 0—External head smaller than internal head, external head attached by tendon to internal head; State 1—as state 0, except internal and external heads displaced from each other; State 2—external head absent. Character states unordered.

Character 15. Adductor longus muscle. State 0—well developed, insertion on or near knee; State 1—poorly developed, insertion on adductor magnus muscle; State 2—absent. Character state order 0-1-2.

Character 16. Quadratojugal. State 0—present, contacting maxilla; State 1—absent.

Character 17. Nasal contact with maxilla. State 0—present; State 1—absent.

Character 18. Nasal contact with frontoparietal. State 0—absent; State 1—present, not fused; State 2—present, fused. Character states unordered.

Character 19. Frontoparietal fontanelle exposed. State 0—not exposed; State 1—exposed.

Character 20. Squamosal. State 0—zygomatic ramus about same length as otic ramus; State 1—otic ramus developed into plate; State 2—as State 1 and zygomatic ramus articulates with maxilla; State 3—otic ramus much smaller than zygomatic ramus, latter articulates with maxilla; State 4—otic ramus much larger than zygomatic ramus. Character states unordered.

Character 21. Vomerine teeth. State 0—present; State 1—absent.

Character 22. Median contact of vomers. State 0—absent; State 1—present.

Character 23. Prootic fusion with frontoparietal. State 0—absent; State 1—present.

Character 24. Occipital condyles. State 0—confluent; State 1—approximate; State 2—widely separated. Character state order 0-1-2.

Character 25. Anterior process of hyale. State 0—present; State 1—absent.

Character 26. Posterior sternum. State 0—cartilaginous plate, broadens posteriorly; State 1—cartilaginous plate, parallel or narrow; State 2—as State 1 with mesosternal mineralization; State 3—sternal style. Character state order 0-1-2-3.

Character 27. Length of last presacral transverse processes relative to sacrum. State 0—about equal; State 1—last presacral processes ≪ sacrum.

Character 28. Sacral diapophyses. State 0—expanded; State 1—rounded.

Character 29. Terminal phalanges. State 0—simple, knobbed, or claw-shaped; State 1—T-shaped.

Character 30. Ilial dorsal crest. State 0—absent; State 1—present.

Character 31. Diploid number of karyotype. State 0—greater than or equal to 26; State 1—24.

	Character																													
	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
Adelotus	0	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	1	0	0	1	?
Crinia	0	0&1&2	1	0	0	1	1&3	0	0&2	2	0	2	0	2	0	0	1	0	1	0	0&1	0	0	2	0	0	1	0	0	0	1
Ceratophrys	0	0&1&2	1	0	0	1	0	1	0	0	0	1	1	1	1	0	0	2	0	3	0	1	1	0	1	0	1	0	0	0	0
Batrachyla	0	0	1	0	1	0	2	0	1	0	1	0&1	0	1	2	1	1	0	1	1	0	0	0	2	1	1	0	0	1	0	0
Cycloramphus	0	2	0&2	2	0	0	0&2&3	0	1	0	1	1	0	1	0	0	0	1	0	1	0	1	0	2	1	1	1	0&1	0	1	0
Eleutherodactylus	0	0	0	0	2	0	2	3	0	1	2	2	0	2	0	0	0	0	0	1	0	0	1	2	0	2	0	1	1	1	0
Eupsophus	0	0&1&2	1	0	0	1	0&2	0	1	0	0&3	0&1	0&1	1	1	0	0	0	1	1	0&1	0	0	1	0&1	2	1	0	0	0	0&1
Hylorina	1	0	1	3	0	?	1	2	?	?	?	?	?	?	?	1	0	0	1	1	0	1	0	1	?	?	0	0	?	?	0
Megaelosia	0	0	0	0	3	2	1	0	1	0	1	1	0	0	1	0	0	0	0	4	0	0	0	1	1	2	0	1	1	1	0
Rupirana	0	0	1	0	0	1	2	?	0	0	2	2	0	0	0	0	1	0	1	1	0	0	0	2	0	1	0	0	0	1	?
Thoropa	0	0	1&2	0	1	0&1	0&2	0	0&1	0	1	1	0	0	1	0	1	0	1	1	0	0	0	2	1	1&3	0	0	1	1	0

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A new species of cardinalfish (Perciformes: Apogonidae) from the Bay of Bengal, Indian Ocean

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Abstract.—A new species, *Apogon oxina,* is described from the Bay of Bengal, Indian Ocean. The preserved color pattern suggests a close relationship with *Apogon ventrifasciatus* from the West Pacific. The new species lacks the white spot at the posterior base of the second dorsal fin present in several other species and has darker and sharper stripes on the head and upper body and well-developed bars on the sides reaching to or above the lateral line.

New species of the large cardinalfish genus *Apogon* continue to be recognized and described at a surprisingly high rate. Most of these species are from the Indo-Pacific region, with the majority in the large subgenus *Ostorhinchus.* There are about 111 valid species in this subgenus, of which about 21 undescribed species are known to me. Relationships within this large group are not well understood. Gon (1996) proposed phyletic relationships within his concept of the *Apogon* subgenus *Jaydia.* His detailed analysis illustrates the complexities of developing a robust hypothesis for relationships within species groupings of *Apogon* prior to testing with an inclusive analysis all of proposed subgenera, other species groupings of *Apogon* and other genera. Fraser (1972) suggested that a more complete understanding of supra-specific relationships, within and without *Apogon,* was dependant on well developed systematics of the species. Such a critical mass of information and material is emerging.

Color patterns and variations of those patterns appear to be the best distinguishing features of closely related species of *Apogon.* New species usually are first recognized by unique color patterns. Consistent color pattern differences between closely related species may be accompanied by a few morphometric differences, such as body depth, caudal peduncle length, spine lengths, soft fin-ray lengths, jaw length and eye diameter, or modally different counts for gill rakers and pectoral fin-rays. Other differences have been noted by many authors, such as meristic changes in the spine count of the first dorsal fin and soft rays of the second dorsal and anal fins; loss of the supramaxilla, supraneurals at the anterior end of the dorsal fin, one pair of epipleural ribs and uroneurals in the caudal skeleton; fusion of some hypurals in the caudal skeleton; character of spination of the postemporal, preopercle, infraorbitals; coloration of the stomach, intestine and peritoneum; presence or absence of known or potential bioluminescent ability; shape of the caudal fin; elongation of individual vertical fin rays; position of the anal opening between the pelvic and anal fins; general scale size, elaboration of pore architecture on scales as a simple pore, complex pores, or pit in scale; and the degree of ossification of the preopercle. *Apogon* and the family, in general, are replete with internal and external character variation not usually seen within a single percoid family. Nevertheless, some allopatric species pairs, for example, *Apogon abrogramma-Apogon exostigma* and *Apogon taeniopterus-Apogon menesemus* proposed by Fraser & Lachner (1985) differ only in color pattern. No morphometric, internal, or meristic differences within those species pairs are known.

The new species belongs in the subgenus *Ostorhinchus* Lacepède, 1802 as defined by Fraser (1972) using the name *Nectamia* Jordan, 1917. Gon (1987) designated a neotype for *Apogon fleurieu* (Lacepède 1802) and effectively relegated *Nectamia* as a synonym.

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. The following acronyms are used to designate institutions and collections cited and follow general usage given in Eschmeyer (1998); BPBM Bernice P. Bishop Museum, Honolulu; CAS California Academy of Sciences, San Francisco; MNHN Muséum National d'Histoire Naturelle, Paris; USNM collections of the former United States National Museum, deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Field station numbers are listed for additional collection information, for example PCH-69-279.

Apogon oxina, new species
Fig. 1

Material examined.—Holotype: *Apogon oxina* CAS 33959, 55.9 mm SL; India, Madras; in 15–22 m; April–June 1975; K. V. Rama Rao. Paratypes: India: CAS 98101; 7(43–71); data same as holotype. Sri Lanka: USNM 213364 55(44–58); Trincomalee; 10 m; PCH 69-277; 29 Sep 1969; Phillip C. Heemstra. USNM 213345 (43–44); PCH 69-279; 30 Sep 1969; Phillip C. Heemstra. Other material: Sri Lanka: USNM 213346 4(19–28); Trincomalee; CCK 69-135; 10–20 m; Christopher C. Koenig; 4 Apr 1970.

Comparative material.—Paratypes *Apogon ventrifasciatus* BPBM 34136 7(35–49); Indonesia, Flores I., Maumere Bay; 8 m; J. E. Randall; 19 Sep 1988. BPBM 34085 5(27–41); Indonesia, Flores I., Maumere Bay; 3–4 m.; J. E. Randall; 17 Sep 1988. Other material. USNM 328265 (45); Papua New Guinea, D'Entrecasteau Is., Normandby I.; 16 Dec 1993. BPBM 30132 (40–53); Indonesia, Lombok I., Sorongjunkung; J. E. Randall; 21 Feb 1974. Holotype *Apogon moluccensis* MNHN 8707; 60.3 mm SL, 76 mm TL; Amboina; Quoy and Gaimard.

Diagnosis.—An *Apogon* of the subgenus *Ostorhinchus* with 14 pectoral fin-rays, usually 23–24 total gill rakers on the first arch, no white spot behind the second dorsal fin, dark vertical bars present on body reaching to or past the lateral line, dark stripes present on head and upper body, and caudal peduncle length 20–25% SL.

Description.—For general body shape see Fig. 1. Range of proportions (as percentages of standard length) with the holotype in parentheses: greatest body depth 36–39 (39); head length 38–41 (41); eye diameter 12–13 (12.2); snout length 8–9 (9.5); bony interorbital width 7–8 (7.5); upper jaw length 18–20 (19); caudal peduncle depth 15–17 (16); caudal peduncle length 20–25 (23); first dorsal-fin spine length 2.8–3.8 (2.8); second dorsal-fin spine length 7.9–9.7 (8.0); third dorsal-fin spine length 17–20 (20); fourth dorsal-fin spine length 16–21 (21); second dorsal spine 12–16 (15); first anal-fin spine length 1.9–3.3 (2.3); second anal-fin spine length 11–12 (11); pectoral fin length 23–27 (23); pelvic fin length 23–26 (26).

Dorsal fin VII–1,9; anal fin II,8, last anal ray much longer than preceding fin-ray; pectoral fin-rays 14–14; pelvic fin 1,5; principal caudal fin-rays 9 + 8; pored lateral line scales 24; transverse scale rows above lateral line 2; transverse scale rows below lateral line 6; median predorsal scales 3–4 (4); circumpeduncular scale rows 12 (5+2+5); total gill rakers 23–24 (24), usually 20–22 (21) well developed 1–2+4–5 upper, 15–17+0–2 lower (2+5–16+1).

Villiform teeth in a band on premaxilla; two to three rows on dentary; one row on palatine and vomer; none on ectopterygoid, endopterygoid or basihyal.

Fig. 1. The holotype of *Apogon oxina,* 55.9 mm SL, from Madras, India, CAS 33959.

Vertebrae 10 + 14. Five free hypurals, one pair of slender uroneurals, three epurals, a free parhypural. Three supraneurals, two supranumerary spines on first dorsal pterygiophore. Basisphenoid present. Supramaxilla absent. Posttemporal serrate on posterior margin. Preopercle serrate on vertical and horizontal margins. Infraorbital shelf present on third bone. Scales ctenoid. Simple pored lateral-line scales from posttemporal to caudal fin, pored scales usually 24.

Life colors.—Unknown.

Preserved color pattern.—In 70% ethyl alcohol: Adult pattern: five dark stripes on each side of head with one (unpaired) mid-nape from snout to origin of first dorsal fin, two stripes over eye extending onto body above lateral line, the dorsal stripe along base of first dorsal fin reaching to or just beyond origin of second dorsal fin, the ventral one reaching well past origin of second dorsal fin; two stripes behind eye, neither extending onto body, the upper one reaching below the posttemporal and the lower one from snout, continuing behind eye along midline of head to edge of opercle above pectoral fin; one stripe extending from lower lip below eye onto opercle ending near pectoral fin base; four or five narrow dark bars from abdomen to first stripe above lateral line on body, first bar just behind and below pectoral fin reaching to lateral line, second bar beginning on abdomen near mid-pelvic fin length reaching past lateral line merging with first stripe above lateral line, third bar beginning on abdomen near posterior tip of pelvic fin reaching above lateral line merging with first stripe above lateral line, fourth bar beginning above anterior end of anal fin reaching above lateral line, and a faint indication of a fifth bar beginning about mid-anal fin base reaching above lateral line; first dorsal fin dusky; melanophore patterns indicate stripe may be present in second dorsal fin and in anal fin; faint dark mark at posterior base of second dorsal; edges of caudal fin pale, melanophore patterns indicate remains of mid-stripe on caudal fin; outer edge of pelvic fin dusky; stomach and intestine black, peritoneum pale. Juvenile pattern: mid-body lateral stripe extending from snout, continuing behind eye along midline of head and body onto caudal fin; 3–5 vertical bars reaching nearly to stripe just above lateral line; no melanophore patterns in the second dorsal or anal fin; other preserved patterns similar to adults.

Distribution.—Known from Madras, India and Sri Lanka.

Etymology.—The Greek word *oxina*

meaning rake or harrow, a feminine noun in apposition, referring to the vertical bars on the side reaching the stripe.

Remarks.—This new species of *Apogon* has a combination of characters suggesting a close relationships with *Apogon ventrifasciatus* Allen, Kuiter & Randall, 1994. *Apogon oxina* differs in lacking the white spot behind the second dorsal fin, having vertical bars reaching to or past the lateral line, a shorter caudal peduncle length (20–25% SL versus 25–31% SL), stronger and darker stripes and bars at all sizes, and an apparently larger size (71 mm SL versus 53 mm SL). Total gill-raker counts for the first arch overlap at 23–24 for *Apogon oxina* and 22–25 for *Apogon ventrifasciatus.* Both species have 20–22 well developed gill-rakers and have 15–17 well developed lower arch gill rakers.

Allen et al. (1994) compared their new species, *Apogon ventrifasciatus,* with *Apogon moluccensis* Valenciennes, 1832 mentioning some similarities in color pattern and a difference in the well developed lower arch gill raker count of 15–17 for *Apogon ventrifasciatus* and 20–21 for *Apogon moluccensis.* However, the type of *Apogon moluccensis* has 16 well developed lower arch gill rakers with no remaining color pattern other than a white spot at the posterior base of the second dorsal fin based on my examination. Valenciennes (1832) describes the type of *Apogon moluccensis* as having stripes on the nape, blackish lips, first dorsal fin with blackish tip and a reddish body lacking any marks or spots on or near the caudal fin. Two species with basal second dorsal-fin white spots and differing gill-raker counts exist and more species may be present based on color patterns. There are two Bleeker names which need to be considered in this group besides *Apogon ventrifasciatus: Apogon chrysosoma* Bleeker, 1852 and *Apogon monochrous* Bleeker, 1856. Gon (1987) identified *Apogon moluccensis* from the Maldives at Rasdu Atoll. He described the 38 mmSL specimen as having 6–7 vertical rows of spots on the body from the lateral line to the abdomen, stripes in the soft dorsal and anal fin, a white spot at the posterior base of the second dorsal fin, 21 well developed gillrakers on the first arch and 24(6+18) total gill rakers. The redescription of types and valid species of this group are under study by J. E. Randall, G. R. Allen and me. None of these white-spot nominal or possibly undescribed species have the combination of characters of *Apogon oxina.*

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A new species of deep-water skate, *Rajella eisenhardti*, (Chondrichthyes: Rajidae) from the Galápagos Islands

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Abstract.—A new species of skate, *Rajella eisenhardti,* is described from two specimens collected from deep-slope (757–907 m) areas off the Galápagos Islands. It is similar to another eastern Pacific species, *Rajella nigerrima* de Buen 1960, but differs in part by having more precaudal vertebrae and more pectoral radials, a wider and longer disc, a longer snout, larger gill openings with wider interspaces, longer anterior and shorter posterior pelvic lobes, and in coloration and spination.

The skate fauna of the eastern central Pacific, extending from southern Mexico to northern Peru, contains at least 12 species (McEachran & Miyake 1984, 1990; McEachran 1995). Galápagos records are limited to those of *Bathyraja spinossima, Gurgesiella furvescens* and *Raja velezi* (McEachran & Compagno 1979; McEachran 1995; Grove & Lavenberg 1997). McEachran and Miyake (1984) also reported a specimen of *Bathyraja* cf. *richardsoni* from near the Galápagos Islands (00°11.3′S, 97°27.7′W, 1710 m), but not within the archipelago. The recent capture of two specimens of an undescribed *Rajella* using the manned submersible *Johnson Sea-Link* during deep-water dives around the Galápagos Islands (McCosker et al. 1997) has prompted this paper.

Methods

Abbreviations: CAS = California Academy of Sciences, ichthyological collections; TCWC = Texas Cooperative Wildlife Collection; TL = total length.

Measurements and meristic counts follow current methodology in McEachran & Miyake (1984, 1988) and Stehmann (1995). Measurements were made with dial calipers and recorded to the nearest 0.1 mm. Vertebral and radial counts were made from radiographs.

Rajella eisenhardti, new species
Figs. 1–2; Table 1

Diagnosis.—The new species can be distinguished from other *Rajella* species by a combination of its moderately long tail (tail length greater than distance from snout to cloaca) that is largely free of denticles on the ventral side; three rows of caudal thorns that begin at level of anterior pelvic lobe; 67–68 predorsal caudal vertebrae; 68–69 pectoral radials; disc width 55.0–58.5% of TL and disc length 50.0–51.2% of TL; snout-vent length 44.1–46.4% of TL; preorbital snout length 13.4–14.1% of TL; and ventrum darker than dorsum, with distinct light areas around mouth and nasal areas, gill openings, abdomen, cloaca, and tips of rostrum, tail, and pectoral fins.

Holotype: CAS 86817, an immature male (384.5 mm TL) caught with a siphon hose on the bottom at 757 m off Cabo Rosa (01°04.74′S, 91°11.08′W), Isla Isabella, Galápagos Islands, by J. E. McCosker abroad the submersible *Johnson Sea–Link* on 11 Nov 1995.

Paratype: CAS 86561, an immature male (254.1 mm TL) caught with a siphon hose

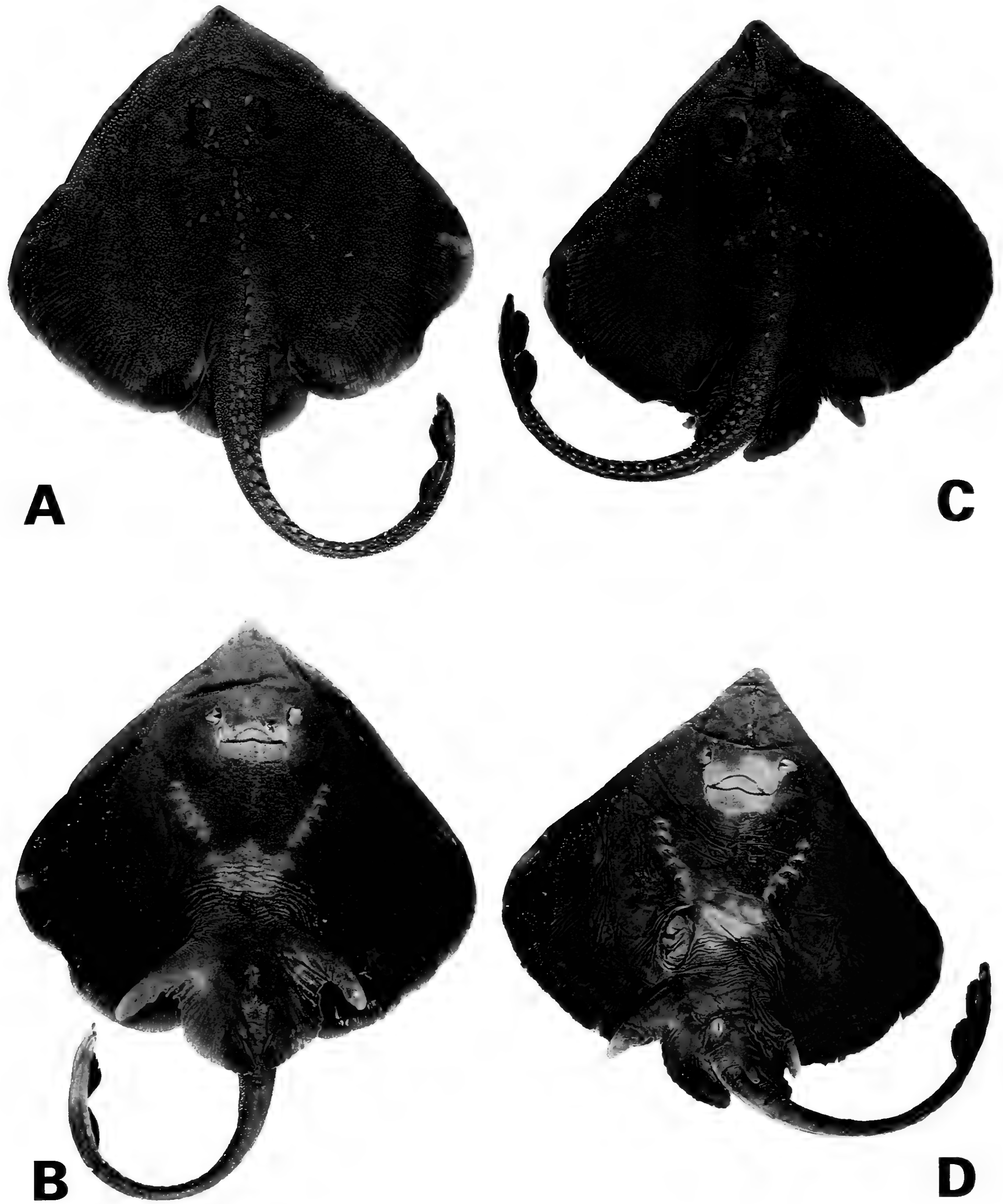

Fig. 1. Preserved types of *Rajella eisenhardti.* A–B, dorsal and ventral views of holotype, CAS 86817 (384.5 mm TL); C–D dorsal and ventral views of paratype, CAS 86561 (254.1 mm TL).

on the bottom at 907 m off James Bay (0°26.46′S, 90°19.04′W), Isla San Salvador (Santiago Island), Galápagos Islands, by J. E. McCosker aboard the submersible *Johnson Sea–Link* on 26 Nov 1995.

Comparative material: *Rajella nigerrima,* TCWC 3881-01, 273 mm TL, juvenile female, trawled off Chile (35°53.5′S, 72°44′W) at 780–925 m, *Anton Brunn* cruise 18A, sta. 40, 9–10 Aug 1966; TCWC 3885-01, 239 mm TL, juvenile female, trawled off Peru (03°15′S, 80°55′W) at

Fig. 2. *Rajella eisenhardti.* Underwater photograph of living paratype (CAS 86561) taken from the submersible *Johnson Sea-Link* on the bottom at 907 m off James Bay, Isla San Salvador (Santiago Island) Galápagos Islands.

945–960 m, *Anton Brunn* cruise 18A, sta. 120, 10 Sep 1966.

Description.—See Table 1 for meristics and measurements. Meristic values described below are listed for the holotype, and values for the paratype are shown in parentheses.

A medium-sized species of *Rajella* (sensu Stehmann 1970, 1978; McEachran & Dunn 1998), its disc heart-shaped and moderately broad, with broadly-rounded outer corners. Disc length 0.88 (0.91) in disc breadth. Anterior margin of disc weakly concave near tip of rostrum, straight to slightly convex to widest part of pectorals. Axis of greatest width 0.83 (0.84) times distance from tip of snout to axil of pectoral fins. Snout to mid-cloaca 2.15 (2.26) times in total length.

Preorbital length 4.0 (3.5) times orbit length; preoral length 1.87 (1.98) times internarial distance. Interorbital distance 1.16 (0.96) times orbit length; orbit length 1.48 (1.85) times spiracle length. Anterior nasal lobe laterally expanded to form a nasal curtain, weakly convex anteriorly and finely-fringed laterally and posteriorly. Posterior nasal flap well-developed, extending to near corner of mouth; a single projection on lateral side of flap with fine fringes on the lateral posterior edges, with a smooth margin medially; length of flap 0.32 (0.29), and width 0.59 (0.57), into preoral length; space between fimbriae 0.30 (0.29) into preoral length.

Distance between first gill slits 1.95 (2.15) times distance between nares; distance between fifth gill slits 1.22 (1.33) times distance between nares; length of first gill slit 1.20 (1.11) times length of fifth gill slit. Third gill slit largest, 0.26 (0.27) times distance between nares, fifth gill slit 0.16 (0.19) times distance between nares, only slightly smaller than first, 0.19 (0.21) times distance between nares.

Pelvic fins deeply incised; anterior lobe long and moderately narrow, bluntly tapered and rounded distally; length of anterior lobe 1.59 (1.46) times length of posterior lobe. Tail long, gradually tapering to tip; distance from mid-cloaca to caudal tip 1.15 (1.26) times distance from snout to cloaca. Base of tail moderately narrow, 9.3% (9.2%) of cloaca to caudal tip length, and moderately convex dorsally, weakly concave ventrally becomming flattened distally. Lateral folds originating well behind the base of tail and continue along length to just anterior of caudal tip where it ends as small lobed flap. Dorsal fins low and rounded; first fin only slightly larger than second and similarly shaped, no space between dorsal fins or between second dorsal and epichordal caudal lobe.

Dorsum entirely covered with fine denticles, including tail and dorsal fins, except on the lateral and posterior margins of the pectoral fins; pelvic fins free of denticles and anterior pelvic lobes smooth, but base of pelvic with fine denticles in the paratype. Larger denticles and thorns with oval or oblong bases, often with weak longitudinal ridges and anteriorly curving tips. Larger denticles on rostral shaft; one to two thorns anterior to each orbit, three posterior to each orbit, and one thorn on each side of the inner orbit. Five thorns on nuchal midline, three on each scapular lateral to the midline, 6–7 thorns on post-scapular midline anterior to the tail. Three rows of thorns on the dorsal surface of the tail be-

Table 1.—Measurements (in mm) and percentages of total length (in parentheses) of *Rajella eisenhardti* compared to percentages of total length of *R. nigerrima* (5 males, 6 females; data from McEachran & Miyake, 1984).

	Raja eisenhardti		*R. nigerrima* (*n* = 11)	
	Holotype CAS 86817	Paratype CAS 86561	Range	Mean
Total length	384.5	254.1	139–374	—
Snout to mid-cloaca	178.5 (46.4)	112.3 (44.1)	40–44	43
Disc width	225.0 (58.5)	140 (55.0)	51–53	52
Disc length	197.0 (51.2)	127.0 (50.0)	46–49	48
Head length	104.8 (27.3)	63.0 (24.8)	NA	NA
Snout length (preorbital)	54.3 (14.1)	34.3 (13.4)	10.2–12.8	11.0
Snout length (preoral)	57.5 (14.9)	35.9 (14.1)	12.6–14.5	13.9
Snout to maximum width	132.0 (34.3)	78.0 (30.6)	31–35	32
Snout to pectoral axis	164.5 (42.8)	104.8 (41.2)	NA	NA
Prenasal length	47.7 (12.4)	31.4 (12.3)	9.6–11.5	11.0
Orbit diameter	13.5 (3.5)	9.8 (3.8)	3.7–4.8	4.3
Interorbital distance	15.7 (4.0)	9.5 (3.7)	3.3–3.6	3.5
Spiracle length	9.1 (2.3)	5.8 (2.2)	1.5–2.3	1.8
Orbit and spiracle length	19.4 (5.0)	12.3 (4.8)	3.4–5.2	4.6
Distance between spiracles	28.0 (7.2)	17.7 (6.9)	6.1–6.8	6.3
Mouth width	28.7 (7.4)	18.7 (7.3)	6.2–7.2	6.9
Distance between nostrils	30.8 (8.0)	18.1 (7.1)	6.5–7.1	7.0
Nasal curtail length	18.6 (4.8)	10.3 (4.1)	NA	NA
Nasal curtail width	34.0 (8.8)	20.5 (8.1)	NA	NA
Width of 1st gill opening	5.9 (1.5)	3.8 (1.4)	1.0–1.5	1.2
Width of 3rd gill opening	8.1 (2.1)	4.9 (1.9)	1.0–1.5	1.2
Width of 5th gill opening	4.9 (1.2)	3.4 (1.3)	0.6–1.1	0.8
Distance betw. 1st gill openings	60.3 (15.6)	38.9 (15.3)	13.0–14.5	13.8
Distance betw. 5th gill openings	37.6 (9.7)	24.1 (9.4)	8.1–8.8	8.5
Length of anterior pelvic lobe	63.9 (16.6)	41.3 (16.2)	10.4–14.7	12.9
Length of posterior pelvic lobe	40.2 (10.4)	28.3 (11.1)	11.8–16.0	14.9
Cloaca to 1st dorsal fin	142.8 (37.1)	100.2 (39.4)	41–44	42.0
Cloaca to caudal origin	188.5 (49.0)	134.3 (52.8)	47–57	54.0
Cloaca to caudal tip	206.1 (52.5)	141.8 (55.8)	50–60	57.0
Caudal lobe length	11.6 (3.0)	8.9 (3.5)	NA	NA
1st dorsal height	21.7 (5.6)	15.0 (5.9)	NA	NA
1st dorsal base	22.5 (5.8)	16.1 (6.3)	NA	NA
2nd dorsal height	21.1 (5.5)	12.6 (5.0)	NA	NA
2nd dorsal base	22.8 (5.9)	16.5 (6.5)	NA	NA
Tail width at base	19.2 (5.0)	13.1 (5.2)	NA	NA
Tail width at 1st dorsal origin	6.9 (1.8)	5.0 (2.0)	NA	NA
Tail thickness at base	13.6 (3.5)	7.8 (3.1)	NA	NA
Tail width at 1st dorsal origin	4.5 (1.2)	3.2 (1.3)	NA	NA
No. of upper/lower tooth rows	48/32	46/42	36–46/36–46	42.4
No. of trunk vertebrae	29	28	27–30	28.6
No. of predorsal caudal vert.	67	68	59–65	62.6
No. of pectoral radials	69	68	61–65	63.0
No. of pelvic radials	19	17	NA	NA

ginning at the mid-level of the pelvic fins and continuing to first dorsal fin; median caudal thorns 24 (23); lateral caudal thorns numbering 38–39 (19–20), thorns diminishing along the tail. Ventral surface of holotype entirely smooth and bare of denticles; ventral surface of paratype smooth except for some small denticles on ventrolateral margins of tail.

Upper and lower jaws slightly arched;

teeth in quincunx arrangement with small short median crowns becoming more blunt and flattened distally; upper tooth rows 48 (46), lower rows 32 (42). Trunk vertebrae 29 (28), predorsal caudal vertebrae 67 (68). Pectoral radials 69 (68), pelvic radials 19 (17).

Color after preservation: Holotype purplish gray and paratype light brownish gray dorsally; both with whitish blotch on the dorsal edge of the pectoral fin tip; ventral surface darker except for distinct whitish areas on the anterior tip of the rostrum, anterior and posterior to the mouth, around the nostrils, around each gill opening, around the cloaca, on the abdomen, on the tips of the anterior pelvic fin lobes, and at the tip of the tail; light area between abdomen and gill openings connected by a V-shaped mark. Thorns and large denticles whitish, smaller denticles same color as surrounding skin. Color in life (based on an underwater photo of the paratype): dorsal interior of disc, pelvic base, and tail pale brown to grayish; rostrum, dorsal fins, and margins of pectoral and pelvic fins blue-gray.

Etymology.—Named in honor of E. Roy Eisenhardt, director emeritus of the California Academy of Sciences, who has generously assisted us and our colleagues.

Discussion

The subgenus *Rajella* was recently elevated to full generic status (McEachran & Dunn 1998), and includes 14 species found in the Atlantic, Pacific, and Indian oceans. These are: *R. annandalei* Weber, 1913; *R. barnardi* (Norman 1935); *R. bathyphilia* (Holt & Byrne 1908); *R. bigelowi* (Stehmann 1978); *R. caudaspinosa* (Von Bonde & Swart 1923); *R. dissimilis* (Hulley 1970); *R. fuliginea* (Bigelow & Schroeder 1954); *R. fyllae* (Lütken 1887); *R. kukujevi* (Dolganov 1985); *R. leopardus* (Von Bonde & Swart 1923); *R. nigerrima* (de Buen 1960); *R. purpuriventralis* (Bigelow & Schroeder 1962); *R. ravidula* (Hulley 1970); and *R. sadowskii* (Krefft & Stehmann 1974). Our specimens differ from all of these species by a combination of morphometrics, meristics, spination, and coloration. It most closely resembles the only other eastern Pacific *Rajella, R. nigerrima,* a species that ranges from Peru to Chile (McEachran & Miyake 1984).

Rajella nigerrima has a checkered taxonomic history. It was first placed in the genus *Breviraja* (de Buen 1960; Stehmann & Seret 1983), later placed in the subgenus *Malacoraja* (McEachran & Compagno 1982) which was subsequently elevated to generic rank (McEachran 1984; McEachran & Miyake 1984; Ishihara & Ishiyama 1986), later reclassified in *Raja,* subgenus *Rajella* (McEachran & Miyake 1990; Pequeño & Lamilla 1993), and has recently been elevated to generic status (McEachran & Dunn 1998). The types of *R. nigerrima* are believed lost and a neotype was designated by McEachran & Miyake (1984).

Our comparisons with the original description of *R. nigerrima,* specimens described by McEachran & Miyake (1984), and preserved specimens we examined, show significant meristic and morphological differences (Table 1). *Raja nigerrima* has fewer predorsal caudal vertebrae and fewer pectoral radials. There are several important proportional differences between *R. eisenhardti* and *R. nigerrima* including the latter's smaller preorbital length in relation to orbit length, and its first gill slit is longer than its fifth gill slit. And (in relation to total length) *R. nigerrima* has a shorter snout, a shorter snout to mid cloaca length, a reduced disc length and width, a narrower mouth, narrower interorbital and interspiracular distances, shorter anterior pelvic lobes, larger posterior pelvic lobes, and narrower third and fifth gill openings.

Rajella nigerrima has three rows of dorsal thorns posterior to the suprascapular, but *R. eisenhardti* has three rows beginning at the middle edge of the pelvic fin; *R. nigerrima* has three dorsal and lateral rows of thorns from the base of the tail to the first dorsal fin, but in *R. eisenhardti* the caudal thorns begin at the level of the anterior pelvic lobes. The underside of the tail in *R. nigerrima* has many small, sharp denticles except for a very narrow strip along the midline, which is bare; in *R. eisenhardti,* the underside is completely bare (holotype) or has spinelets only on the lateral margins of the tail's underside (paratype).

The color of *R. nigerrima* is brown, with some indistinct lighter areas on the underside around the mouth, vent, abdomen, and around the gills; in *R. eisenhardti,* the body color is gray to brownish gray with very distinct whitish areas around the nares, mouth, gills, vent, and abdomen, and on the tips of the rostrum, tail, and pectoral fins and pelvic lobes.

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A new genus of the subfamily Cubacubaninae (Insecta: Zygentoma: Nicoletiidae) from a Mexican cave

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Abstract.—A new genus and species (*Squamigera latebricola*) of the subfamily Cubacubaninae from a Mexican cave is described. The new genus is distinguished from almost all the genera of this subfamily by having scales. It differs from *Texoreddellia,* the only other genus of this subfamily with scales, by the morphology of scales and other characters, which are discussed.

The family Nicoletiidae is a frequently encountered group in caves of México and Central America (Reddell 1981), but with few exceptions, most species await description. During exploration of several caves in the states of Guerrero and Morelos, México, several specimens of this family were collected. A specimen collected from "Pozas Azules" cave is a previously undescribed genus with scales of the subfamily Cubacubaninae. Available material is of particular interest because most members of the subfamily lack scales. Only two genera have them: *Texoreddellia* (Wygodzinsky 1973) and the new genus described here. However, the morphology of the scales among other characteristics is drastically different for these two genera; therefore, they are probably not closely related.

Study Area

The material was collected in "Pozas Azules" cave (Taxco de Alarcón Municipality, Guerrero State, México, 18°36′40″N, 99°33′25″W). The cave is 1399 m long and +53 m deep. This cave is the resurgence of a cave system formed by Isote cave and Cueva de las Pozas Azules. Total length of system is almost three kilometers and depth is 230 m (for a detailed description of both caves' topography, see Espinasa-Pereña 1989).

This cave system has a very peculiar fauna. Apart from the new genus described here, a freshwater polychaete has been described as a troglobite (Solís-Weiss & Espinasa 1991). Some undescribed copepods living in association with the polychaete will probably be characterized as troglobites. Other organisms collected in the system are troglophile ricinulids (*Cryptocellus boneti*), collembola of the families Entomobridae and Sminthuridae, beetles, two species of spiders, millipedes, mites, protozoa and bacteria (*Salmonella, Klebsiella,* and *Bacillus*). To date, physical connection between Isote cave and Cueva de las Pozas Azules has not been explored because both ends of the caves end in sumps. Connection is assumed in part on geohydrological evidence (Espinasa-Pereña 1989), by the proximity of the two final sumps found in each cave (less than 20 m apart), and most importantly, by the shared fauna mentioned above.

Cave formation.—The limestone rock was formed during the lower Cretaceous period (Albian, Cenomanian, and Turonian). Elevation occurred at the end of Cretaceous (Maastrichtian), when erosion began. Presence of an igneous rock (Riolite tilzapotla) overlaying the limestone from which the water that formed the cave comes, seems to indicate that the cave was not formed until late Oligocene (López-Ramos 1974). It is also known that the cave was already formed in the Quaternary because there is evidence in cave sediments of climatic changes related to this period (Espinasa-Pereña, pers. comm.). Thus, if the cave was formed at some point between Oligocene and Quaternary, there is reason to assume that the troglobites in this cave system separated from the outside communities at more or less the same time.

Materials and Methods

The specimen was found crawling on the cave wall. It was placed into a vial with 70% alcohol. 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 the aid of a camera lucida attached to a compound microscope.

The type is 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-2.

Squamigera, new genus

Diagnosis.—A member of the subfamily Cubacubaninae with scales. Cerci of male with modified spines. Parameres with a cleft on apex.

Description.—Body robust, long, approximately parallel-sided, thorax slightly but distinctly wider than abdomen. Scales present, numerous, and multiradiate. Form mucronate to emarginate, with borders slightly serrated. Head, thorax, and abdomen with scales and setae. Legs with scales on proximal articles. Mouthparts and abdominal stylets only with setae.

Pedicellus of male with unicellular glands and a small spur on its base. Mouthparts not specialized. Mandibles strongly sclerotized apically and with usual teeth. Galea apically with several sensory pegs. Lacinia heavily sclerotized distally; first process of lacinia pectinate. Labium without prominent lateral lobes.

Tarsi with 4 articles. Praetarsi with 3 simple claws, median claws glabrous, slender, and smaller than lateral claws.

Abdominal sterna II (apparently)-III-VII subdivided into coxites and sternite. Sterna VIII and IX of male entire. Sterna II–VII with 2 + 2 macrochaetae. Coxites on segments II–IX with stylets. Eversible vesicles on segments II–VI, pseudovesicles on VII. Urosternum VIII with a wide and not too deep posterior emargination. Posterior projections acute to slightly rounded, pointing slightly outward. Tergum X protruding, almost straight on posterior border, posterior angles with 2 or 3 subequal macrochaetae. Urosterna III and IV simples. Cerci of male with modified spines.

Parameres with a cleft and specialized setae on apex. Opening of penis longitudinal.

Type species.—Squamigera latebricola.

Etymology.—Latin *Squamigera* = scale bearing, scaly. Here treated as a noun in the nominative singular. Gender, feminine. Makes reference to its body covered with scales.

Distribution.—The only individual found is from "Cueva de las Pozas Azules" cave, Taxco de Alarcón Municipality, Guerrero State, México, 18°36′40″N, 99°33′25″W.

Remarks.—Squamigera belongs to a group of nicoletiid genera, the Cubacubaninae (Mendes 1988), characterized by subdivided abdominal sterna II–VII and fused coxites of VIII and IX abdominal segments of the male. *Squamigera* is distinguished from almost all genera of this subfamily by having scales. It differs from *Texoreddellia,* the only other genus with scales, by the morphology of scales, having scales on head, morphology of parameres, and modified spines in male cerci.

The genus shares with *Anelpistina* (Silvestri 1905 as subgenus), *Prosthecina* (Silvestri 1933), and *Cubacubana* (Wygodzinsky & Hollinger 1977), the presence of spines in cerci and a posterior emargination on urosternum VIII, which are absent in

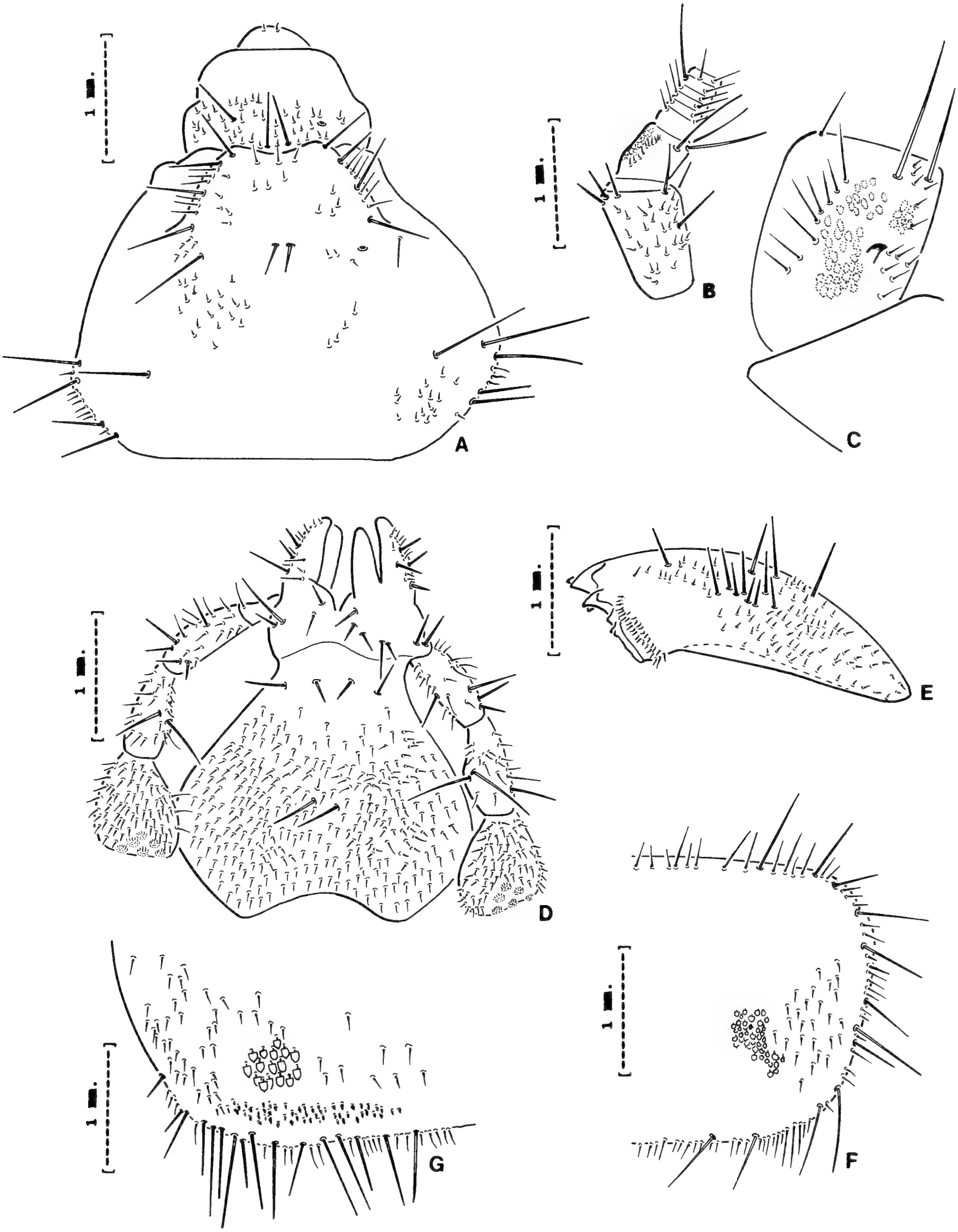

Fig. 1. *Squamigera latebricola* new genus. (Male): A, Head; B, Basal article and pedicellus of antenna; C, Small spur of pedicellus; D, Labial palp and labium; E, Mandible; F, Thoracic tergum (scales and setae partially shown); G, Posterior border of metanotum (scales partially represent).

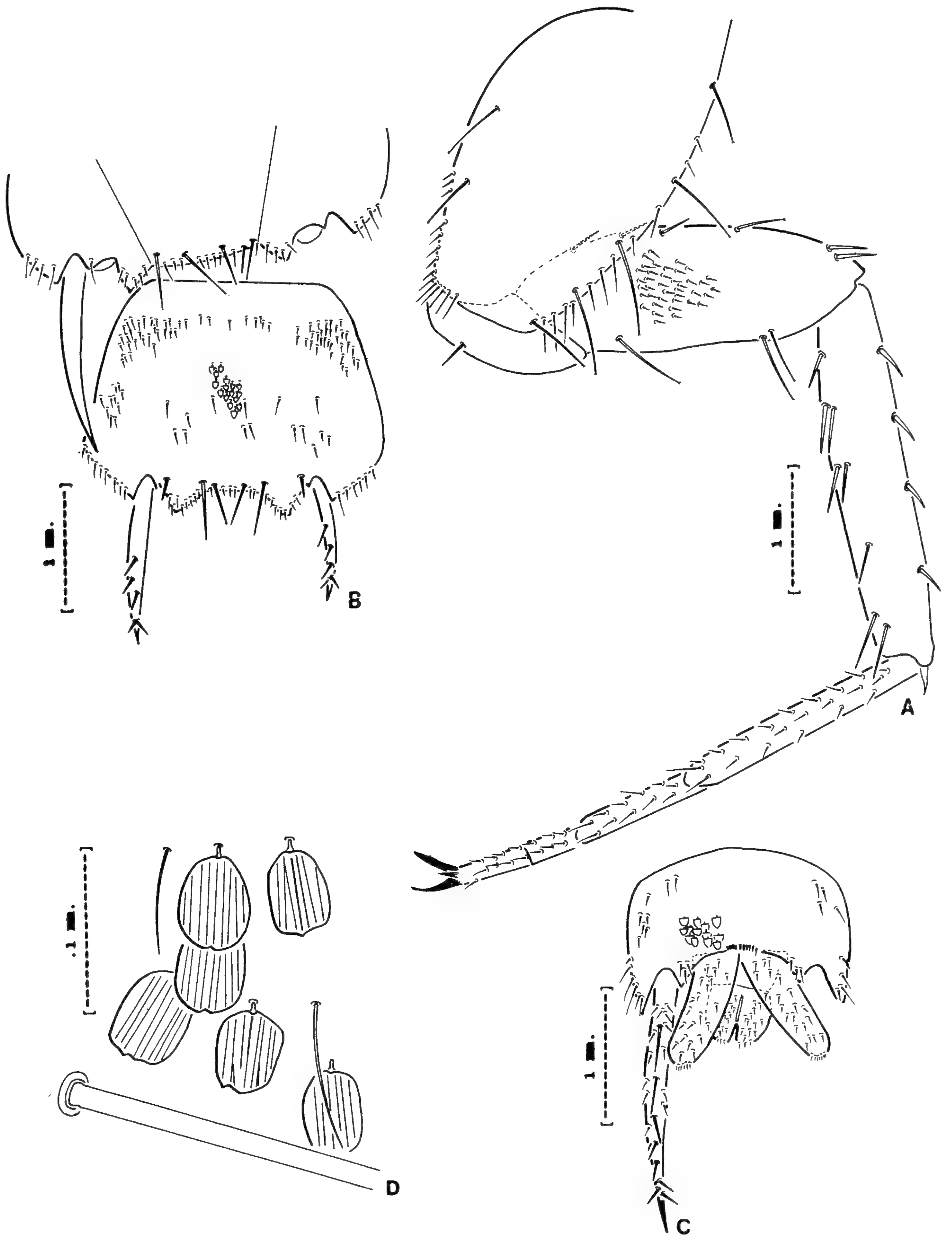

Fig. 2. *Squamigera latebricola* new genus. (Male): A, Hind leg, microchaetae partially shown, scales not shown; B, Urosternum VII and VIII (scales and setae partially shown); C, Genital area; D, Scales of head.

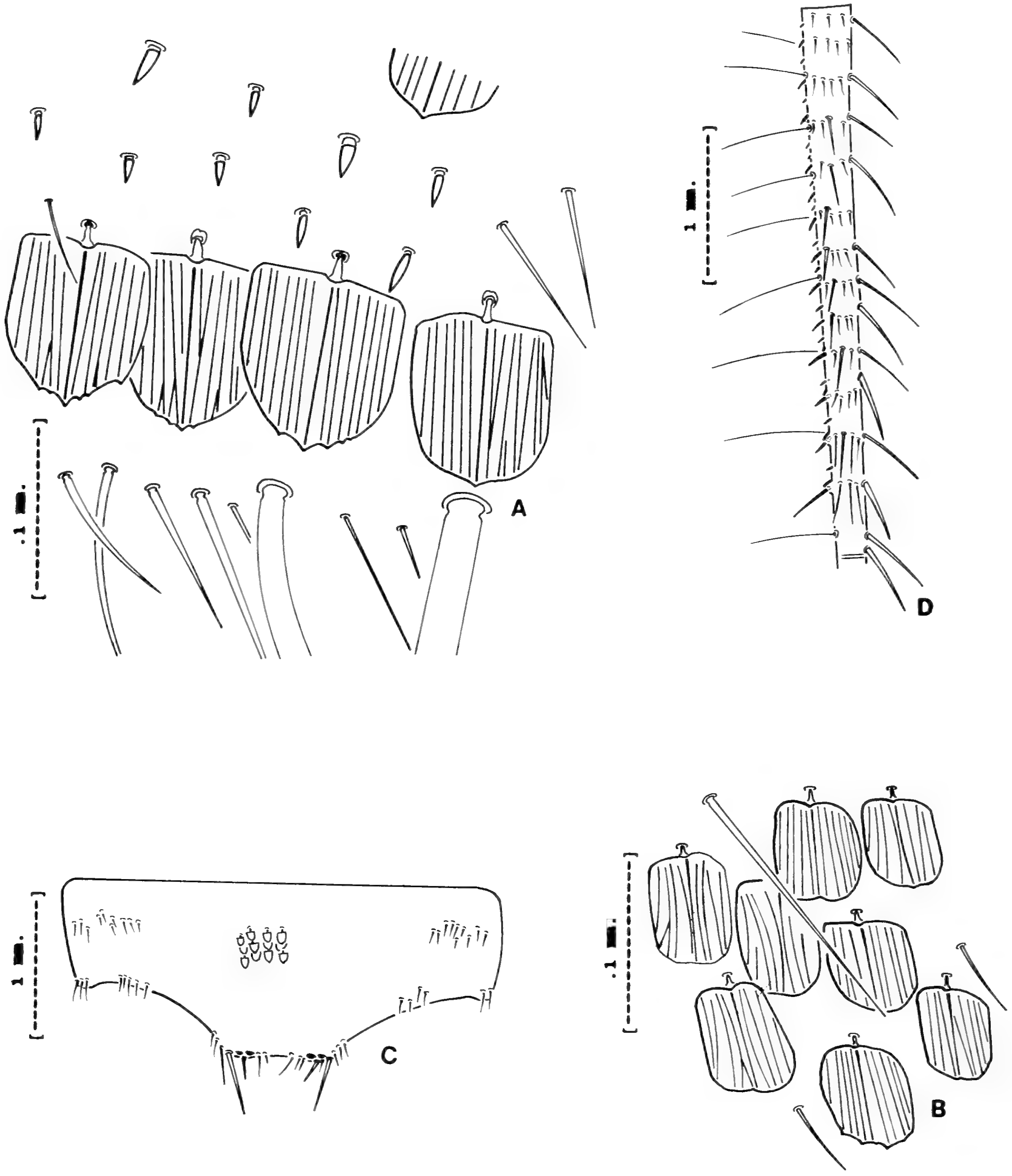

Fig. 3. *Squamigera latebricola* new genus. (Male): A, Scales and spines of the posterior border of the metanotum; B, Scales of urotergum I; C, Urotergum X (scales and setae partially shown); D, Cercus basal portion.

Texoreddellia. It is possible that *Squamigera* has closer affinities with this group of species than with *Texoreddellia.*

Squamigera latebricola, new species
Figs. 1A–G, 2A–D, 3A–D

Material examined.—México. Guerrero: Taxco de Alarcón, Cueva de las Pozas Azules (+53 meters deep, 1399 meters long). 3 Dec 1988, R. Espinasa-Closas col. Male holotype.

Description.—Maximum body length 22.0 mm. Maximum length of antennae unknown (broken), of caudal appendages 28.0 mm. Body and legs robust. Head, thorax, abdomen, and proximal articles of legs covered by scales (Figs. 2D, 3A, B). General color light yellow to white.

Head with macrochaetae and microchaetae as shown in Fig. 1A. Basal article of antennae in males has a small projection with 2 macrochaetae. Pedicellus of antennae of male as shown in Fig. 1C, with 5 clusters of unicellular glands and a small sclerotized spur. Mouthparts relatively long. Apex of maxillary palp similar to *Texoreddellia,* but with a third very small extra conule. Labial palp long, apical article barely longer than wide, labium and first article of labial palp with macrochaetae (Fig. 1D). Mandible without very small pegs over the bigger tooth. Setae as shown in Fig. 1E. Legs as shown in Fig. 2A, relatively long; hind tibia approximately 5 times longer than wide; claws of normal size.

Cerci of male with a longer than wider basal article and a very long second article, followed by short articles of subequal size. In the very long article the spines start almost at its base until they become a more prominent group; the relatively long spines are inserted on distinct tubercles (Fig. 3D). Compared with other genus of the subfamily, spines are relatively small.

Thoracic terga with long macrochaetae (Fig. 1F), very abundant on all borders. Also, on the posterior border they show a series of small sclerotized spines (Figs. 1G, 3A). Tergum X protruding, almost straight on the posterior border (Fig. 3C).

Urosterna III and IV of male without modifications. Urosternum VIII with a wide and not too deep posterior emargination. Posterior projections acute to slightly rounded, pointing slightly outward (Fig. 2B).

Urosternum IX of male slightly curved behind and centrally on the posterior border with macrochaetae slightly more sclerotized (Fig. 2C). Point of insertion of parameres in urosternum IX is deep, with internal face of coxal processes with macrochaetae more sclerotized (Fig. 2C) similar to some members of the genus *Anelpistina.*

Stylets IX bigger than the others, with 6 macrochaetae and an extra subapical pair. The other stylets only have 3 macrochaetae and an extra subapical pair. In males, styles IX without other modifications.

Penis and parameres as in Fig. 2C. Parameres curved outward, attaining less than ½ the length of stylets IX. Surface of parameres with a cleft and short setae.

Etymology.—Latin *latebricola* = One who dwells in lurking places. Gender masculine. Makes reference to the cavernicole habitat where this species dwells.

Remarks.—Despite several trips to Pozas Azules cave, only a single male was collected. Because of its size, this specimen is probably an adult with all the secondary sexual characters developed. Individuals at different stages of the postembryonic development might differ in characters, such as the number and size of spines in cerci.

Many caves in this area of Guerrero, México, have been explored and have yielded many individuals of the family Nicoletiidae (Espinasa 1991), but all from different genera. The one locality where *S. latebricola* has been found is in this single cave. Therefore it is probably a troglobite with a very restricted geography.

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Two new species of the genus *Anelpistina* (Insecta: Zygentoma: Nicoletiidae) from Mexican caves, with redescription of the genus

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Abstract.—Two new species of the genus *Anelpistina* are described, *A. inappendicata* and *A. cuaxilotla.* Of these two, *A. inappendicata* lacks the articulated submedian appendages found in urosternite IV of males, which are diagnostic characters of genus *Anelpistina.* Analysis of other characters shows that this species has close affinities with members of genus *Anelpistina,* and therefore a new re-description of the genus is provided to include this species.

Insects of the family Nicoletiidae are common inhabitants of caves in México. Numerous species of troglobites and troglophiles have been collected from this area, but with few exceptions, they await description (Reddell 1981). During the exploration of several caves in the states of Guerrero and Morelos, México, several specimens of this family were collected and are described here, thus contributing to the knowledge of the cave fauna of the region.

Definition of genus *Anelpistina* by Silvestri (1905) is based on the articulated submedian appendages found in urosternite IV of males. Organisms who are closely related to species of genus *Anelpistina,* but lack such appendages, would be incorrectly placed in genus *Cubacubana* (Wygodzinsky & Hollinger 1977). For this reason, genus *Anelpistina* is redescribed using more characters to include species, such as the one described in this paper, that lack the appendages.

Materials and Methods

Detailed descriptions of the caves can be found in Hoffman et al. (1986), Diamant & Espinasa-Pereña (1991), and in Espinasa-Pereña (1989). Organisms collected were crawling on floor or under rocks. They were placed into a vial with 70% alcohol or were taken alive to the laboratory. Dissections were made with aid of a stereo microscope and the different parts of the body were mounted in fixed preparations with Hoyer's solution.

Comparison with *A. boneti* was done with specimens collected by author from their type localities of Juxtlahuaca cave, Colotlipa, Guerrero, México, and from a new locality, the cave of "Iglesia-Mina superior", San Juan, Tepoztlán, Morelos, México. Comparison with other species was based on published material. 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 numbers: ZYG-3 for *Anelpistina inappendicata* and ZYG-4 for *Anelpistina cuaxilotla.*

Anelpistina Silvestri, 1905

Diagnosis.—Member of subfamily Cubacubaninae without scales. Submentum without conspicuous lateral lobes bearing glandular pores. Urosternite IV of adult male with 1 + 1 articulated submedian appendages and/or with point of insertion of parameres in urosternum IX deep, normally with internal face of coxal processes with macrochaetae more or less sclerotized.

Description emending.—Body slender, approximately parallel-sided, thorax slightly but distinctly wider than abdomen. Antennae and body are of similar length. Head with approximately 8 + 8 macrochaetae in border of insertion of antennae. Pedicellus of male normally with 3 clusters of unicellular glands, one of them very long.

Mouthparts not specialized. Mandibles strongly sclerotized apically and with usual teeth, typically with more than 4 macrochaetae. Galea apically with several sensory pegs. Lacinia heavily sclerotized distally; first process of lacinia pectinate. Labium without prominent lateral lobes. Next to last article of labial palp more or less with a rounded bulkiness.

Tarsus longer or equal in length to tibia. Tarsi with 4 articles. Praetarsi with 3 simple claws, median claws glabrous, slender, and smaller than lateral claws.

Abdominal sterna II–VII subdivided into coxites and sternite. Sterna VIII and IX of male entire. Coxites on segments II–IX with stylets. Eversible vesicles on segments II–VI, pseudovesicles on VII. Urosterna III simple. Urosterna IV in males with or without 1 + 1 articulated submedian appendages. Point of insertion of parameres in urosternum IX generally deep except in *A. weyrauchi* (Wygodzinsky 1959) and to certain degree in *A. ruckeri* (Silvestri 1905), normally with internal face of coxal processes with macrochaetae more or less sclerotized. Cerci of male with modified spines.

Normal parameres, not subdivided or somewhat constricted apically. With specialized setae on apex. Opening of penis longitudinal.

Type species.—*Anelpistina wheeleri* Silvestri 1905.

Remarks.—According to Silvestri's (1905) definition of genus *Anelpistina,* the main difference between this genus and the other members of the subfamily Cubacubaninae is the articulated submedian appendages in the urosternite IV of males. Specimens that are closely related to species of the genus *Anelpistina,* but lack such appendages could incorrectly be placed in the genus *Cubacubana.* Therefore a broader re-description is given to include these specimens.

With the new re-description, genus *Anelpistina* differs from *Texoreddellia* (Wygodzinsky 1973) by the absence of scales and of a conspicuous process of the pedicellus in males, as well as by the presence of modified spines on the cerci of males. From *Allonicoletia* (Mendes 1992) by the presence of stylets in urosternite II. From *Neonicoletia* (Paclt 1979) by the aspect of the endopodium. *Prosthecina* (Silvestri 1933) and *Cubacubana* agree with *Anelpistina* in the possession of modified spines on the cerci of males, but *Prosthecina* has a submentum with conspicuous lateral lobes bearing numerous glandular pores. *Cubacubana* lacks 1 + 1 articulated submedian appendages in urosternite IV and the point of insertion of parameres in urosternum IX is shallow without more or less sclerotized macrochaetae in the internal face of coxal processes. *Anelpistina* has either or both the appendages and the deep insertion.

Anelpistina inappendicata, new species
Figs. 1A–F, 2A–G

Type material.—México, Guerrero State, Tetipac municipality, Agua Brava cave (17 meters deep, 819 meters long). ex soil, 7 Aug 1988, 25 Mar 1989 and 15 Mar 1991, L. Espinasa col. Male holotype, 4 male paratypes and ten female paratypes.

Description.—Maximum body length 13.5 mm. Maximum length of antennae 9.0 mm, of caudal appendages 9.0 mm. When complete, antennae and caudal appendages measure more or less the length of body. General color light yellow to white.

Head with macrochaeta and microchaeta as shown in Fig. 1F, with approximately 8 + 8 macrochaetae on border of insertion of

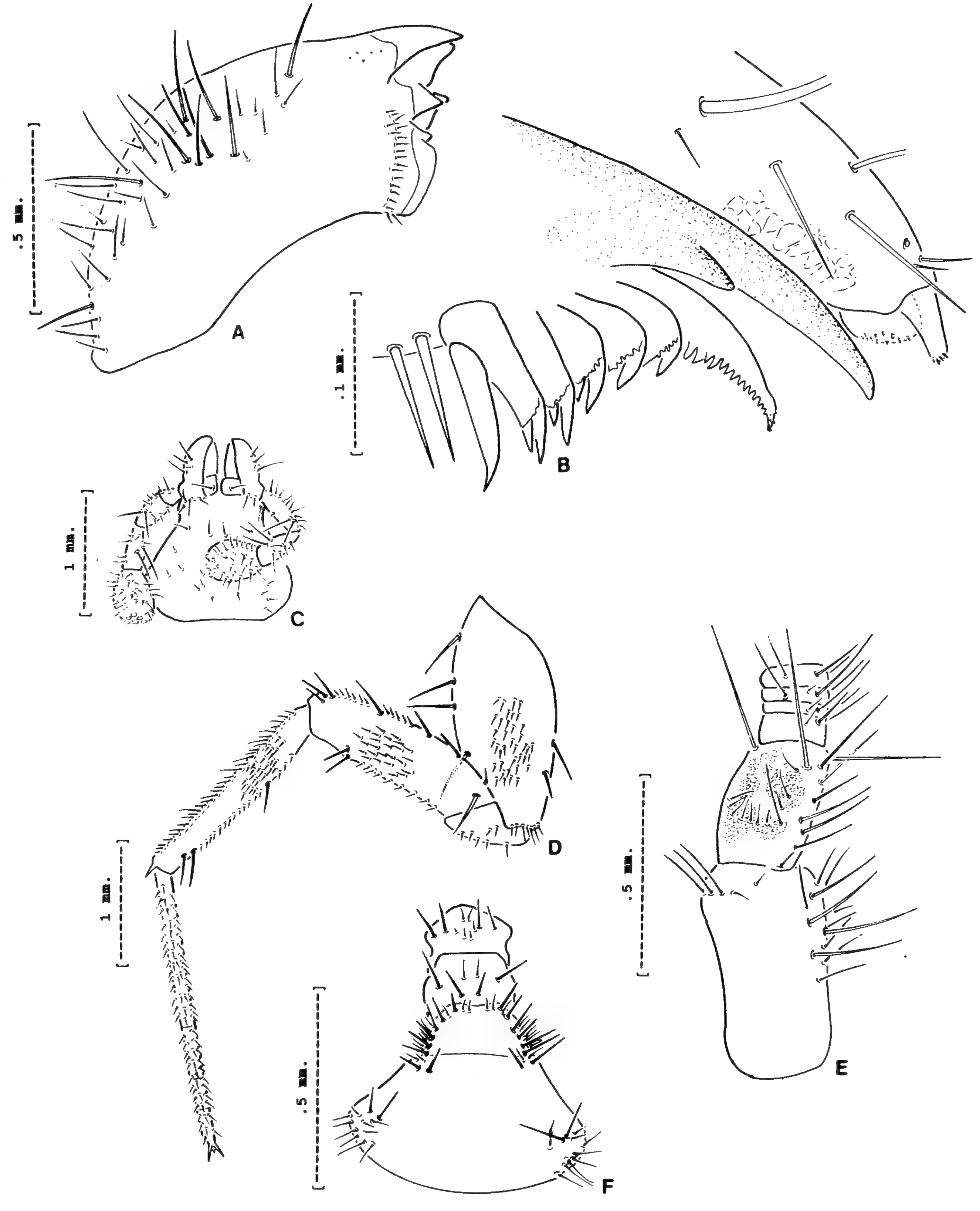

Fig. 1. *Anelpistina inappendicata* n. sp.: A, Mandible; B, Apical portion of maxilla; C, Labium with palp; D, Hind leg, microchaetae partially shown; E, Male. Basal portion of antenna; F, Head.

antennae. Basal article of antennae in males without projections. Pedicellus of antennae of male as shown in Fig. 1E, with numerous clusters of unicellular glands. Female basal articles of antennae simple.

Mouthparts relatively long, apex of maxilla as shown in Fig. 1B. Labial palp long, apical article longer than wide. Labium and first article of labial palp with macrochaetae. Mandibles with approximately 8 ma-

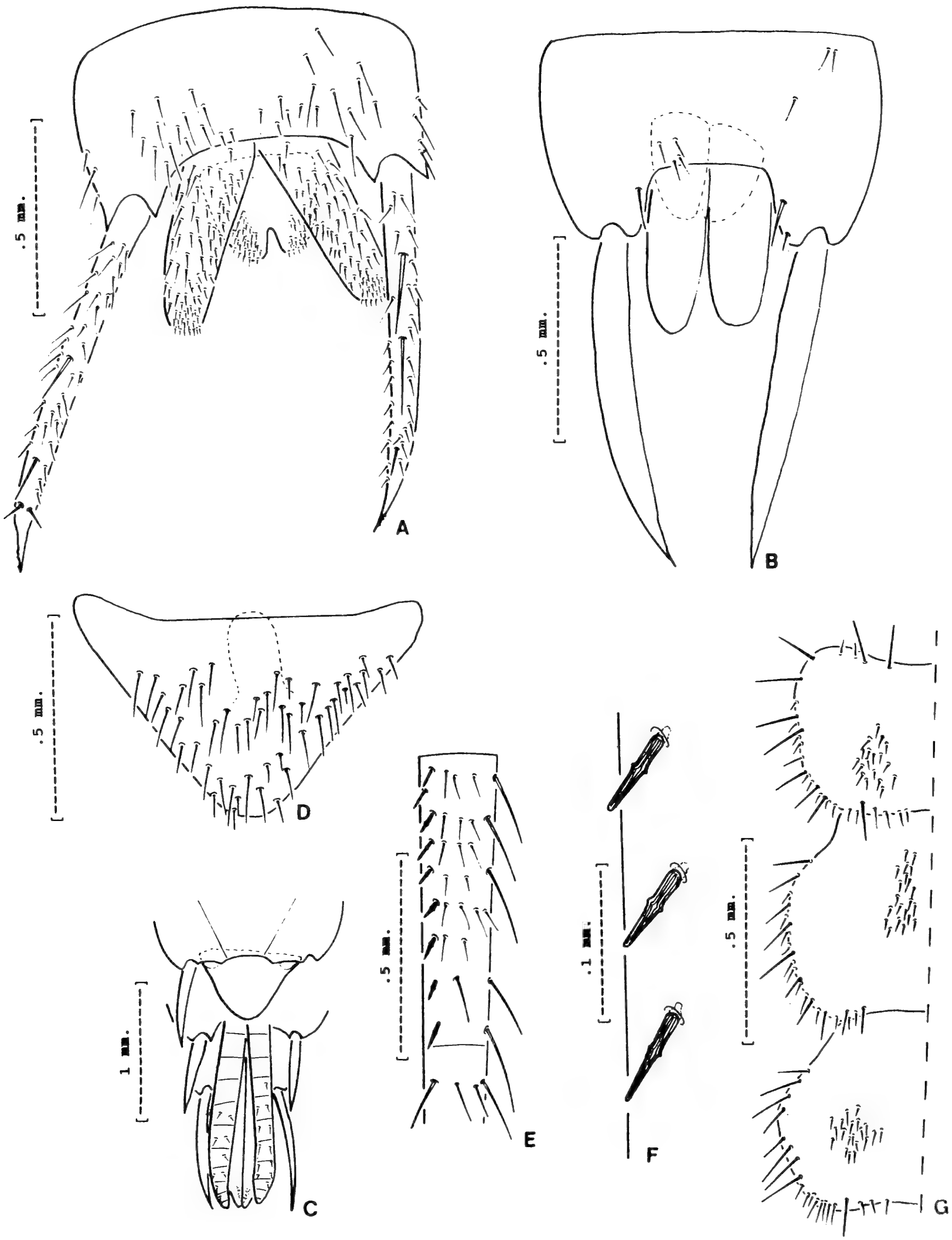

Fig. 2. *Anelpistina inappendicata* n. sp.: A–B, Male. Genital area; C, Ovipositor and subgenital plate; D, Subgenital plate; E, Basal portion of cercus; F, Modified spines of cercus, higher magnification; G, Thoracic nota. dorsal.

crochaetae, some very small pegs on larger tooth (Fig. 1A). Legs as shown in Fig. 1D, moderately elongate; hind tibia approximately 7× longer than wide. Claws of normal size.

Cerci of male with a longer than wide basal article, a very long second one bearing numerous spines, followed by numerous short articles of simple chaetotaxy. Spines along most of second article and of similar size. Spines with medial enlargement in form of ring (Fig. 2E, F). Female cerci simple.

Thorax with short macrochaetae, very abundant on lateral borders, 1 + 1 submedian distinct macrochaetae, apart from several setae of varied sizes, in posterior border of pro-, meso- and metanotum. 2 + 2 also on anterior border of pronotum (Fig. 2G).

Urotergite X almost straight in both sexes, posterior angles with 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. Urosternum IX of male straight behind without a row of sensory cones, but point of insertion of parameres in urosternum IX is deep, with internal face of coxal processes with macrochaetae more sclerotized (Fig. 2A, B). Stylets II–VIII as usual for subfamily. Stylets IX larger than others, with 2 or 3 macrochaetae and an extra subapical pair. Terminal spine with small teeth. In males and females styles without modifications.

Penis and parameres as shown in Fig. 2A, B. Parameres attaining ½ of stylets IX, divergent and slightly concave. Surface of parameres with short setae. Subgenital plate of female triangular, twice as wide as it is long (Fig. 2C, D). Ovipositor barely surpassing apex of stylets IX. Gonapophyses with approximately 12 articles.

Postembryonic development not very complex, with younger instars almost identical to older ones except for size. In smaller sized males (9 mm.), spines on cerci lack medial enlargement in form of a ring (it is unknown if younger instars than those collected lack spines). In females, length of ovipositor increases proportionally with body size until at body length of 9.5 mm, ovipositor barely surpasses apex of stylets IX. Longer body sizes of up to 13.5 mm. did not bring an increase of size of ovipositor when compared to stylets IX.

Etymology.—In/appendicata = without/appendages. Makes reference to the lack of articulated submedian appendages in this species, which are normally found in the urosternite IV of males in the genus *Anelpistina.*

Remarks.—The characters that allow us to identify *A. inappendicata* as more closely related to species of the genus *Anelpistina* than to *Cubacubana,* even though it lacks such appendages are: Antennae and body are of similar length, as in *Anelpistina,* while in *Cubacubana* the antennae are twice as long; Pedicellus of antennae with three clusters of unicellular glands, one of them very long. This is in general the case in *Anelpistina.* The norm in *Cubacubana* is four clusters bordered by a "U" shaped row of microchaetae; Head with approximately 8 + 8 macrochaetae in the border of insertion of the antennae, as in some *Anelpistina,* while *Cubacubana* normally has 5 + 5; Lateral borders of thoracic nota with approximately eight macrochaetae. This is closer to most *Anelpistina,* with approximately five macrochaetae, than to *Cubacubana,* with approximately three; Mandibles with more than four macrochaetae, as in some *Anelpistina,* while in *Cubacubana* there are typically four; The next to last article of the labial palp without a rounded bulkiness. In this character *A. inappendicata* is, on the contrary, more similar to species of the genus *Cubacubana* whose article is straighter, while in *Anelpistina* they are bulky. This character could be explained by a loss of bulkiness in *A. inap-*

pendicata; Tarsus longer than the tibia. Although this is generally the case for *Cubacubana,* in *Anelpistina* it is longer to equal; Point of insertion of parameres in urosternum IX deep, with internal face of coxal processes with macrochaetae sclerotized. This deep insertion and the sclerotized macrochaetae are absent in *Cubacubana.* On the contrary, the deep insertion is present in all the species of *Anelpistina,* except *A. weyrauchi,* and the sclerotized macrochaetae are present in most of the species.

Anelpistina inappendicata and the other North American species of *Anelpistina* have in common a deep insertion of the paramers and other intermediate characteristics, which are absent in the South American species (*A. weyrauchi*). It is likely therefore that the divergence of *A. inappendicata* from the species of this genus happened after the separation of *A. Weyrauchi* from the group, but before the radiation of the other described North American species of *Anelpistina.*

Anelpistina decui (Wygodzinsky & Hollinger 1977), new combination *Cubacubana decui* Wygodzinsky & Hollinger, 1977:320–322, figs. 4–6; Mendes, 1986: 341; Espinasa, 1991:6, 14.

Remarks.—Although *A. decui* lacks the articulated submedian appendages on urosternite IV of the male, this species has closer affinities with members of *Anelpistina* than it does to *Cubacubana* because its point of insertion of parameres in urosternum IX is deep and the internal face of coxal processes has sclerotized macrochaetae.

An analysis of other characters present in *A. decui* that allow us to identify it as more closely related to species of genus *Anelpistina* than to *Cubacubana,* even though it lacks such appendages, is given based on the illustrations and description of Wygodzinsky (1977): Antennae twice as long the length of the body, as in *Cubacubana,* while in *Anelpistina* antennae are of similar length. Even though this character would appear to make it closer to *Cubacubana,* its longer antennae may be due to a secondary adaptation to its cavernicole environment; Pedicellus of antennae with two long clusters of unicellular glands and no "U" shaped row of microchaetae. In *Anelpistina,* normally there are three clusters, one of them very long. The norm in *Cubacubana* is four clusters bordered by a "U" shaped row of microchaetae; Lateral borders of thoracic nota with approximately five macrochaetae, as in most *Anelpistina,* while *Cubacubana* approximately has three; The next to last article of the labial palp with a somewhat rounded bulkiness, as in *Anelpistina,* while in *Cubacubana* it is straighter; Cerci of male with four spines; a small one, a long and strong one, another small and a very long curved one. Although in both *Anelpistina* and *Cubacubana* there is diversity in morphology of spines, this particular arrangement of four spines is exactly the same for most species in genus *Anelpistina.*

Other characteristics that could further establish to whom the species is more closely related, such as the number of macrochaetae on mandibles and on the border of the insertion of antennae, regrettably could not be obtained from the illustrations of Wygodzinsky (1977).

Anelpistina cuaxilotla, new species
Figs. 3A–G, 4A–D

Type material.—Type locality: México. Guerrero: Apetlanca, Cuaxilotla town, in the penumbra zone (Entrance to 120 m) of "Cuaxilotla" cave, under rocks. 6 Jun 1987 and 23 Aug 1987. L. Espinasa col. Male holotype, ten male paratypes and 12 female paratypes. Other localities: México, Morelos state, Tepoztlán municipality, San Juan town, "San Juan" or "Sistema Ferrocarril-Mina inferior" volcanic cave system, under rocks. 21 Jan 1979. R. García col. One male paratype.

Description.—Maximum body length 12.0 mm. Maximum length of antennae 6.0 mm, of caudal appendages 5.0 mm. When complete, antennae and caudal appendages

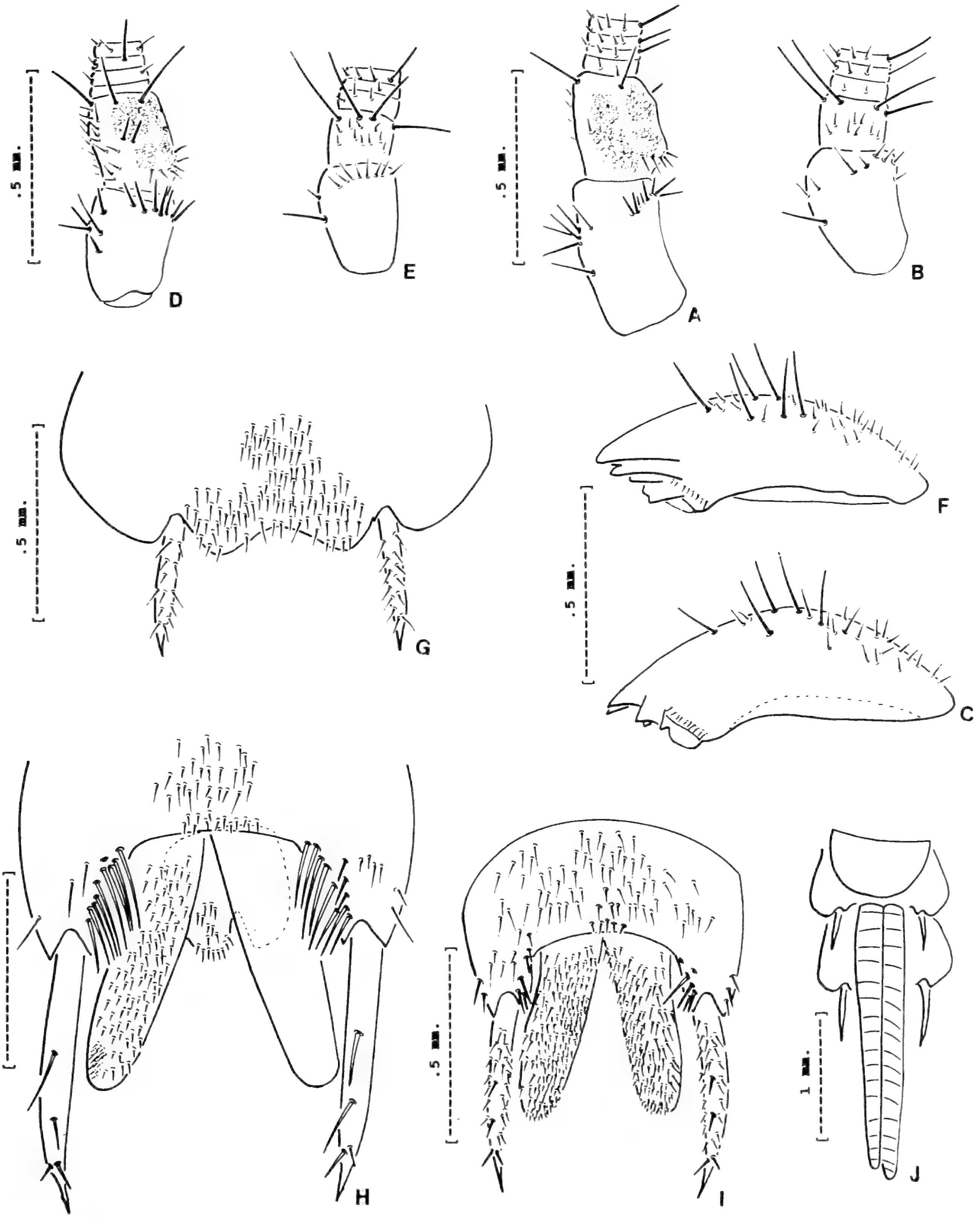

Fig. 3. A–C, *Anelpistina boneti* (Wygodzinsky), D–G, *Anelpistina cuaxilotla* n. sp.: A, Male, basal portion of antenna; B, Female, basal portion of antenna; C, Mandible. D, Male, basal portion of antenna; E, Female, basal portion of antenna; F, Mandible; G, Male, abdominal sternum VIII; H, Male from "San Juan" cave, genital area; I, Male from "Cuaxilotla" cave, genital area; J, Ovipositor and subgenital plate.

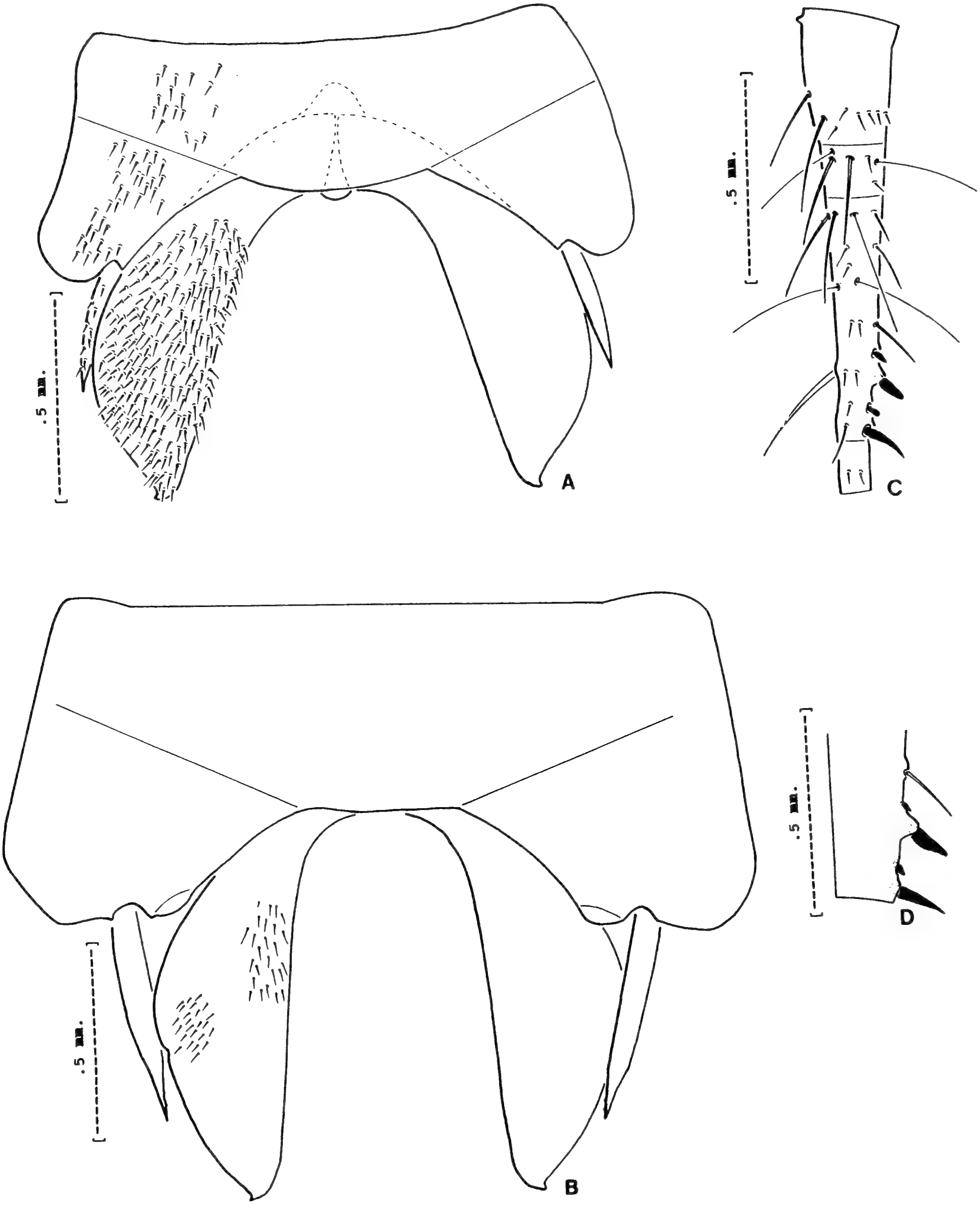

Fig. 4. *Anelpistina cuaxilotla* n. sp.: A, Male from "Cuaxilotla" cave, appendages of urosternite IV; B, Male from "San Juan" cave, appendages of urosternite IV; C, Male from "Cuaxilotla" cave, modified spines of cercus; D, Male from "San Juan" cave, modified spines of cercus.

measure less than length of the body. Setae on body strong, long and very abundant. General color light yellow to white.

Head with macrochaetae and microchaetae similar to Fig. 1F. Basal article of antennae in males slightly longer than pedicellus, but shorter than in *A. boneti.* In the female it is also shorter than in *A. boneti*

(Fig. 3A, B, D–E). Pedicellus of male as shown in Fig. 3D, with numerous clusters of unicellular glands. Female basal articles of antennae simple.

Mouthpart appendages relatively long, very similar to *A. boneti.* Apex of maxillary palp with two conules, one longer than wider and the other wider than longer. Labial palp long, apical article barely longer than wide and only slightly longer than next to last article. This penultimate article with bulkiness with two macrochaetae. Labium and first article of labial palp with macrochaetae. Mandibles without very small pegs on bigger tooth and chaetotaxy as in Fig. 3F. Legs as in *A. boneti,* with sclerotized macrochaetae on tibia. Claws of normal size.

Cerci of male with a longer than wide basal article, second article wider than longer and a very long third one bearing 4 spines in distal portion, followed by numerous short articles of simple chaetotaxy. Spines consist of a very small one, a strong, subacute one, another very small, and a long, acute and slightly curved one (Fig. 4C, D). Cerci of female simple.

Abdominal sterna and terga as in other members of the genus. Setae long and numerous. Thorax with shorter setae than on urosterna. Lateral borders as in *A. boneti,* with 4–5 macrochaetae. Urotergite X long and almost straight in both sexes, posterior angles with 2 + 2 macrochaetae and a few relatively strong setae.

Appendages of urosternum IV of male very long and robust, acute on apex. Their longest diameter equals the length of the stylets of this segment (Fig. 4A, B).

Urosternum VIII of male long and shallow shallowly emarginate on the posterior margin (Fig. 3G), slightly deeper than in *A. boneti.*

Urosternum IX of male with setae abundant. Behind insertion of parameres, in the center, with a small group of short, sclerotized and spiniform setae. Internal face of coxal processes with irregular row of 5 spiniform macrochaetae highly sclerotized (Fig. 3I). In the only male individual collected from cave of San Juan (Sistema Ferrocarril-Mina inferior), this row is of ten macrochaetae (Fig. 3H). It is not known if this difference is due to population differences or because the individual of San Juan, being the biggest (12.0 mm) corresponds to an older instar.

Stylets similar to *A. boneti.* Stylets IX bigger than the others. Penis and parameres as shown in Fig. 3H, I. Parameres attain the length of stylets IX. Surface of parameres with short setae.

Subgenital plate of female rounded, with the apex slightly flat (Fig. 3J). Ovipositor surpassing apex of stylets IX by twice the length of stylets. Gonapophyses with approximately 17 articles.

Postembryonic development not very complex with younger instars almost identical to older ones except for size. In male, appendages of urosternite IV appear very small at a length of approximately 6.0 mm and acquire adult morphology at a length of 7.0 mm. In the longest individual (12.0 mm) only a slight increase in the proportions of sexual secondary characters is observed.

Female development not well known because all females collected measure more than 7.5 mm, when length of ovipositor already surpasses apex of stylets IX by one and a half to two times its size.

Etymology.—Cuaxilotla. Makes reference to the type locality, "Cuaxilotla" cave.

Remarks.—The closest species to *Anelpistina cuaxilotla* are *A. bolivari, A. anophtalma,* and *A. boneti.* In males of *A. cuaxilotla,* urosternum VIII is shallowly emarginate on posterior margin, while in *A. bolivari,* emargination is narrow and deep. Other characteristics that differentiate these two species are the spines in the cerci and the abundance of setae in terga and sterna. From *A. anophtalma* it differs because in this species, urotergite X is deeply emarginate on the posterior margin, appendages of urosternite IV are thin and ovipositor is short, while in *A. cuaxilotla,* urotergite X is almost straight, appendages are broad and ovipositor is long. For *A. boneti,* the closest species to *A. cuaxilotla,* the main difference is that in *A. boneti* the appendages of urosternite IV are thin, while in *A. cuaxilotla* they are broad. Other characteristics that differentiate them are that in the former, the cerci have three spines (although some individuals from "Iglesia-Mina superior" cave in Morelos have 4) while in *A. cuaxilotla* they have four; the basal article of the antennae in males and females is proportionally longer than the pedicellus in *A. boneti* than it is in *A. cuaxilotla* (Fig. 3A, B, D, E); and the chaetotaxy of the mandible (Figs. 3C and F). To establish these differences with precision, a large number of individuals of *A. boneti* collected from the type locality by the author were compared to the individuals of *A. cuaxilotla.*

The somewhat overlapping distribution of *A. cuaxilotla* and *A. boneti* is intriguing. The latter was reported to a wide distribution comprising the states of Guerrero, Morelos, D.F. and even Habana island in the Gulf of California (Wygodzinsky 1946), while *A. cuaxilotla* has been found in Guerrero and Morelos. Wygodzinsky (1946) initially distrusted such a big geographic distribution of *A. boneti,* although repeated studies failed to show differences between samples of different origins ("Desconfiamos inicialmente da grande distribução da espécie, repetidos exames detalhados falharam de demostrar diferenças entre os exemplares de procedência diferente").

Regardless of whether organisms from the Gulf of California are indeed *A. boneti,* the author of the present paper has found a locality where both species can be found in close proximity. Individuals that clearly belong to *A. boneti* have been collected in the cave system of the "Iglesia-Mina superior" (Morelos, Tepoztlán, San Juan). This cave system is only tens of meters away from the cave system of Ferrocarril-Mina inferior, where an individual of *A. cuaxilotla* was found. Individuals of both species from these two caves can clearly be differentiated morphologically, especially because samples of both contain mature males.

It is currently not known if the presence of four spines on the cerci in males of *A. boneti* from Iglesia-Mina superior cave, instead of three spines as it is the norm for this species, reflects variation within the species, or if it instead reflects local hybridization between both species in these neighboring caves.

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Anacroneuria from northeastern South America (Insecta: Plecoptera: Perlidae)

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Abstract.—Descriptions are given for ten new species of *Anacroneuria* from Venezuela, Guyana, and Suriname, and records are given for ten species previously described from this region. The following 10 new species are described (type locality in parenthesis): *Anacroneuria achagua* (Venezuela. Portuguesa: Guanare), *A. arawak* (Suriname. Brokopondo: Brownsberg Naturpark, Mazaroni Plateau), *A. chaima* (Venezuela. Sucre: Rio Cocollar, 1.5 km SE Las Piedras de Cocollar), *A. claudiae* (Venezuela. Zulia: Rio Yasa (3 km E Kasmera), Estacion Biologica), *A. karina* (Venezuela. Sucre: Rio Cocollar, 1.5 km SE Las Piedras de Cocollar), *A. makushi* (Guyana. Kanuku Mountains, Moco Moco River), *A. paria* (Venezuela. Sucre: Rio Cocollar, 1.5 km SE Las Piedras de Cocollar), *A. perija* (Venezuela. Zulia: Parque Nacional Perija, Rio Negro, Toromo), *A. timote* (Venezuela. Tachira: Quebrada Los Mirtos, 8 km S El Cobre), and *A. wapishana* (Guyana. Potaro River, Kaieteur Falls). *Anacroneuria phantoma* (Banks) and *A. pictipes* Klapálek are redescribed and a modified key to regional males is presented.

Stark (1995) provided descriptions of Venezuelan *Anacroneuria* based on collections made primarily through 1985. Recently a series of Venezuelan and Guyanan specimens collected in 1994–97 were made available by O. S. Flint and R. Holzenthal, and a few specimens were provided by the California Academy of Science. This material includes nine new species, new records for eight previously described species, and a few unassociated females described under informal designations. Also included are redescriptions of *A. pictipes* Klapálek and *A. phantoma* (Banks) from holotypes and an additional new species from Suriname. Holotypes are deposited in the National Museum of Natural History, Washington, D.C. (USNM) or the California Academy of Science, San Francisco, CA (CAS). Paratypes and other specimens are deposited in the Universidad Central de Venezuela, Maracuy (UCV), the University of Minnesota, Saint Paul (UMSP) or the collection of the author (BPS). Additional material was examined from the Museum of Comparative Zoology, Harvard University (MCZ) and the National Museum of Natural History, Prague (NMH).

Anacroneuria achagua, new species

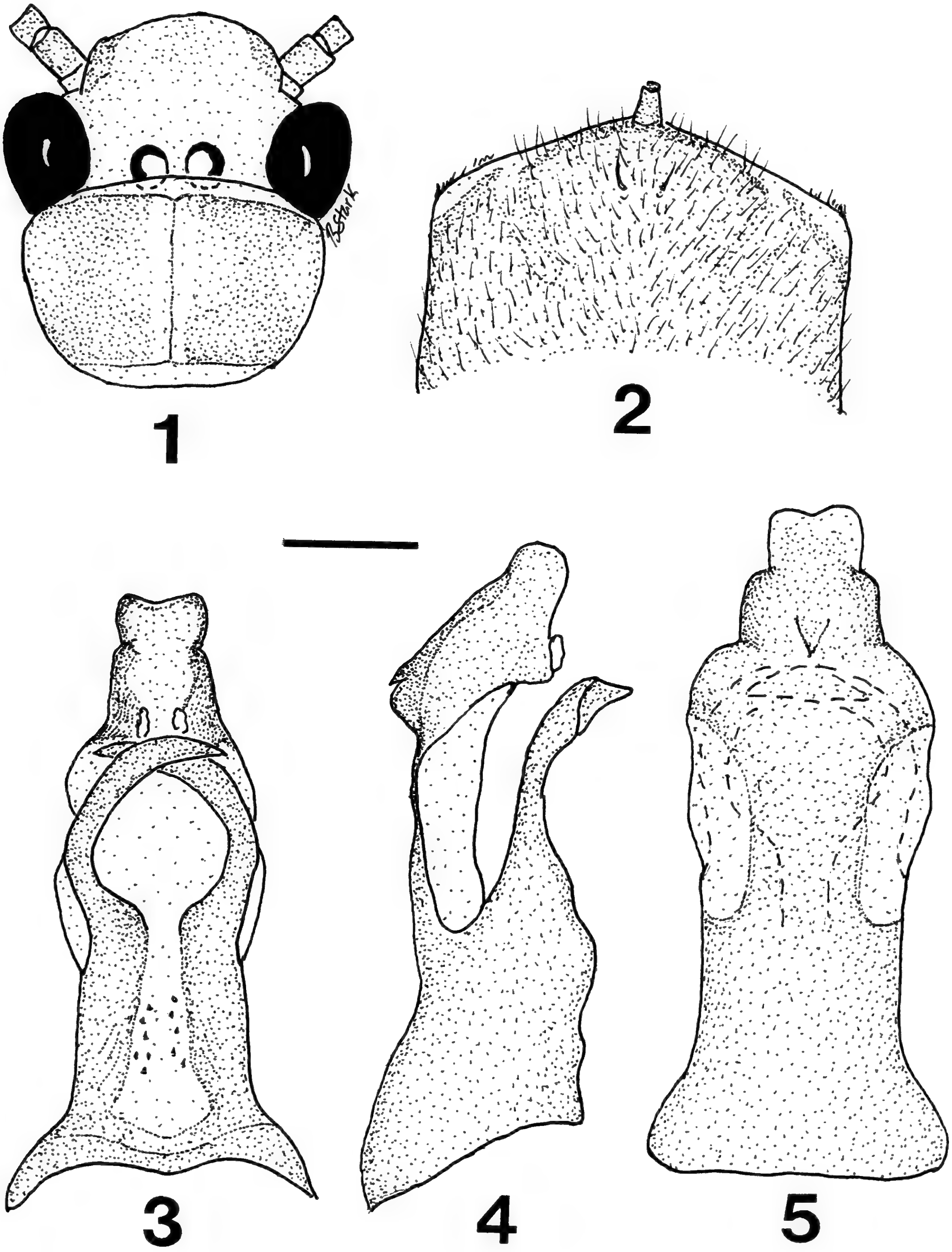
Adult habitus.—Head with an obscure brown pattern over anterior half of frons; lappets brown. Median pronotal stripe pale, broad irregular lateral bands brown (Fig. 1). Wing membrane transparent, veins pale.

Male.—Forewing length 8 mm Hammer thimble shaped, height greater than basal diameter (Fig. 2). Aedeagal apex short, with wide, emarginate tip offset from shoulders; ventral aspect with an obscure pair of membranous lobes; dorsal keel triangular; shoulders somewhat quadrate, hooks stout (Figs. 3–5).

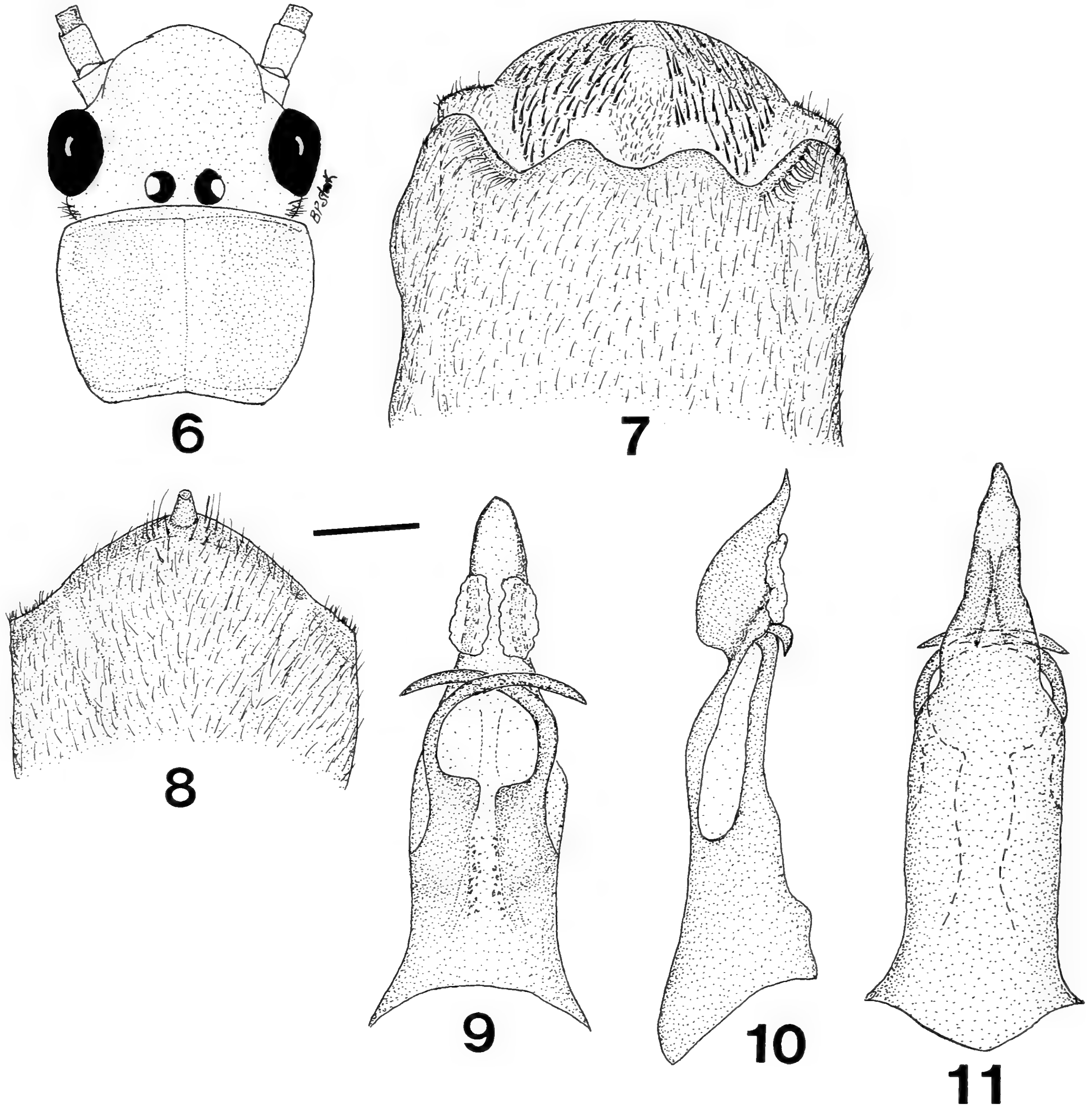
Female.—Unknown.

Nymph.—Unknown.

Etymology.—The name honors the



Figs. 1–5. *A. achagua* structures. 1. Head and pronotum. 2. Male sternum 9. 3. Aedeagus, ventral. 4. Aedeagus, lateral. 5. Aedeagus, dorsal. Scales: 0.6 mm (1), 0.3 mm (2), 0.15 mm (3–5).



Figs. 6–11. *A. arawak* structures. 6. Head and pronotum. 7. Female sterna 8 and 9. 8. Male sternum 9. 9. Aedeagus, ventral. 10. Aedeagus, lateral. 11. Aedeagus, dorsal. Scales: 0.6 mm (6), 0.3 mm (7, 8), 0.15 mm (9–11).

Achagua people of Venezuela and is used as a noun in apposition.

Types.—Holotype ♂ and ♂ paratype from Venezuela, Portuguesa, Guanare, 10–13 Sep 1957, B. Malkin (CAS).

Diagnosis.—This species has a V-shaped aedeagal keel and apex somewhat like that of *A. pictipes* but these species are easily distinguished by the distinctive wing and pronotal pigmentation of that species (Figs. 48, 53).

Anacroneuria arawak, new species

Adult habitus.—Head with diffuse yellow brown area extending forward from ocelli; pronotum with diffuse brown lateral bands and a narrow pale median band (Fig. 6). Wing membrane transparent, veins pale.

Male.—Forewing length 9 mm. Hammer thimble shaped, height subequal to basal diameter (Fig. 8). Aedeagal apex slender, scoop shaped with a pair of subapical ventral membranous lobes. Apex curved slightly dorsad; hooks slender, dorsal keel long and narrow (Figs. 9–11).

Female.—Forewing length 10.5 mm. Subgenital plate four lobed, median lobes shorter than lateral lobes; inner margins of lateral lobes bearing a short setal fringe. Sternum 9 with a broad transverse sclerite and a trilobed median setal patch; median lobe clothed with minute setae, lateral lobes with prominent setae (Fig. 7).

Nymph.—Unknown.

Etymology.—The name honors the Arawak people of Guyana and Suriname and is used as a noun in apposition.

Types.—Holotype ♂ and ♀ paratype from Suriname, Brokopondo District, Brownsberg Naturpark, Mazaroni Plateau, 400–500 m, 16 Aug 1982, W. E. Steiner (USNM).

Diagnosis.—This species does not appear to be closely related to other regional *Anacroneuria.* The aedeagal shape and pale habitus are somewhat similar to *A. isleta* (Stark 1994) but that species has a triangular keel and a shorter and more rounded aedeagal tip. In dorsal aspect the aedeagus is similar to that of *A. bari* (Stark 1995), but that species does not have membranous ventral lobes on the aedeagus. The female is distinctive by virtue of the setal fringe on the lateral subgenital plate lobes (Fig. 7).

Anacroneuria aroucana Kimmins

Anacroneuria aroucana Kimmins, 1948: 105. Holotype ♂, Arouca River, Trinidad.
Anacroneuria aroucana: Stark, 1994:173.

Material.—Venezuela: Sucre, Quebrada Zapateral, 1.5 km SE Las Piedras de Cocollar, 810 m, 9 Apr 1995, R. Holzenthal, O. S. Flint, 4 ♂ (USNM, UCV). Sucre, Rio Cocollar, 1.5 km SE Las Piedras de Cocollar; 810 m, 7–8 Apr 1995, R. Holzenthal, O. S. Flint, 10 ♂ (USNM).

Comments.—These are the first mainland records for this species.

Anacroneuria bari Stark

Anacroneuria bari Stark, 1995:226. Holotype ♂, El Tucuco, 45 km SW Machiques, Zulia, Venezuela.

Material.—Venezuela: Guarico, Parque Nacional Guatopo, Quebrada Guatopo, 0.5 km NE La Colina, 600 m, 22 Jan 1994, R. Holzenthal, C. Cressa, Rincón, 3 ♂ (UMSP, UCV). Trujillo, Quebrada Potrerito, 7.5 km NE Bocono, 1530 m, 29–30 Apr 1995, R. Holzenthal, C. Cressa, Gutic, 2 ♂ (BPS).

Comments.—This species was previously reported from the Venezuelan states of Barinas, Miranda, and Zulia (Stark 1995).

Anacroneuria bifasciata (Pictet)

Perla bifasciata Pictet, 1841:231. Holotype ♀, Moritz, Colombia.
Anacroneuria bifasciata: Zwick, 1972: 1154.
Anacroneuria bifasciata: Stark, 1995:239.

Material.—Venezuela: Distrito Federal, Rio Camuri Grande, 1 km S Camuri (nucleo USB), 30 m, 24 Jan 1994, R. Holzenthal, C. Cressa, Rincón, 1 ♂, 1 ♀ (BPS).

Comments.—This species was previously reported from the Venezuelan states of Aragua, Distrito Federal, and Lara (Stark 1995).

Anacroneuria caraca Stark

Anacroneuria caraca Stark, 1995:228. Holotype ♂, Rio Limon, Parque Nacional Henri Pittier, Aragua, Venezuela.

Material.—Venezuela: Guárico, Parque Nacional Guatopo, Quebrada Guatopo, 0.5 km NE La Colina, 600 m, 22 Jan 1994, R. Holzenthal, C. Cressa, Rincón, 1 ♂ (UMSP).

Comments.—This species was previously reported from the Venezuelan states of Aragua and Barinas (Stark 1995).

Anacroneuria chaima, new species

Adult habitus.—Head with a wide brown area forward of ocelli extending to M-line;

lappets and anterior margin of head brown. Median pronotal stripe pale; broad lateral stripes dark brown (Fig. 12). Wing membrane and veins brown.

Male.—Forewing length 8 mm. Hammer cylindrical, height greater than basal diameter (Fig. 13). Aedeagal apex simple, scoop shaped, slender and rounded at the tip; ventral aspect with a small circular pair of membranous lobes; dorsal aspect with a low wide keel; hooks slender (Figs. 14–16).

Female.—Unknown.

Nymph.—Unknown.

Etymology.—The name honors the Chaima people of Venezuela and is used as a noun in apposition.

Types.—Holotype ♂ (pinned) from Venezuela, Sucre, Rio Cocollar, 1.5 km SE Las Piedras de Cocollar, 810 m, 7–8 Apr 1995, R. Holzenthal, O. S. Flint (USNM).

Diagnosis.—This species is similar to *A. perija* in general aedeagal structure but differs in having small, circular membranous aedeagal lobes (Fig. 14) and in having the arms of the dorsal aedeagal keel divergent (Fig. 16). The dark color pattern of *A. perija* is also much more prominent, particularly over the occiput (Fig. 38).

Anacroneuria chorrera Stark

Anacroneuria chorrera Stark, 1995:230. Holotype ♂, La Chorrera Canyon, Merida, Venezuela.

Material.—Venezuela: Merida, Rio La Gonzalez, between Merida and Jaji, 1870 m, 25 Apr 1995, R. Holzenthal, C. Cressa, Gutic, 3 ♂ (UCV). Merida, Rio Albarregas, 1 km NW Universidad de los Andes, 1980 m, 17 Jan 1994, R. Holzenthal, C. Cressa, Rincón, 3 ♂ (UMSP). Merida, Parque Nacional Sierra Nevada, Quebrada La Mucuy, 7 km E Tabay, 2200 m, 18 Jan 1994, R. Holzenthal, C. Cressa, Rincón, 4 ♂ (BPS). Trujillo, Quebrada Potrerito, 7.5 km NE Boconó, 1530 m, 20–30 Apr 1995, R. Holzenthal, C. Cressa, Gutic, 4 ♂ (UMSP). Tachira, tributary to El Valle, 3.8 km SE El Zumbador, 2730 m, 21 Apr 1995, R. Holzenthal, C. Cressa, Gutic, 7 ♂ (UMSP). Tachira, Quebrada Los Mirtos, 8 km S El Cobre, 2400 m, 22 Apr 1995, R. Holzenthal, C. Cressa, Gutic, 1 ♂ (UCV).

Comments.—This species was previously reported from the Venezuelan states of Aragua, Distrito Federal, and Merida (Stark 1995).

Anacroneuria claudiae, new species

Adult habitus.—Head yellow with diffuse brown pattern extending from ocelli to anterior margin but interrupted by three pale areas at M-line; lappets brown. Median pronotal stripe pale, lateral stripes dark, anterolateral margins with pale spot (Fig. 17). Wing membrane transparent, veins brown.

Male.—Forewing length 8 mm. Hammer thimble shaped, height greater than basal diameter (Fig. 18). Aedeagal apex simple, scoop shaped, slender and truncate at the tip; ventral aspect with a small pair of membranous lobes; dorsal aspect with a narrow keel, hooks slender (Figs. 19–21).

Female.—Unknown.

Nymph.—Unknown.

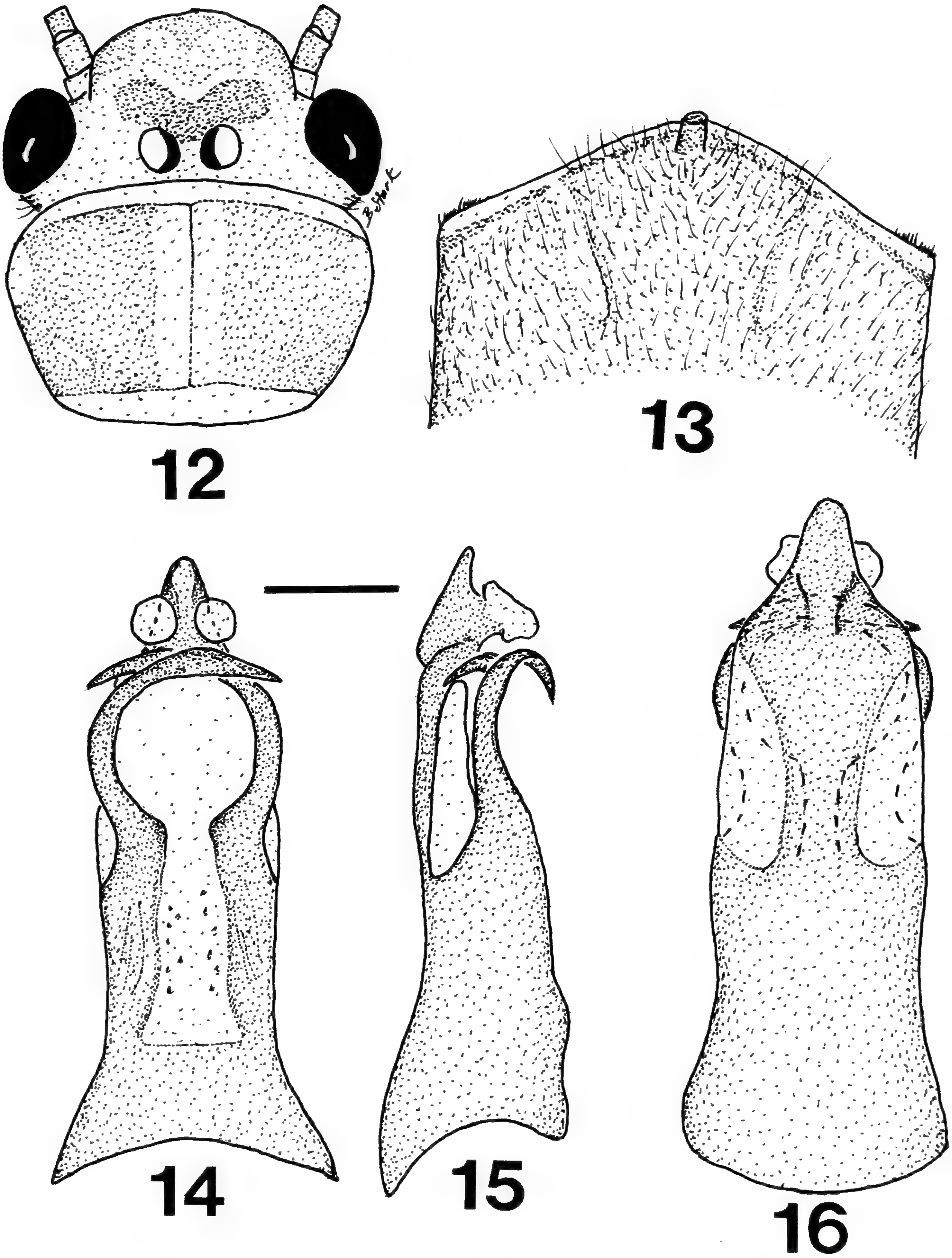
Etymology.—The matronym honors Claudia Cressa of the Universidad Central de Venezuela, Caracas.

Types.—Holotype ♂ from Venezuela, Zulia, Rio Yasa, 3 km E Kasmera (Estacion Biologica), 150 m, 14 Jan 1994, R. Holzenthal, C. Cressa, Rincón (USNM). Paratype ♂ from Venezuela, Zulia, Parque Nacional Perija, Rio Negro, Toromo, 360 m, 15 Jan 1994, R. Holzenthal, C. Cressa, Rincón (UCV).

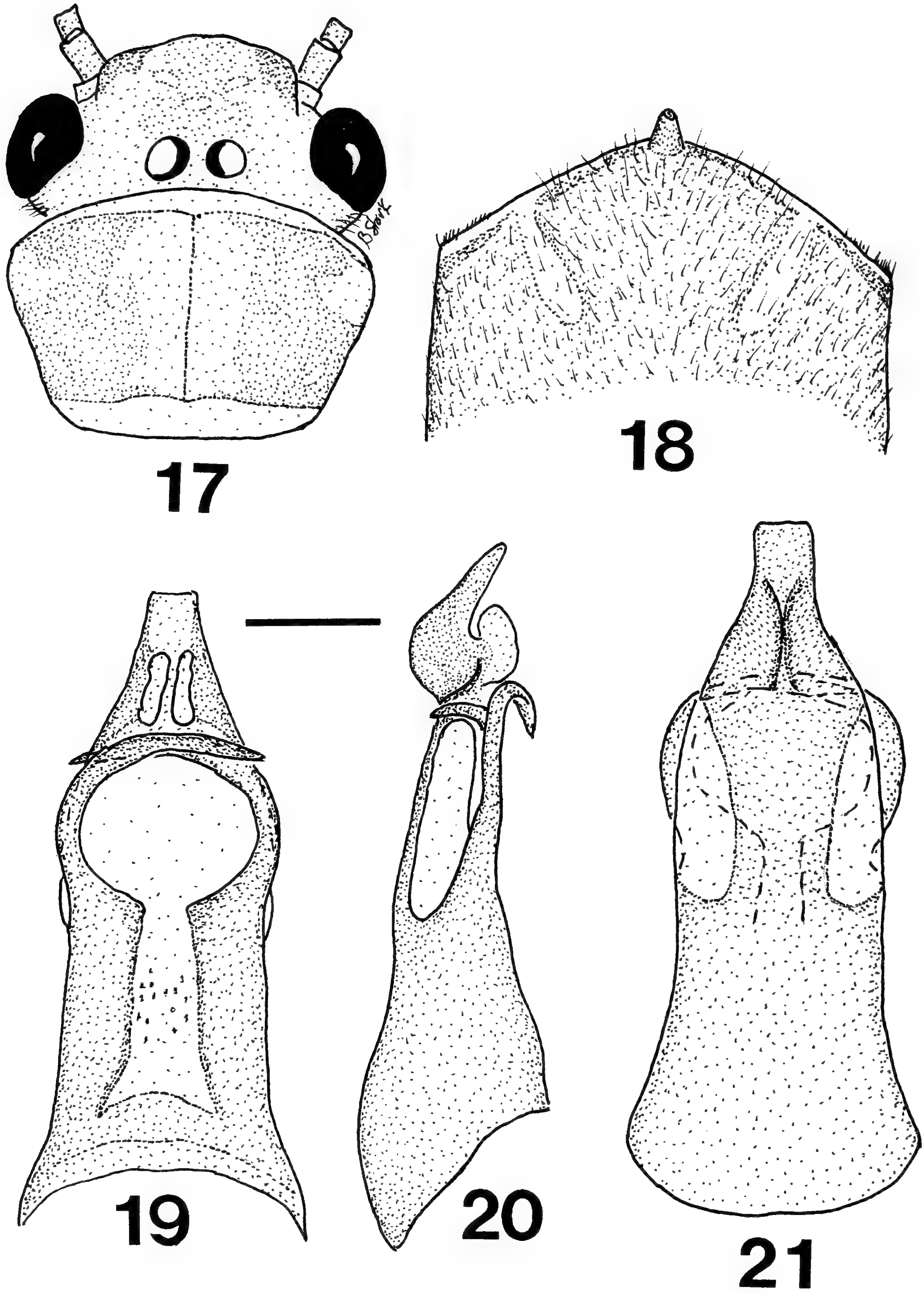
Diagnosis.—This species is similar to *A. chiquita* in general aedeagal structure but differs from that species in having small paired membranous ventral lobes (Fig. 17) and in having unmodified aedeagal hook apices (Fig. 17).

Anacroneuria cruza Stark

Anacroneuria cruza Stark, 1995:231. Holotype ♂, Exp. Culebra, N Duida, Territorio Federal Amazonas, Venezuela.



Figs. 12–16. *A. chaima* structures. 12. Head and pronotum. 13. Male sternum 9. 14. Aedeagus, ventral. 15. Aedeagus, lateral. 16. Aedeagus, dorsal. Scales: 0.6 mm (12), 0.3 mm (13), 0.15 mm (14–16).



Figs. 17–21. *A. claudia* structures. 17. Head and pronotum. 18. Male sternum 9. 19. Aedeagus, ventral. 20. Aedeagus, lateral. 21. Aedeagus, dorsal. Scales: 0.6 mm (17), 0.3 mm (18), 0.15 mm (19–21).

Material.—Guyana: Kanuku Mountains, Kumu River, 28–30 Apr 1995, O. S. Flint, 2 ♂ (USNM). Kanuku Mountains, Moco Moco River, 29 Apr 1995, O. S. Flint, 1 ♂ (USNM). Venezuela: Sucre, Rio Cocollar, 1.5 km SE Las Piedras de Cocollar, 810 m, 7–8 Apr 1995, R. Holzenthal, O. S. Flint, 4 ♂ (USNM, UCV).

Comments.—This species was previously known from Territorio Federal Amazonas, Venezuela (Stark 1995).

Anacroneuria karina, new species

Adult habitus.—Head yellow with a diffuse brown spot forward of ocelli; lappets brown. Irregular midlateral pronotal bands dark brown, median field pale, grading to pale brown (Fig. 22). Wing membrane pale brown, veins brown, R and Sc dark brown.

Male.—Forewing length 11 mm. Hammer thimble shaped, height greater than basal diameter (Fig. 23). Aedeagal apex simple, scoop shaped and broadly rounded; ventral membranous lobes narrow; dorsal keel well developed; hooks slender (Figs. 24–26).

Female.—Unknown.

Nymph.—Unknown.

Etymology.—The name honors the Kariña people of Venezuela and is used as a noun in apposition.

Types.—Holotype ♂ (USNM) and 7 ♂ paratypes (USNM, UCV) from Venezuela, Sucre, Rio Cocollar, 1.5 km SE Las Piedras de Cocollar, 810 m, 7–8 Apr 1995, R. Holzenthal, O. S. Flint.

Diagnosis.—Many species of *Anacroneuria* share the color pattern of *A. karina* and the aedeagus also bears a general similarity to that of other species such as *A. bari* and *A. arcuata* (Stark 1995). *Anacroneuria karina,* however, lacks the transverse dorsal aedeagal keel found in *A. arcuata* and the aedeagal apex is much longer and narrower in *A. bari.*

Anacroneuria llana Stark

Anacroneuria llana Stark, 1995:234. Holotype ♂, La Escalera, 108 km S Rio Cuyuni, Bolivar, Venezuela.

Material.—Guyana: Potaro River, Kaieteur Falls, 1350′, 21–23 Aug 1997, O. S. Flint, 9 ♂, 58 ♀ (USNM).

Comments.—This species was previously known from the holotype. The Guyana males agree with the holotype in all respects except in having falcate aedeagal hooks. The females collected with these males share the same color pattern (Fig. 63) and are associated on that basis. These females have eggs with a terminal spine similar to those of *A. blanca* (Stark 1995) and they also are similar in color pattern, size and in having an intersegmental band of microtrichia.

Female.—Forewing length 13–14 mm. Subgenital plate four lobed, outer lobes slightly longer. Median sclerite of sternum 9 densely hirsute, hairs slightly longer laterally. Intersegmental membrane covered with a dense microtrichia band (Fig. 64).

Anacroneuria makushi, new species

Adult habitus.—Head yellow; pronotum with diffuse midlateral brown bands (Fig. 27). Wing membrane transparent, veins pale.

Male.—Forewing length 9.5 mm. Hammer laterally compressed, height greater than basal diameter (Fig. 28). Aedeagal apex scoop shaped, tip blunt; ventral aspect with a pair of subapical membranous lobes; dorsal aspect with a long, low keel; dorsal sclerite basal to keel bearing an arcuate process; hooks irregularly scalloped on inner margin (Figs. 29–31).

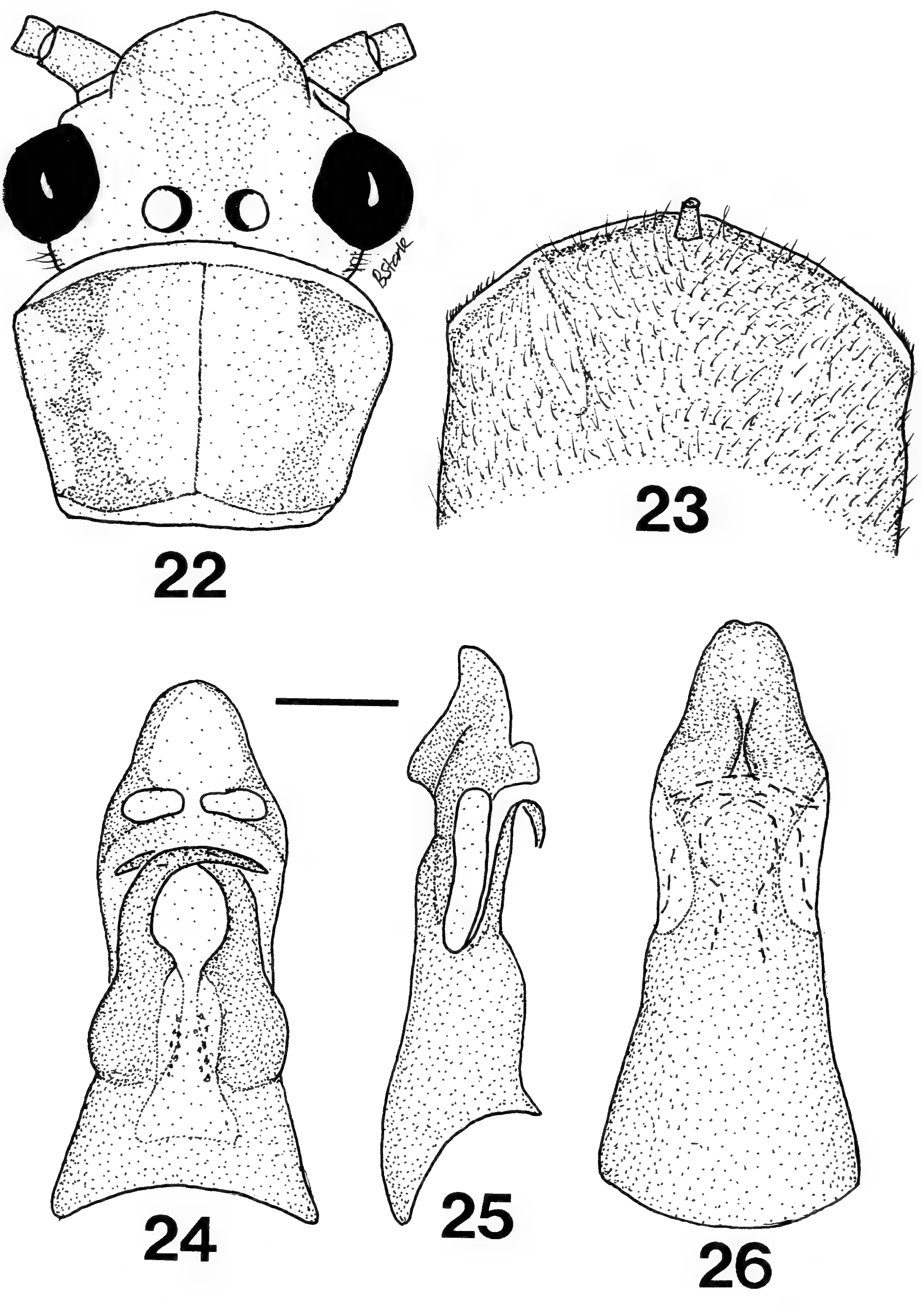
Female.—Unknown.

Nymph.—Unknown.

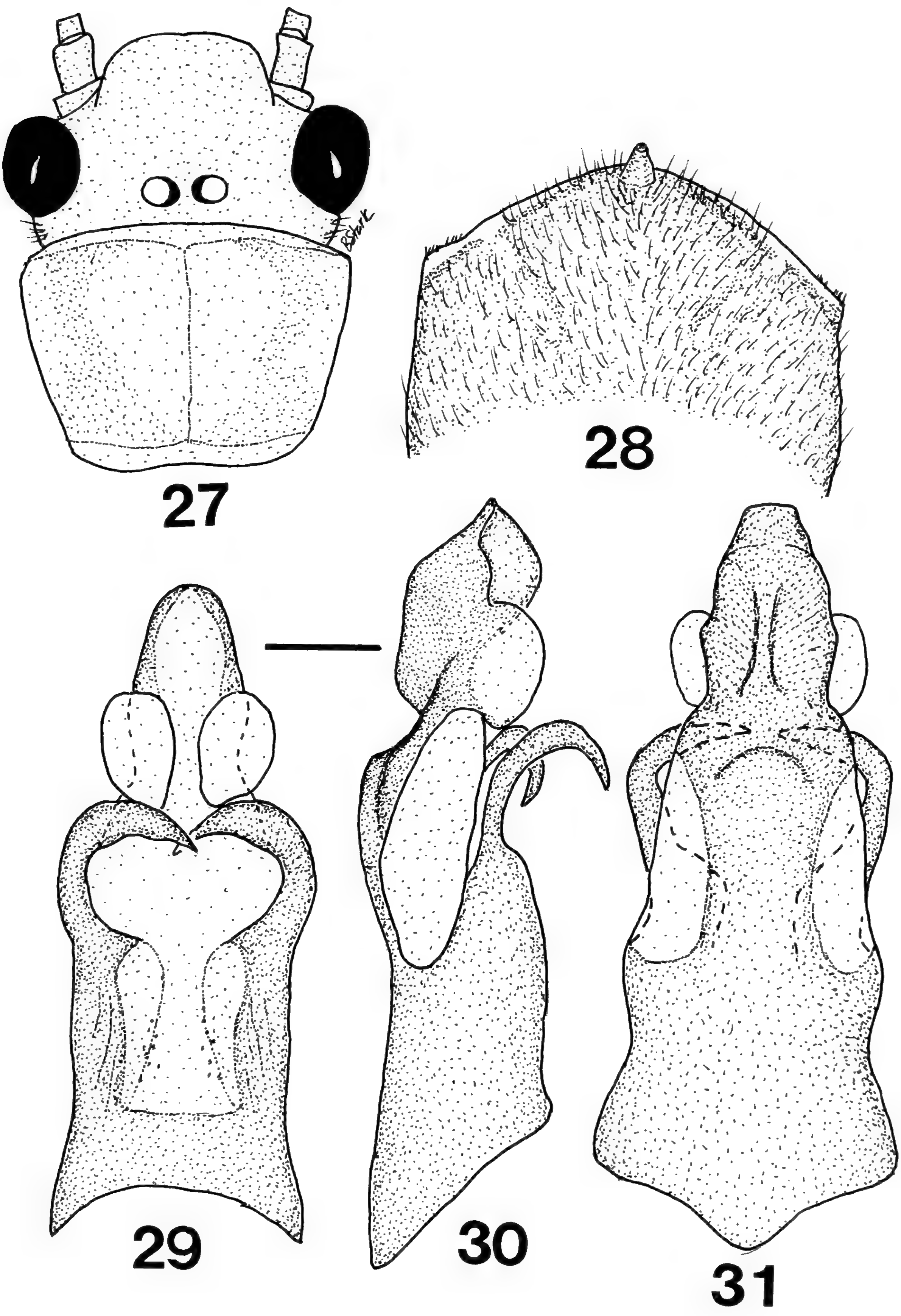
Etymology.—The name honors the Makushi people of Guyana and is used as a noun in apposition.

Types.—Holotype ♂ (pinned) and 2 ♂ paratypes from Guyana, Kanuku Mountains, Moco Moco River, 29 Apr 1995, O. S. Flint (USNM).

Diagnosis.—*A. makushi* is similar to *A. baniva* in aedeagal structure (Stark 1995). The most conspicuous difference between



Figs. 22–26. *A. karina* structures. 22. Head and pronotum. 23. Male sternum 9. 24. Aedeagus, ventral. 25. Aedeagus, lateral. 26. Aedeagus, dorsal. Scales: 0.6 mm (22), 0.3 mm (23), 0.15 mm (24–26).



Figs. 27–31. *A. makushi* structures. 27. Head and pronotum. 28. Male sternum 9. 29. Aedeagus, ventral. 30. Aedeagus, lateral. 31. Aedeagus, dorsal. Scales: 0.6 mm (27), 0.3 mm (28), 0.15 mm (29–31).

these species is the arcuate process on the dorsal aedeagal sclerite in *A. makushi* (Fig. 31).

Anacroneuria paleta Stark

Anacroneuria paleta Stark, 1995:236. Holotype ♂, 4 km S Santo Domingo, Merida, Venezuela.

Material.—Venezuela: Trujillo, Quebrada Potrerito, 7.5 km NE Bocono, 1530 m, 29–30 Apr 1995, R. Holzenthal, C. Cressa, Gutic, 31 ♂ (UMSP, UCV, BPS).

Comments.—This species was previously recorded from the Venezuelan states of Barinas and Merida (Stark 1995).

Anacroneuria paria, new species

Adult habitus.—Very diffuse brown pattern over ocelli and midlaterally on pronotum (Fig. 32). Wing membrane pale with distinctive longitudinal brown band extending from anal cell to tip; band narrow in proximal half, expanded at the cord, but interrupted by a large circular "window" beyond the cord (Fig. 37).

Male.—Forewing length 10 mm. Hammer thimble shaped, height less than basal diameter (Fig. 33). Aedeagal apex with five dorsal lobes and a short narrow keel; ventral aspect of mesal lobe scoop shaped, without membranous lobes; hooks slender (Figs. 34–36).

Female.—Forewing length 12 mm. Subgenital plate four lobed; lateral lobes larger than inner lobes, mesal notch deep and V-shaped. Transverse sclerite of sternum 9 wide, sinuate and prominent, mesal sclerite T-shaped; lateral lobes of mesal sclerite with prominent setae, stalk covered with minute setae (Fig. 54).

Nymph.—Unknown.

Etymology.—The name is based on the Paria Peninsula and is used as a noun in apposition.

Types.—Holotype ♂ (pinned) and 9 ♀ paratypes from Venezuela, Sucre, Rio Cocollar, 1.5 km SE Las Piedras de Cocollar, 810 m, 7–8 Apr 1995, R. Holzenthal, O. S. Flint (USNM). Additional paratypes; Venezuela: Sucre, Parque Nacional Peninsula de Paria, Uquire, Rio La Vidua, 15 m, 30 Mar–1 Apr 1995, R. Holzenthal, O. S. Flint, C. Cressa, 3 ♀ (UCV). Sucre, Peninsula de Paria, Puerto Viejo, "Rio el Pozo", 20 m, 3 Apr 1995, R. Holzenthal, O. S. Flint, C. Cressa, 6 ♀ (USNM).

Diagnosis.—This species is similar to *A. bifasciata* (Pictet) and *A. vistosa* Stark in displaying a distinctive wing pigmentation pattern, however *A. paria* is readily distinguished from both species on the basis of color pattern, aedeagal shape and details of female sternum 9 (Stark 1995). *Anacroneuria bifasciata* adults have tiny ocelli, a prominent dark mesal pronotal band and the wing pigmentation is separated into three distinct transverse bands. The aedeagal apex of *A. bifasciata* also bears five dorsal lobes but the mesal lobe lacks a keel and the mesal sclerite of the female 9th sternum is triangular and evenly setose. The aedeagal apex of *A. vistosa* is trilobed and the mesal sclerite of the female 9th sternum is evenly setose.

Anacroneuria perija, new species

Adult habitus.—Center of frons bright yellow, anterior head margin, posterolateral head margins, and ocellar area dark brown. Median pronotal stripe pale, lateral third brown (Fig. 38). Wing membrane brown, veins dark brown, Sc pale.

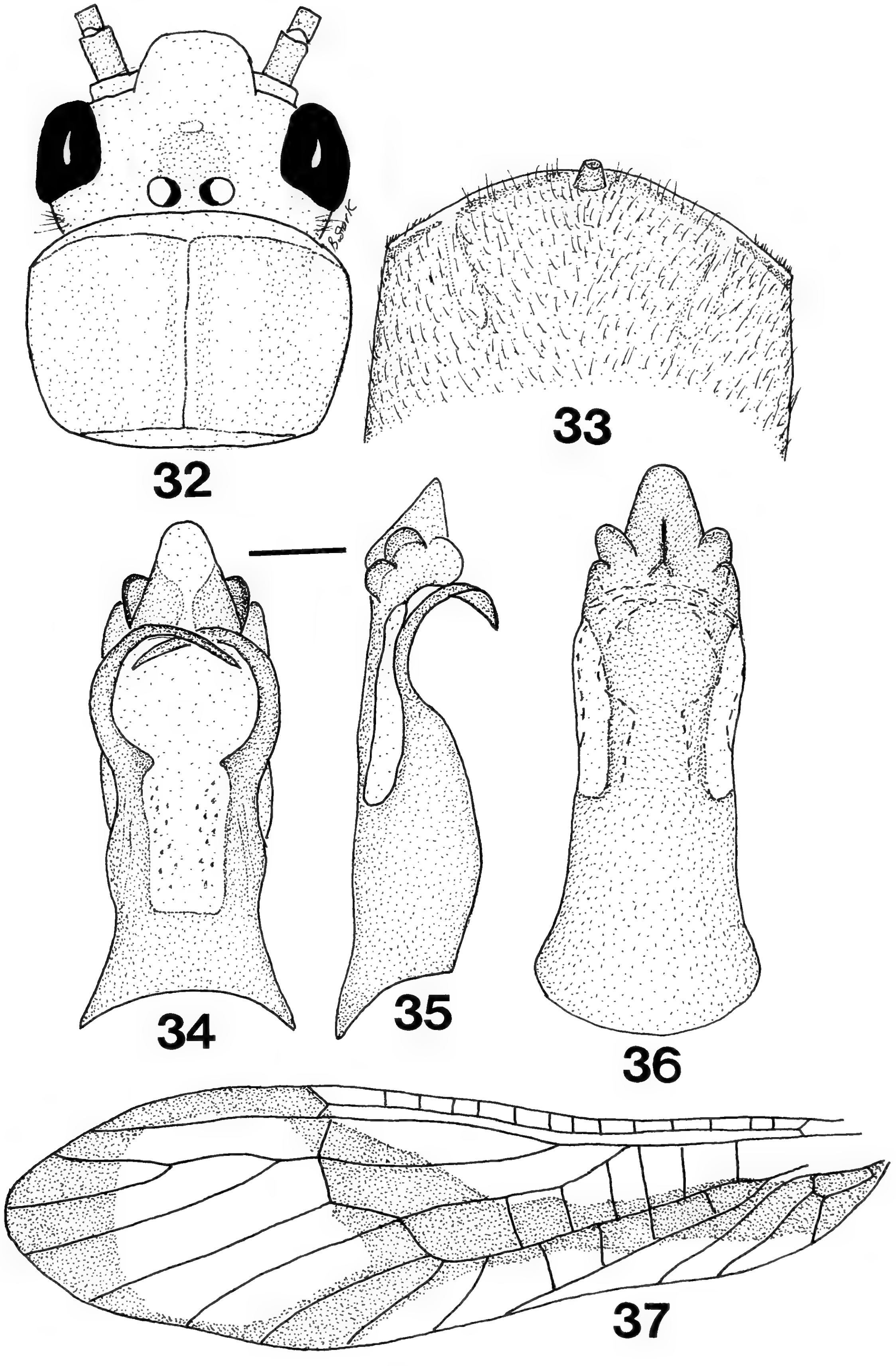
Male.—Forewing length 9 mm. Hammer cylindrical, height greater than basal diameter (Fig. 39). Ventral aedeagal apex a short scoop covered with a pair of membranous lobes; dorsal aspect with a wide keel and a low U-shaped region; hooks slender (Figs. 40–42).

Female.—Unknown.

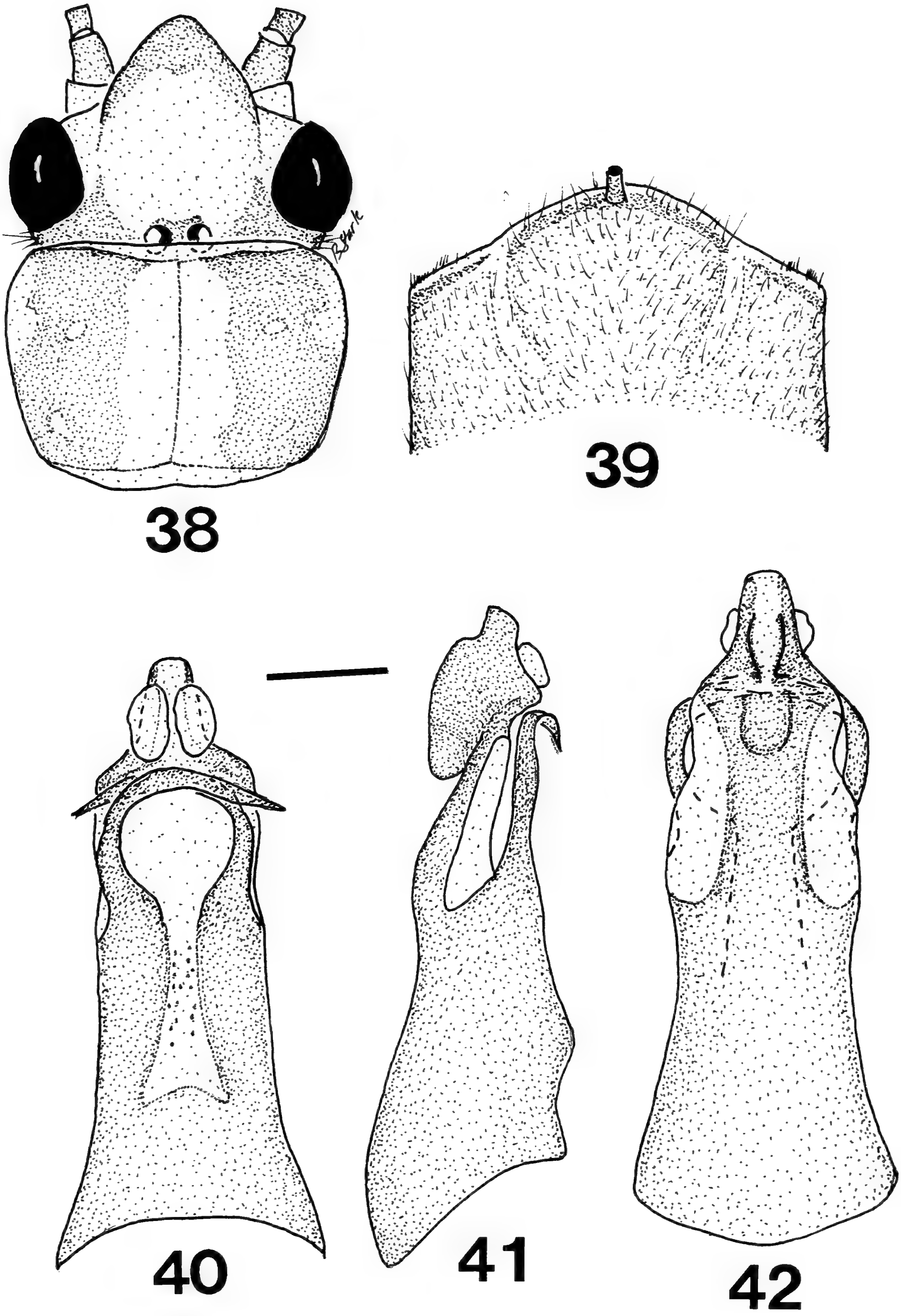
Nymph.—Unknown.

Etymology.—The name is based on the type locality and is used as a noun in apposition.

Types.—Holotype ♂ from Venezuela,



Figs. 32–37. *A. paria* structures. 32. Head and pronotum. 33. Male sternum 9. 34. Aedeagus, ventral. 35. Aedeagus, lateral. 36. Aedeagus, dorsal. 37. Forewing. Scales: 1.2 mm (37), 0.6 mm (32), 0.3 mm (33), 0.15 mm (34–36).



Figs. 38–42. *A. perija* structures. 38. Head and pronotum. 39. Male sternum 9. 40. Aedeagus, ventral. 41. Aedeagus, lateral. 42. Aedeagus, dorsal. Scales: 0.6 mm (38), 0.3 mm (39), 0.15 mm (40–42).

Zulia, Parque Nacional Perija, Rio Negro, Toromo, 360 m, 15 Jan 1994, R. Holzenthal, C. Cressa, Rincón (USNM).

Diagnosis.—This species keys to *A. baniva* in Stark (1995) but the aedeagal apex is much shorter and narrower than in that species, and the dorsal keel and subapical U-shaped process of *A. perija* also will distinguish the two. Although the condition of *A. baniva* type material left much of the color pattern obscured, it is clear that species lacks the distinctive head pattern of *A. perija.*

Anacroneuria phantoma (Banks)

Neoperla phantoma Banks, 1914:609. Holotype ♂, Mallali, Guyana.

Adult habitus.—Head yellow with diffuse yellow brown lappets. Pronotum with pale median stripe and broad, diffuse brown midlateral bands; lateral margins pale (Fig. 43). Wing membrane and veins pale.

Male.—Forewing length 9–10 mm. Hammer laterally compressed, height greater than basal diameter (Fig. 44). Aedeagal apex bluntly pointed, shoulders undeveloped. Dorsal keel long, ventral membranous lobes large. Hooks scalloped along inner margins (Figs. 45–47).

Female.—Unknown.

Nymph.—Unknown.

Material.—Guyana: Mallali, Mar, H. S. Parish, 1 ♂ (holotype) (MCZ). Potaro River, Kaieteur Falls, 1350′, 21–23 Aug 1997, O. S. Flint, 4 ♂ (USNM).

Diagnosis.—This species is quite similar to and perhaps synonymous with *A. baniva* (Stark 1995). The subtle differences in aedeagal structure include a small apical notch, decurved apex and low dorsal keel in *A. baniva.* The holotype of *A. phantoma* has a blunt aedeagal apex, straight in lateral aspect and a more pronounced dorsal keel (Figs. 45–47). *Anacroneuria makushi* represents another member of this complex with a more robust aedeagal apex and a transverse arcuate keel (Figs. 29–31).

Comments.—The type locality above Linden on the Demerara River is one of the H. S. Parish sites of 1912–13 (Adams, pers. comm.).

Anacroneuria pictipes Klapálek

Anacroneuria pictipes Klapálek, 1923:21. Holotype ♀, Haut-Carsevenne, Guyana.

Adult habitus.—(Modified from Klapálek, 1923) Body ochre yellow, pronotum darker brown along the posterior margins and near lateral margins (Fig. 48). Wing membrane and veins brown; R dark brown, costal border pale (Fig. 53).

Male.—Forewing length 10 mm. Hammer laterally compressed at tip, height greater than basal diameter (Fig. 49). Aedeagal apex truncate to emarginate, arising from low broadly rounded shoulders; dorsal keel triangular, hooks slender (Figs. 50–52).

Female.—Forewing length 11 mm. Subgenital plate weakly four-lobed. Median field of sternum nine weakly sclerotized and sparsely hirsute. Posterior margin of nine without transverse sclerite (Fig. 55).

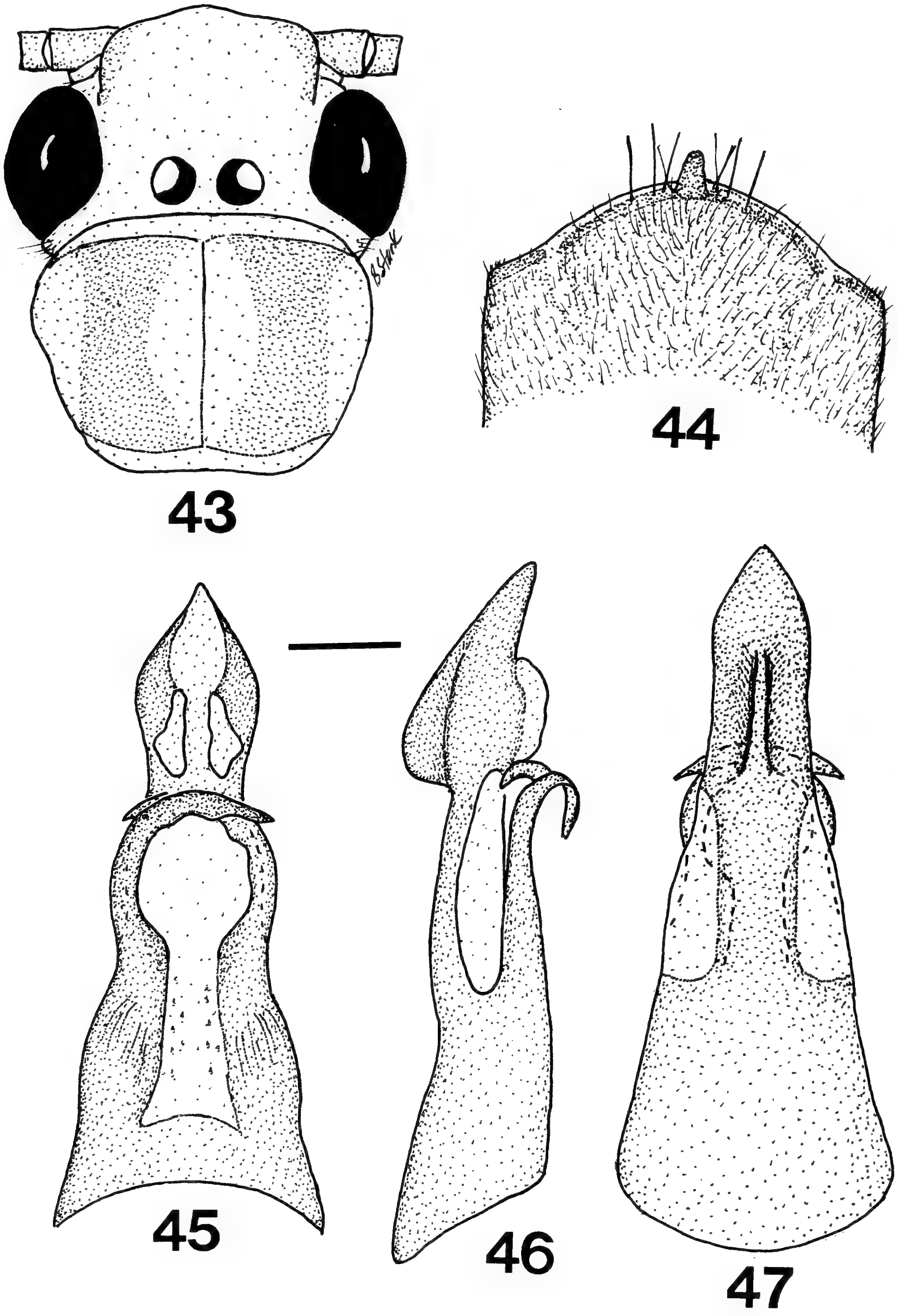
Nymph.—Unknown.

Material.—Guyana [French Guiana ?]: Haut-Carsevenne, 1878, F. Geay, 1 ♀ (holotype) (NMH). Guyana: Kanuku Mountains, Moca Moca River, 29 Apr 1995, O. S. Flint, 2 ♂ (USNM). Paramaketoi Village, 2350′, 24–25 Aug 1997, O. S. Flint, 3 ♂ (USNM).

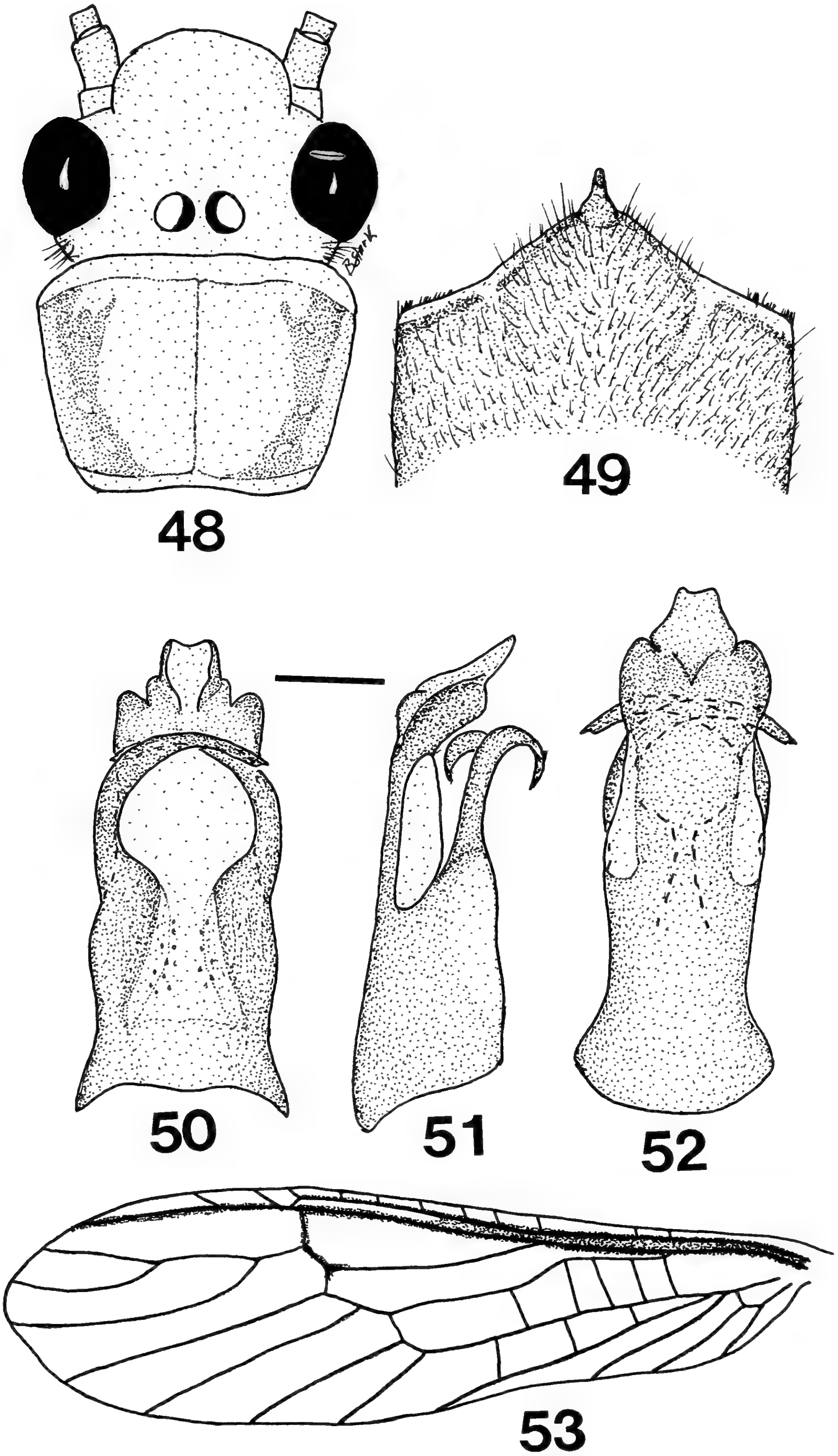
Comments.—This association of males with the holotype female is based on the distinctive wing pigmentation pattern. Females collected with the males at Moca Moca River represent another species, described below as "GU-1" which lacks this wing pattern.

Anacroneuria timote, new species

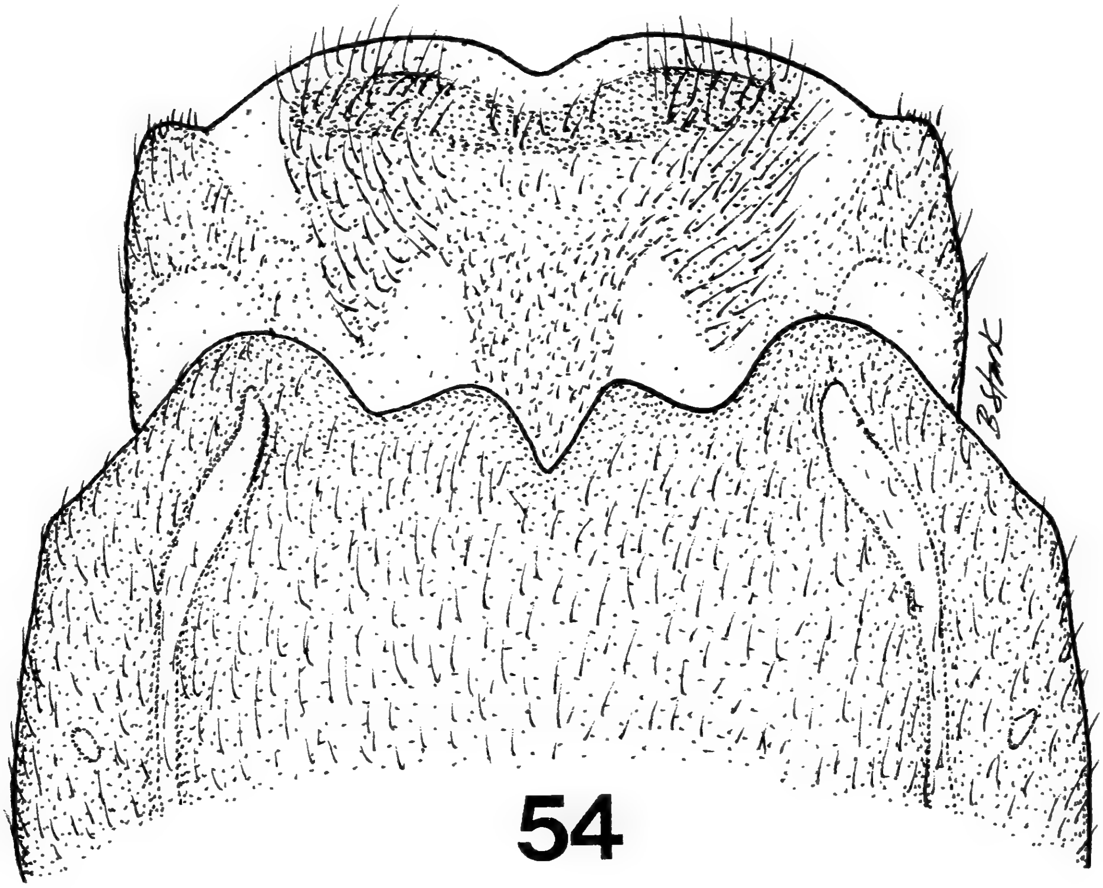
Adult habitus.—Head yellow with diffuse brown area forward of ocelli and M-line; lappets brown. Broad median pronotal stripe pale, irregular midlateral stripes brown, lateral margins pale (Fig. 56). Wing membrane transparent, C and Sc veins pale, R vein dark brown.



Figs. 43–47. *A. phantoma* structures. 43. Head and pronotum. 44. Male sternum 9. 45. Aedeagus, ventral. 46. Aedeagus, lateral. 47. Aedeagus, dorsal. Scales: 0.6 mm (43), 0.3 mm (44), 0.15 mm (45–47).



Figs. 48–53. *A. pictipes* structures. 48. Head and pronotum. 49. Male sternum 9.50. Aedeagus, ventral. 51. Aedeagus, lateral. 52. Aedeagus, dorsal. 53. Forewing. Scales: 1.2 mm (53), 0.6 mm (48), 0.3 mm (49), 0.15 mm (50–52).



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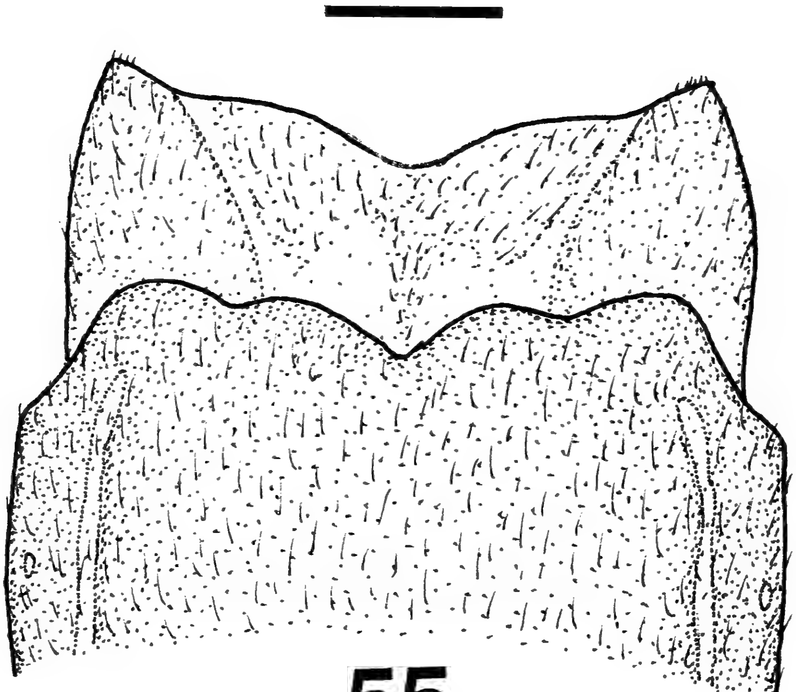

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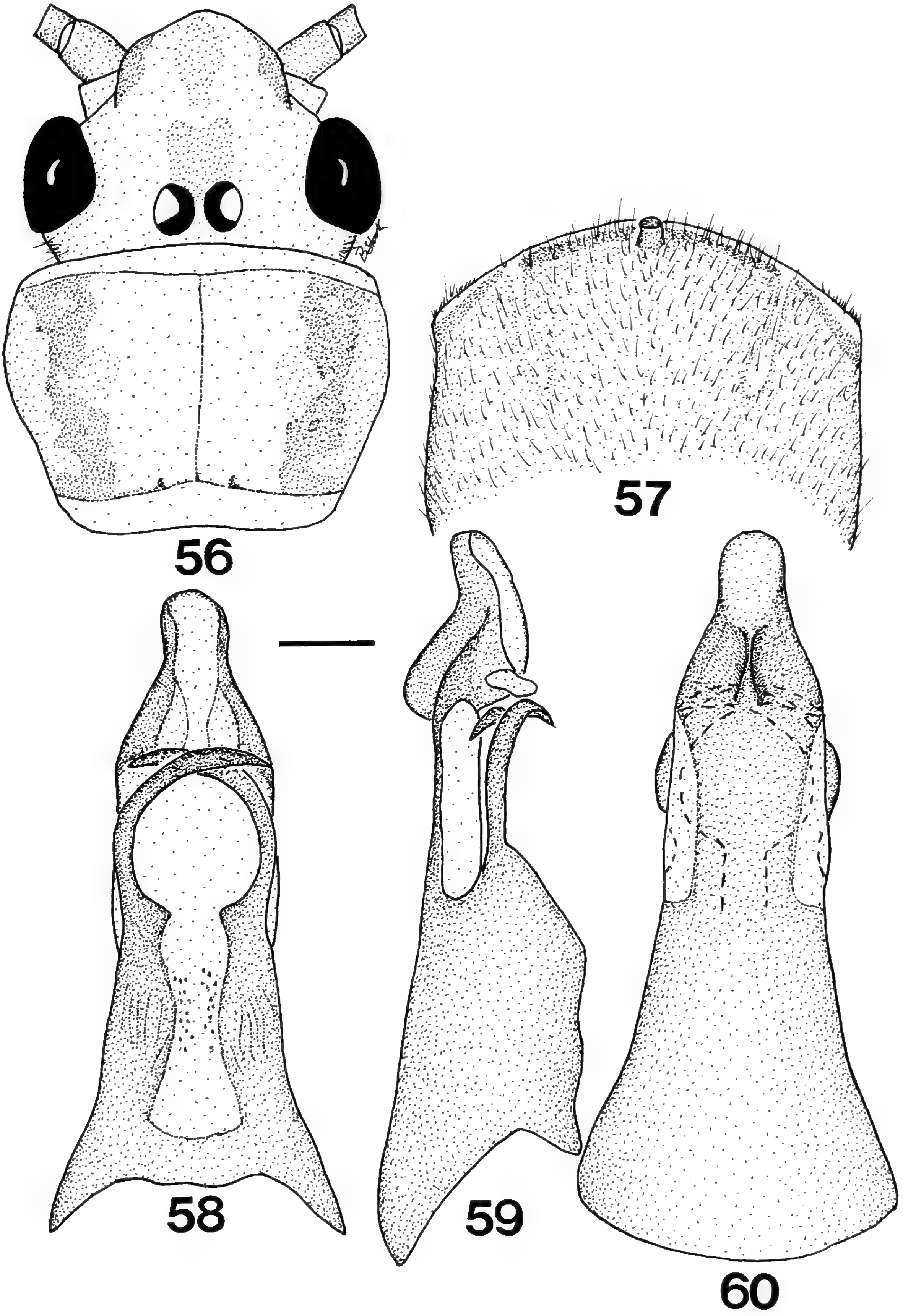
Figs. 54–55. *Anacroneuria* female sterna 8 and 9. 54. *A. paria.* 55. *A. pictipes.* Scale: 0.3 mm.



Figs. 56–60. *A. timote* structures. 56. Head and pronotum. 57. Male sternum 9. 58. Aedeagus, ventral. 59. Aedeagus, lateral. 60. Aedeagus, dorsal. Scales: 0.6 mm (56), 0.3 mm (57), 0.15 mm (58–60).

Male.—Forewing length 17 mm. Hammer thimble shaped, height less than basal diameter (Fig. 57). Aedeagal apex simple, scoop shaped with broadly rounded tip; ventral aspect with an inconspicuous pair of membranous lobes; dorsal keel well developed, hooks slender (Figs. 58–60).

Female.—Unknown.

Nymph.—Unknown.

Etymology.—The name honors the Timote people of Venezuela and is used as a noun in apposition.

Types.—Holotype ♂ (USNM) and 4 ♂ paratypes (UCV, UMSP) from Venezuela, Tachira, Quebrada Los Mirtos, 8 km S El Cobre, 2400 m, 22 Apr 1995, R. Holzenthal, C. Cressa, Gutic.

Diagnosis.—The head and pronotal pattern, size, and general aedeagal structure of this species is similar to *A. shamatari* (Stark 1995). The most conspicuous difference in aedeagal structure involves the membranous area between the hooks. In *A. shamatari* this area terminates well short of the aedeagal base whereas in *A. timote* it extends almost to the aedeagal base (Fig. 58).

Anacroneuria wapishana, new species

Adult habitus.—Head dark brown except for anterior margin and callosities. Pronotum dark brown except for V-shaped median band and small anterolateral areas (Fig. 61). Fore and mid femora and tibiae dark brown; hind femora yellow in basal two thirds, dark brown apically. Wing membrane brown except for transparent window at cord; veins dark brown except for pale costal area; wing tips dark brown.

Male.—Unknown.

Female.—Forewing length 11 mm. Subgenital plate four lobed; outer lobes small, notches shallow; median notch deep. Mesal sclerite of sternum 9 with short broad median field of fine setae, lateral fields with long thick bristles; transverse posterior sclerite indistinct (Fig. 62).

Nymph.—Unknown.

Etymology.—The name honors the Wapishana people of Guyana and is used as a noun in apposition.

Types.—Holotype ♀ from Guyana, Potaro River, Kaieteur Falls, 1350′, 21–23 Aug 1997, O. S. Flint (USNM).

Diagnosis.—The exceptional color pattern of the holotype is the basis for naming this species from a female. The species bears some similarity to *A. dourada* (Jewett 1960) but is much smaller and has a more extensive area of dark pigment on the frons.

Unassociated Females

Anacroneuria GU-1

Adult habitus.—Head yellow, without dark pattern. Pronotum with irregular brown midlateral bands and a broad yellow median band. Wing membrane transparent, veins pale.

Female.—Forewing length 11 mm. Subgenital plate with four subequal lobes. Mesal sclerite of sternum 9 with broad median field of short, fine setae, lateral field with longer thick bristles; posterior margin with a narrow U-shaped median sclerite (Fig. 65).

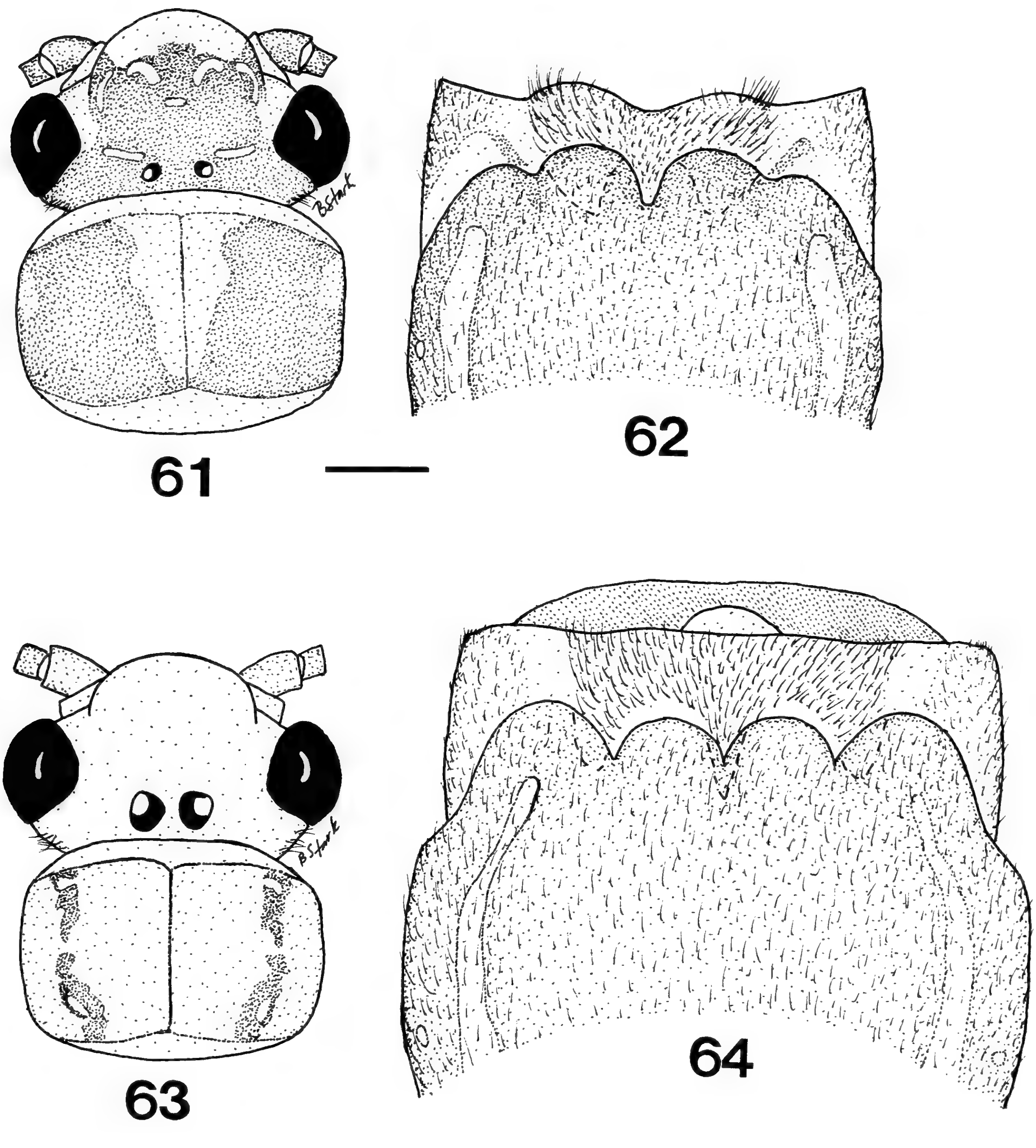
Material.—Guyana: Kanuku Mountains, Moco Moco River, 29 Apr 1995, 4 ♀, O. S. Flint (USNM). Kanuku Mountains, Kumu River and falls, 28–30 Apr 1995, 1 ♀, O. S. Flint (USNM).

Anacroneuria GU-2

Adult habitus.—Head yellow brown, lappets pale. Pronotum with diffuse brown midlateral bands. Wing membrane transparent, veins pale.

Female.—Forewing length 11 mm. Subgenital plate four lobed; lateral lobes wide and offset from narrow median lobes by shallow acute notches. Mesal sclerite of sternum 9 with median field covered with fine short setae which form a sagittate patch separated from lateral patches covered with longer bristles; posterior sclerite absent (Fig. 66).

Material.—Guyana: Dubulay Ranch, Ar-



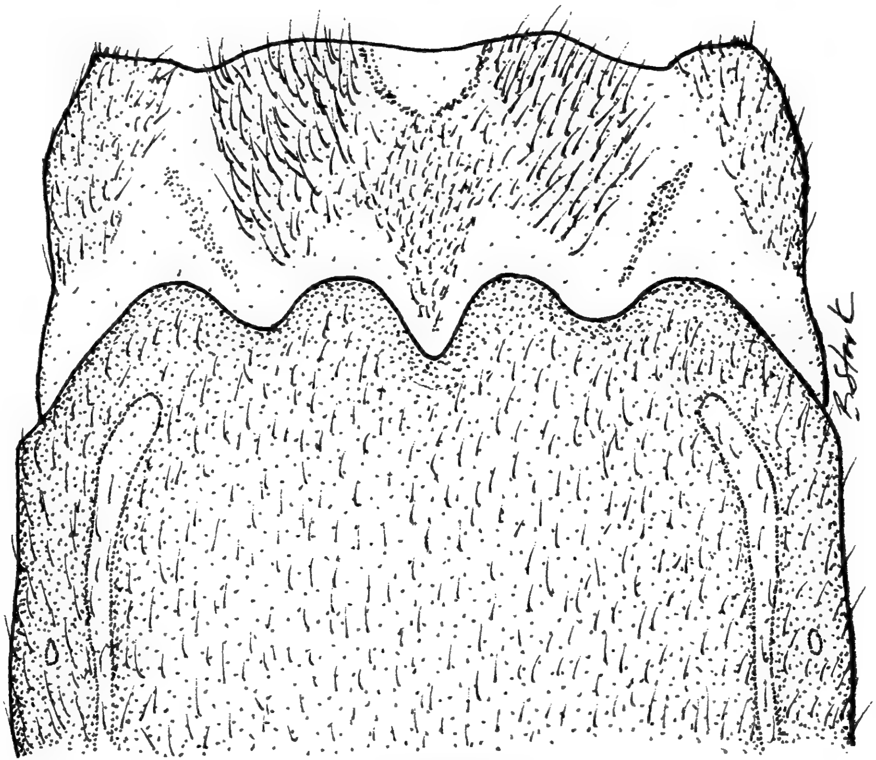
Figs. 61–64. *Anacroneuria* female structures. 61. *A. wapishana* head and pronotum. 62. *A. wapishana* sterna 8 and 9. 63. *A. llana* head and pronotum. 64. *A. llana* sterna 8 and 9. Scales: 0.6 mm (61, 63), 0.3 mm (62, 64).

amatani Creek, 15–18 Apr 1995, 2 ♀, O. S. Flint (USNM).

Anacroneuria GU-3

Adult habitus.—Head yellow with diffuse brown pigment forward of ocelli; lappets brown. Pronotum with irregular diffuse brown spots scattered over midlateral area (Fig. 67). Tibiae banded, basal and apical bands brown, median band pale. Wing membrane transparent except for pale brown tips which accent an obscure window at the cord; veins brown, R darker, costal area pale.

Female.—Forewing length 10 mm. Subgenital plate four lobed; outer lobes small, notches shallow, median notch deep and U-shaped. Median sclerite of sternum 9 with



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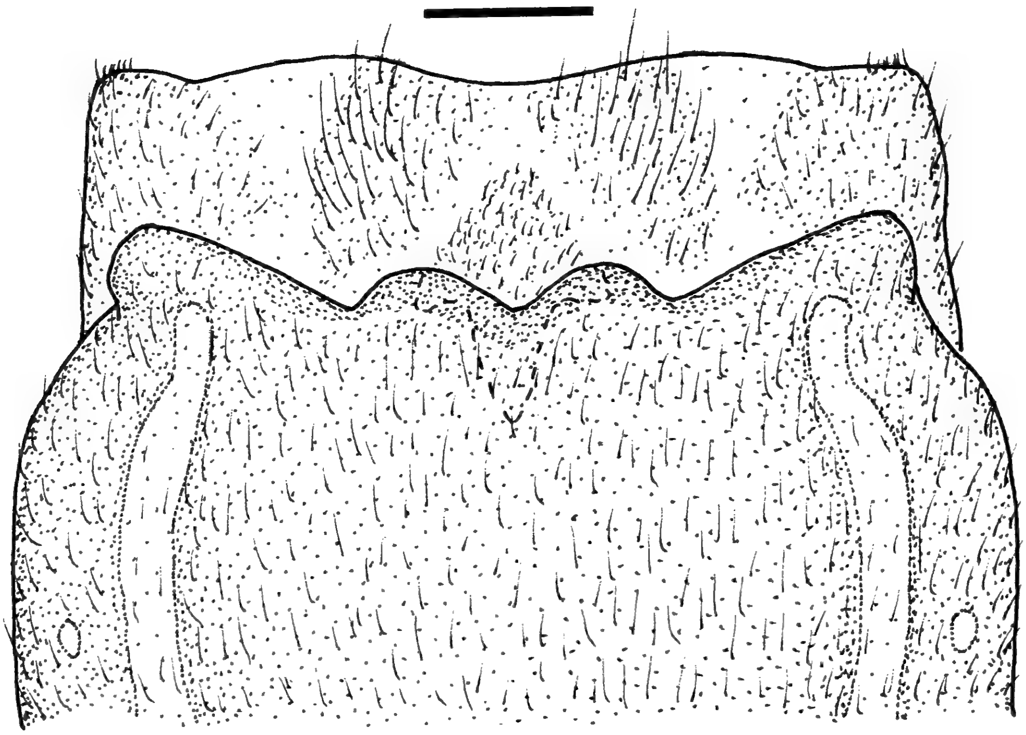

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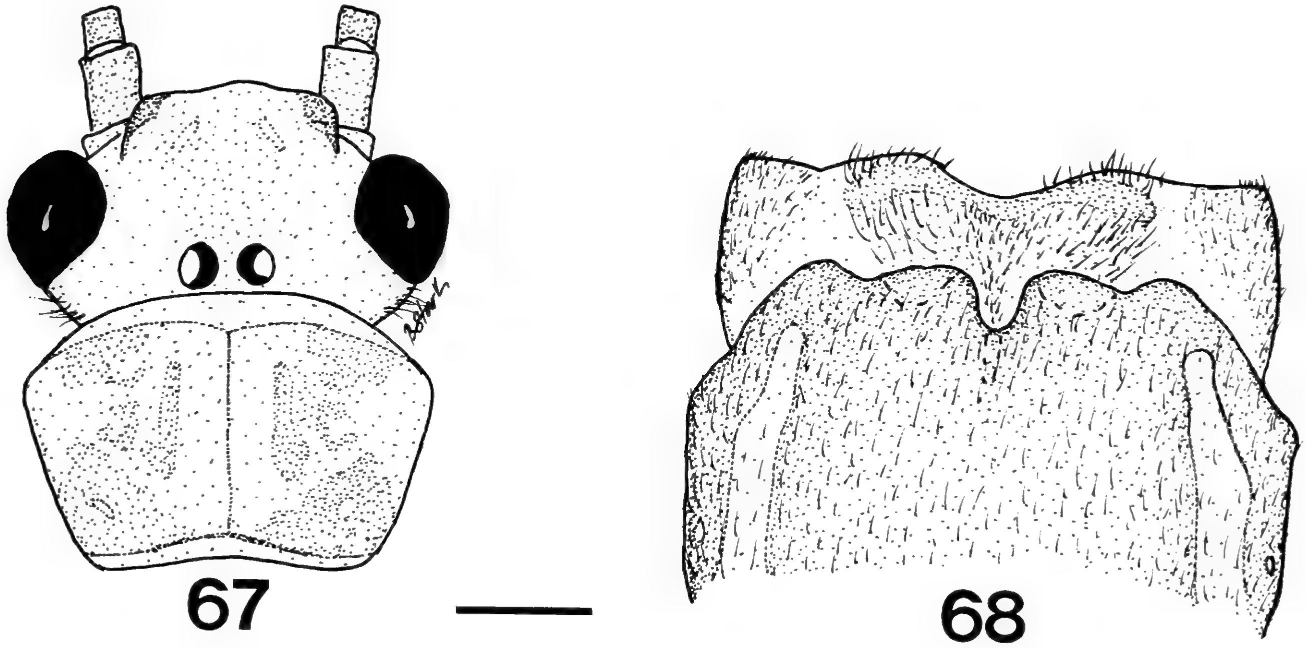
Figs. 65–66. *Anacroneuria* female sterna 8 and 9. 65. *Anacroneuria* GU-1. 66. *Anacroneuria* GU-2. Scale: 0.3 mm.



Figs. 67–68. *Anacroneuria* GU-3 female structures. 67. Head and pronotum. 68. Sterna 8 and 9. Scales: 0.6 (67), 0.3 (68).

long narrow stem; stem and mesal field with short, fine setae, lateral areas with thicker setae. Transverse sclerite sinuate (Fig. 68).

Material.—Guyana: Mazaruni-Potaro District, Takutu Mountains, 20 Dec 1983, P. J. Spangler, 1 ♀ (USNM). Same location, 12 Dec 1983, P. J. Spangler, R. A. Faitoute, P. D. Perkins, 1 ♀ (USNM).

Provisional Key for Male *Anacroneuria* from Venezuela, Guyana, and Suriname (Modified from Stark 1995)

1. Wings banded in amber and dark brown 2
   Wings variable, but without bands . . . 3
2. Dark pigment separated into basal, median and apical bands . . . . . *A. bifasciata*
   Dark pigment forming a narrow longitudinal band from base to cord (Fig. 37) . . . . *A. paria*
3. Forewing length greater than 13.5 mm 4
   Forewing length less than 13 mm . . 11
4. Hammer low, scarcely elevated above sternum . . . . *A. chorrera*
   Hammer length equal to apical diameter 5
5. Hammer apex quadrate; aedeagal hook apices footlike . . . . *A. cuadrada*
   Hammer apex circular; aedeagal hooks without footlike apices 6
6. Dorsum of aedeagus with a transverse, subapical arcuate lobe . . . . . *A. arcuata*
   Dorsum of aedeagus without arcuate lobe 7
7. Hammer tiny; aedeagal apex notched . . . . *A. muesca*
   Hammer thimble shaped; aedeagal apex rounded 8
8. Aedeagal apex strongly trilobed; pale mesal pronotal band not extending laterally beyond ocelli . . . . . *A. fenestrata*
   Aedeagal apex simple; pale mesal pronotal stripe wide, extending laterally beyond ocelli 9
9. Aedeagal apex abruptly narrowed at shoulder (Fig. 58) 10
   Aedeagal apex gradually tapered . . . . *A. paleta*
10. Membranous area between hooks extends almost to aedeagal base (Fig. 58) . . . . *A. timote*
    Membranous area between hooks extends far short of aedeagal base . . . . *A. shamatari*
11. Aedeagal apex simple 12
    Aedeagal apex multilobed 25
12. Aedeagal hooks straight, daggerlike . . . . *A. cruza*
    Aedeagal hooks curved, scythelike . . . 13

13. Apex of aedeagal hooks fingerlike, aedeagal apex surmounting a distinct neck . . . . *A. digitata*
    Apex of aedeagal hooks not fingerlike, subapical area of aedeagus without neck 14
14. Ventral aspect of aedeagus with a conspicuous pair of membranous lobes . . 15
    Ventral aspect of aedeagus with membranous lobes absent or inconspicuous 22
15. Dorsal keel formed by a pair of widely spaced ridges (Fig. 16); head with a conspicuous dark area at ocelli (Fig. 12) 16
    Ridges of dorsal keel closely spaced (Fig. 31); head with diffuse or pale ocellar pigment (Fig. 27) 17
16. Keel arms divergent anteriorly (Fig. 16); occipital area pale (Fig. 12) . . . . *A. chaima*
    Keel arms convergent anteriorly (Fig. 42); occipital area dark (Fig. 38) . . . . *A. perija*
17. Inner margins of aedeagal hooks scalloped (Fig. 29) 18
    Inner margins of aedeagal hooks smoothly curved (Fig. 24) 20
18. Aedeagus with a dorsomesal arcuate keel (Fig. 31) . . . . *A. makushi*
    Aedeagus without dorsomesal arcuate keel 19
19. Aedeagal apex notched, decurved in lateral aspect . . . . *A. baniva*
    Aedeagal apex rounded, straight in lateral aspect (Figs. 45–46) *A. phantoma*
20. Membranous ventral aedeagal lobes wider than long (Fig. 24); submarginal pronotal bands narrow (Fig. 22) . . . . *A. karina*
    Membranous ventral aedeagal lobes longer than wide (Fig. 19); submarginal pronotal bands wide (Fig. 17) . . . 21
21. Aedeagal apex truncate (Fig. 19); ventral membranous aedeagal lobes small (Fig. 19) . . . . *A. claudiae*
    Aedeagal apex pointed (Fig. 9); ventral membranous aedeagal lobes large (Fig. 9) . . . . *A. arawak*
22. Aedeagal apex gradually narrowed to a point . . . . *A. bari*
    Aedeagal apex truncate or broadly rounded 23
23. Aedeagus with a small ventral membranous lobe . . . . *A. chiquita*
    Aedeagus without ventral membranous lobe 24
24. Projecting apex of aedeagus subequal to shoulder . . . . *A. llana*
    Projecting apex of aedeagus about twice as long as shoulder . . . . *A. blanca*
25. Aedeagal apex with a dorsolateral pair of small hornlike processes 26
    Aedeagal apex without hornlike processes 27
26. Hornlike aedeagal processes acute and conspicuous in ventral aspect . . . . *A. caraca*
    Hornlike aedeagal processes rounded and inconspicuous in ventral aspect . . . . *A. aroucana*
27. Dorsal aedeagal keel V-shaped (Fig. 52) 28
    Dorsal aedeagal keel not V-shaped . . . 29
28. R and basal half of Sc vein covered with dark brown pigment (Fig. 53) . . . . *A. pictipes*
    R and basal half of Sc without constrasting pigment band . . . . . *A. achagua*
29. Ventral aspect of aedeagus with a large membranous lobe . . . . *A. pequena*
    Ventral aspect of aedeagus without membranous lobe 30
30. Lateral aedeagal lobes scarcely projecting . . . . *A. menuda*
    Lateral aedeagal lobes distinctly projecting 31
31. Lateral aedeagal lobes about as wide as median lobe 32
    Lateral aedeagal lobes about half as wide as median lobe . . . . . . *A.* sp VZ-10
32. Wings with a large transparent spot beyond cord, and an irregular transparent costal band . . . . *A. vistosa*
    Wings rather uniformly pigmented . . . . *A. pinza*

Acknowledgments

I thank R. Holzenthal, University of Minnesota, and O. S. Flint and N. Adams, United States National Museum, for the loan of specimens. I also thank P. Zwick and curators at the California Academy of Science and the Museum of Comparative Zoology

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112(1):94–96. 1999.

A new species of *Siamosquilla* from Indonesia (Crustacea: Stomatopoda: Protosquillidae)

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Abstract.—*Siamosquilla sexava,* the second species of the genus, is described from Indonesia. It can be distinguished from the type species, *S. hyllebergi* Naiyanetr, from Thailand, by the shorter median rostral spine, the larger ocular scales, the much broader telson, and differences in ornamentation of the fused sixth abdominal somite and telson.

Among the stomatopods collected by one of us (M. V. E.) during a six-year field study in Indonesia was a minute protosquillid which proved to be the second known species of *Siamosquilla* Naiyanetr, 1989. It is described below.

Abbreviations used in the account include: LON, Lembaga Oseanologi Nasional (National Institute of Oceanoraphy), Jakarta, Indonesia; TL, total length, measured on the midline; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

The holotype and some paratypes have been deposited in the USNM; two paratypes are in the LON.

Family Protosquillidae Manning, 1980
Siamosquilla Naiyanetr, 1989
Siamosquilla sexava, new species
Fig. 1

Material examined.—Indonesia: Moromaho, Tukang Besi: 1♀, TL 18 mm (holotype, USNM 260927), 2♀♀, TL 16–17 mm (paratypes, LON).—Gili Meno, Lombok: 1♂, TL 17 mm, 1♀, TL 18 mm (paratypes, USNM 260928).—Melanguane, Sangihe-Talaud: 1♀, TL 17 mm (paratype, USNM 260929).—Taupun, Togian Islands: 1♂, TL 13 mm (paratype, USNM 260930).

Diagnosis.—Size very small, TL less than 20 mm in adults. Cornea broadened, set obliquely on stalk. Ocular scales well developed, produced into triangular lobes laterally, extending nearly to lateral rostral spine in adults.

Rostral plate sharply trispinous, median spine distinctly upturned distally, extending to base of corneas; ventral projection of rostral plate large, obtusely rounded ventrally. Lateral rostral spines extremely long, slender and recurved, length nearly two-thirds that of median spine. Basal part of rostral plate very thin. Anterior margins of lateral plates of carapace concave, anterolateral angles strongly produced to a sharp point, extending anteriorly to base of rostral plate.

Mandibular palp absent. Five epipods present.

Raptorial claw with inflated part of outer margin of dactylus notched. Propodus with single movable spine proximally on inner margin.

Anterior 4 abdominal somites smooth, unarmed, not carinate dorsally. Fifth abdominal somite smooth medially, with single low longitudinal carina laterally above lateral margin, separated from margin by a groove, armed with posterolateral spine. Sixth abdominal somite entirely fused with telson in adults, dorsal surface rough, with shallow, irregularly curved grooves, lacking carinae entirely.

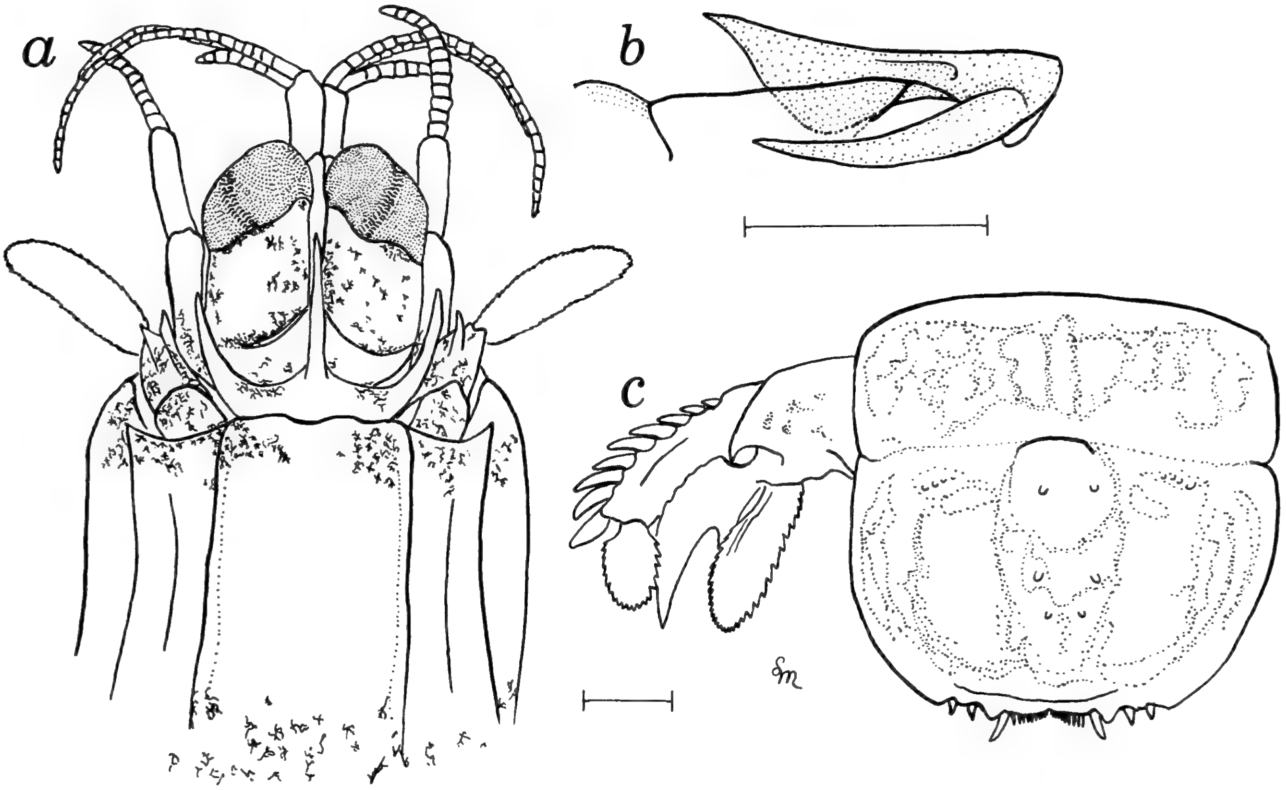

Fig. 1. *Siamosquilla sexava,* new species, female holotype, TL 18 mm. *a,* Anterior part of body, dorsal view (apex of left ocular scale damaged); *b,* Rostral plate, lateral view; *c,* Fused sixth abdominal somite and telson and left uropod, dorsal view. Scales = 1 mm.

Telson much wider than long, dorsal surface rough, slightly inflated, with 3 very indistinct bosses. Median boss outlined by a shallow groove in dorsal surface of telson; boss rounded anteriorly, converging posteriorly; outline of submedian bosses even less distinct, extending posteriorly almost to posterior margin of telson. Median fissure completely fused, no longer visible. Three pairs of marginal teeth, submedians with moveable apices arising submarginally under submedian marginal projections. Intermediate teeth very low and rounded, almost indistinguishable in larger specimens. Lateral teeth more distinctly produced, with rounded apices. Separation between three pairs of marginal telson teeth shallow and rounded. Submedian teeth with 12–14 denticles on either side of midline, increasing noticeably in length laterally, intermediate teeth each with 2 fixed mesial denticles, laterals each with 1 denticle. Lateral margins of telson straight, rounded distally.

Uropods stout, proximal segment of exopod with 9 short movable spines laterally, distalmost extending beyond midlength of distal segment, with fixed distal spine ventrally. Inner margin of uropodal exopod setose; uropodal endopod with normal complement of setae. Inner spine of basal prolongation of uropod much shorter than outer.

Size.—Males (n = 2), TL 13–17 mm. Females (n = 5), TL 13–18 mm.

Remarks.—This small species has a very distinctive rostral plate, with long, recurved lateral spines, and a telson that is most remarkable for its lack of distinguishing features; the sixth abdominal somite is fused to the telson, which has almost indiscernible bosses and a fused median fissure. *Siamosquilla sexava* differs from *S. hyllebergi* in numerous features: the median rostral spine is shorter, extending to, rather than beyond, the cornea and the lateral rostral spines are longer; the ocular scales are broader; in adults the anterolateral angles of the carapace are sharper and more pronounced; the dorsal sculpture of the fused sixth abdominal somite and telson is much more elaborate; and the telson is much broader.

The fixed projections on the posterior margin of the telson are much more pronounced in *S. hyllebergi* than in *S. sexava,* and the submedian projections in the former species probably obscure the submarginal, movable submedian teeth of the telson, which are clearly visible in *S. sexava.*

In *S. sexava,* the size of the ocular scales increases allometrically, and in very small specimens of *S. sexava* the scales resemble those of larger *S. hyllebergii*; they increase in width with increasing TL.

Distribution.—Known only from eastern Indonesia, where it is relatively widespread. Recorded from five regions: Lombok, Sangihe-Talaud, Togian Islands, and Tukang Besi Archipelago.

Etymology.—The species name is from the word *sexava,* which means "mantis" in Bahasa Talaud, the local language in one of the collection localities (Melanguane, Sangihe-Talaud). The local fishermen, school teachers and children there were most helpful in assisting with collecting, and were fully cognizant of the differences between stomatopods and other decapod shrimp, comparing stomatopods to the "sexava" without any solicitation. Their assistance is most appreciated.

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The taxonomic status and zoogeography of *Cambarus bartonii carinirostris* Hay, 1914 (Crustacea: Decapoda: Cambaridae)

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Abstract.—Historically, *Cambarus bartonii carinirostris* was considered a subspecies of *Cambarus bartonii.* Recent studies indicate that *C. b. carinirostris* is indistinguishable from the nominate species and should be relegated to synonymy with *C. bartonii.* In other studies this assignment is not accepted and subspecific status has been maintained for *C. b. carinirostris* when reporting on crayfish closely related to *C. bartonii.* Work in the area of northern Appalachian crayfishes has made it apparent to us that *C. b. carinirostris* should be elevated to full species status based on its unique meristic and morphometric characteristics.

For nearly two decades we have studied the crayfishes of the northern Appalachians. Of the many questions associated with this area, the proper identity and distribution of *C. b. bartonii* (Fabricius 1798) has been and continues to be a principal concern. Ortmann's (1905, 1906, 1931) studies remain the foundation on which the distribution and systematics of northern Appalachian crayfish are presently understood. After Ortmann's death in 1933, Horton H. Hobbs, Jr., shifted the center of crayfish systematic studies to the southern Appalachians (and other southern areas) and the identity of *C. b. bartonii* and its subspecies remained unresolved. In the early 1970s we became interested in the ecology of crayfish in our home state, Ohio. We were immediately confronted with the problem of *C. b. bartonii* and the subspecies associated with it, since both *C. b. carinirostris* (Hay 1914) and *C. b. cavatus* (Hay 1902) are reported from Ohio (Hobbs 1974, 1989; Thoma & Jezerinac 1982). With the unresolved taxonomic problems and a domination by members of the subgenus *Cambarus* in Ohio, it became apparent that a taxonomic study was needed before the study of crayfish ecology could commence.

Materials and Methods

Specimens examined came from the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and the Ohio State University Museum of Biological Diversity, Columbus, Ohio (OSU-MBD). The paratypes, housed at the Museum of Comparative Zoology (MCZ) were not examined. Field collections (now house at OSU-MBD) were made using a 1.3 × 2 m seine or by hand. A total of 95 specimens of *C. carinirostris* (33 Form I males, 27 Form II males, and 35 females) and 191 specimens of *C. b. bartonii* (79 Form I males, 43 Form II males, and 69 females) were measured for this study. Measurements were made to the nearest 0.1 mm using a vernier caliper and followed Hobbs (1981) and Jezerinac (1985). Measurements of regenerated body parts were avoided. Analysis was performed using SYSTAT 5.2.1. Principal component analysis used only Form I male specimens.

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† Deceased, 21 April 1996.

Cambarus (Cambarus) *carinirostris* Hay, new status

Cambarus bartonii carinirostris Hay, 1914: 384.

Cambarus bartonii montanus.—Faxon, 1914:386 (in part).—Newcombe, 1929: 286 (in part).

Cambarus montanus montanus.—Ortmann, 1931:106 (in part).

Cambarus (Cambarus) bartoni carinirostris.—Ortmann, 1931:107.

Cambarus (Cambarus) bartonii carinirostris.—Hobbs 1969: 109, fig. 19m; 1974: 11, fig. 24; 1989: 13 fig. 30.—Thoma, 1982:875.—Thoma & Jezerinac, 1982: 136.—Jezerinac, 1983: 4.—Jezerinac & Thoma, 1984: 120 figs. 8–9.—Jezerinac & Stocker, 1989: 2.—Jezerinac & Stocker, 1990: 1.—Jezerinac, Stocker & Tarter, 1995: 76–83, fig. 35–38.

Diagnosis.—Body pigmented. Carapace subcylindrical, slightly flattened dorsoventrally. Eyes slightly reduced. Rostrum with parallel or slightly concave margins, margins thickened, lacking marginal spines or tubercles, rostrum curved abruptly cephalically and terminating in upturned corneous tubercle; frequently with a median carina. Areola 3.4–12.0 times longer than wide (median = 5.7), comprising 25.2–40.4% of total length of carapace (median = 37.9%), bearing 3 to 4 punctations across narrowest part. Cervical spine absent or reduced to blunt tubercle. Cervical grove uninterrupted. Suborbital angle acute. Postorbital ridge lacking cephalic spine or tubercle. Branchiostegal spine reduced to small knob. Antennal scale approximately 1.5 times as long as broad, with mesial and lateral margins subparallel near and at midlength; distomesial margin strongly sloping. Basiopodite of antenna lacking spine. Ischiopodite of antenna with blunt spine. Chela smooth, robust, length 79.6–111.9% of total carapace length (median = 94.0%) in Form I males (71.8–88.4%, median = 78.8% in females), bering 1 row of 5 to 8 (median = 7.0) adpressed squamous tubercles along mesial margin of palm and 5 to 7 punctations dorsal to such tubercles (occasionally distal 1 to 4 punctations replaced by tubercles). Width of gape of fingers of Form I male 17.4–46.3% of palm length (median = 27.2%), less so in Form II males (median = 16.3%) and females (median = 17.2%). Lateral margin of fixed finger weakly costate; moderately developed dorsomedial ridges on both fingers flanked by parallel rows of punctations; fixed finger impressed at dorsal and ventral lateral bases; dactyl 0.9–2.5 (median = 2.1) times longer than mesial margin of palm; palm width 41.5–51.1% (median = 46.1%) of chela length; third or fourth tubercle of mesial margin of fixed finger enlarged; 1–2 tubercles usually present on mid-subpalmar surface; never with elongated setae at base of fixed finger. Dorsomesial margin of carpus of chela with 1 distal spine and 1 proximal blunt tubercle; ventral surface with 1 or 2 conical tubercles at distal margin. Ventrolateral ridge of merus usually with 2–3 spines. Hook only on ischium of third pereiopod of male. Basal boss on coxa of fourth pereiopod well developed. First pleopods of Form I male contiguous at base, with 2 short terminal elements bent at approximately 90° to main shaft; corneous central projection truncated distally, bearing subapical notch; mesial process inflated, tapering distally; central projection of Form II male pleopods noncorneous, club-shaped. Females with annulus ventralis slightly embedded in sternum, asymmetrical, subrhomboid, slightly movable, lacking cephalolateral prominence; first through fifth pleopods similar in shape.

Color notes.—For the most part, this species is dorsally a uniform brown ranging from chestnut to tan with ventral surfaces fading to cream. Some populations have a greenish hue. The thickened rostral margins and postorbital ridges are a brownish red and the larger tubercles and spines orange. No banding or striping evident.

Types.—"Type" and paratypes USNM 23962 (1 Form I male, 7 Form II male, 15 female); paratypes, MCZ 7399 (1 Form I male, 1 Form II male, 1 female). The Form I male housed at the USNM is herein designated the lectotype of the species.

Type locality.—Hay (1914:385) stated "Gandy Creek, Oceola, Randolph Co., W. Va." in his original description. A visit to this area and discussions with local residents indicated Oceola (38°42′50″N, 79°38′00″W) was the location of a now non-extant school house at the site of a historic lumber camp. The old school house was located near the Sinks of Gandy. We made a topotype collection from Gandy Creek upstream of County Road 40, just west of County Road 29/1 (38°43′22″N, 79°37′38″W). This site is the first road crossing downstream of the mouth of the Sinks of Gandy.

Range.—Found throughout the drainages of the Allegheny and Monongahela rivers in Pennsylvania, New York and West Virginia; tributaries of the Ohio River upstream of Sunfish Creek in Ohio and Fish Creek in West Virginia; southern tributaries of Lake Erie and Lake Ontario from the Grand River, Ohio, to the Gennesse River, New York; throughout the Greenbrier River and tributaries of the New River upstream of the Greenbrier; upper Elk River, West Virginia.

Variation.—In the upper reaches of the Monongahela basin (Cheat and Tygart/Buckhannon basins) *C. carinirostris* probably retains its most plesiomorphic state. This is the only portion of the range in which no other stream dwelling forms of *Cambarus* are found. Here, *C. carinirostris* attains its greatest degree of sculpturing (including the carina) and approaches the body size of members of the subgenera *Cambarus* and *Puncticambarus* that inhabit larger rivers. The plesiomorphic appearance is likely in part due to the larger sizes attained. In the remainder of the range, *Cambarus* (*Puncticambarus*) *robustus* Girard, 1852, or *Cambarus* (*C.*) *sciotensis* Rhoades, 1944, occupy the larger mainstem streams and *C. carinirostris* is confined to the smaller tributaries. In the Casselman River of the Youghiogheny River, Pennsylvania, we have seen specimens with body forms reminiscent of the subgenus *Erebicambarus* Hobbs, 1969, in that they display a more tubular, sausage-shaped carapace that is less dorsoventrally compressed. The chelae remain decidedly within the range of *C. carinirostris,* though they have the least amount of gape between the fingers. Specimens from the southernmost extent of the range display reduced inflation of the rostral margins and lack the 90° angle at the rostral tip. The rostra in this population most closely resemble the probable plesiomorphic state.

Occasionally, a second row of slightly produced tubercles can be found on the palm of the chela. This character does not exhibit a defined geographical pattern but appears in some individuals in most collections. All other populations exhibit the normal characteristics given in the Diagnosis.

Size.—Mature specimens range from 26 to 48.8 mm (median = 34.9 mm) total carapace length (median: Form I males 36.9 mm, Form II males = 31.9 mm, females = 35.4 mm).

Life history notes.—Jezerinac et al. (1995) reported Form I males from late April through early September and ovigerous females from July through mid August. This study found Form I males as late as October and ovigerous females in the reported range of dates. No information exists on longevity, growth rates, thermal preferences or dietary habits.

Habitat and ecology.—The normal habitat occupied by *C. carinirostris* is pools and riffles of high gradient first and second order streams. Populations can be found in intermittent streams but the abundance is greatly reduced. Some burrowing occurs, mostly sub-boulder, in mid-stream or on the edges of streams. This species is a secondary burrower. *Cambarus carinirostris* is capable of expanding its niche in the absence of other species of *Cambarus* that are primary burrowers or mainstem inhabitants.

Often caves, if present, yield specimens, usually in the vicinity of the mouth. This species is sensitive to excess silt, bed load sediments, nutrient enrichment, acid mine impacts, and habitat alterations that reduce cobble and boulder abundance.

Taxonomic status.—Numerous authors have commented on the distribution and taxonomic status of *C. carinirostris.* In his original description Hay (1914: 385) reported the species from Tygart Valley and Cheat River in Randolph County, West Virginia, stating that *C. carinirostris* was "... a well marked subspecies ..." differing from the nominate species in that "... the carapace is a little more cylindrical, the rostrum broader and flatter, and always furnished near the tip with a median longitudinal carina." Faxon (1914: 385), commented that the rostral carina was a rather elusive character and reported additional records for this taxon from the Greenbrier River basin (West Virginia). The next report on *C. carinirostris* was Ortmann (1931: 139) in which he retained the subspecific status for *C. carinirostris,* and stated *C. carinirostris* differs from *C. b. bartonii* only in the presence of the carina. After Ortmann's death, no further comments were published on the taxonomy of *C. carinirostris* until Hobbs (1972: 111) commented that it probably should not be recognized. Bouchard (1976: 588) recognized no subspecies of *C. bartonii,* reporting that no characters separate the currently recognized subspecies. He also noted the instability of the rostral characters. Thoma (1982), Thoma & Jezerinac (1982), Jezerinac (1983), and Jezerinac et al. (1995) continued to use subspecific status for *C. carinirostris.*

We agree with Faxon (1914), Ortmann (1931), and Bouchard (1976) that the carina of *C. carinirostris* is an elusive trait, frequently absent or greatly reduced. In our study of the species we found the population in the vicinity of the type locality exhibited the carina most strongly and frequently, and in this respect one could conclude that *C. carinirostris* is a local variation. When we examined the *bartonii* complex for other traits, we noted clear differences in chela structure between populations of the Atlantic and Mississippi drainages in Pennsylvania (especially in form I males). Thoma & Jezerinac (1982: 137) reported that *C. carinirostris* could be distinguished from *C. bartonii bartonii* (Fabricius, 1798) by the thickened and frequently concave rostral margins; an abruptly ending rostrum that forms a 90° angle with the base of the acumen; more strongly developed postorbital ridges; stronger development of the lateral impression and dorsal ridges of the chela; a slight development of a second row of 2 or 3 tubercles on the mesial margin of the palm; reduced gape between the dactyl and propodus; and an enlarged third tubercle on the mesial margin of the opposable propodus. Continued work throughout the ranges of the two forms (and the rest of the range of the subgenus) revealed that the combination of thickened rostral margins, an enlarged third (or fourth) tubercle on the mesial margin of the opposable finger of the propodus, moderate development of the lateral impression and dorsal ridges of the chela, and less than 2 full rows of palmar tubercles is sufficient to distinguish this species from the nominate species and all other taxa presently known in the *bartonii* complex. The partial second row of palmar tubercles (not consistently present), 90° angled rostral margins, strong postorbital ridges, and dactyl gape are useful in distinguishing this species individually from other species of the *bartonii* complex. Within the subgenus two forms (*C. b. cavatus* Hay, 1902, and *C. sciotensis* Rhoades, 1944) consistently display the development of a second row of tubercles on the mesial margin of the palm. *Cambarus sciotensis* displays a full complement of 5 or 6 tubercles in the second row. Thoma & Jezerinac (1982) reported that *C. b. cavatus* consistently had 3 to 5 tubercles in the second row of palmar tubercles, noninflated rostral margins, and a narrower areola (the narrower areola may relate to the burrowing habits of *C. b. cavatus*).

Principal component analysis of morphometric data for *C. carinirostris* and *C. b. bartonii* (Fig. 1) illustrates slight differences in body structure. The gape of the chela fingers, dactyl width, and areola width are the strongest loading variables (Table 1). Areola and dactyl width tend to be wider and chela gape narrower (Fig. 2) in *C. carinirostris.* No single body proportions are sufficient to separate the two taxa on a consistent basis. The most reliable character traits (using Form I males only) for consistently separating the two taxa are development of an enlarged third tubercle on the inner margin of the opposable propodus, lateral impression of the chela, and dorsal ridges on the chela fingers of *C. carinirostris* (Fig. 2). The northern form of *C. b. bartonii* (Atlantic drainage from the Potomac basin northward) lacks these chela characters altogether while the southern complex of *C. b. bartonii* lacks the lateral impression and thickened rostral margins. Some southern representatives of *C. b. bartonii* have an enlarged third tubercle on the opposable dactyl. This is accompanied by an enlarged first and fourth (occasionally third) tubercle on the opposable finger of the propodus, a characteristic lacking in *C. carinirostris.*

No intergrade populations have been found (using the characters we employed) between *C. carinirostris* and any other closely related taxon. For these reasons we elevate *C. carinirostris* to full species status. Important to note is that the above characteristics are most reliable in Form I males, preferably of a large size.

Evolution, zoogeography and associated variation.—Cambarus carinirostris is primarily an inhabitant of the still extant portions of the preglacial Pittsburgh River (Leverett 1902, Tight 1903) and (in part) the New River basin. This distribution is a reflection of the evolutionary history of the species. *Cambarus carinirostris* was most likely derived from an ancestral stock of the *bartonii* complex that inhabited the New River (Kanawha basin). This stock was intern derived from populations inhabiting the upper Tennessee River basin, in particular the Clinch and Powell systems. Hobbs (1969) concluded that the subgenus *Cambarus* originated in the Tennessee basin and entered the Kanawha River basin from a northward migrating member of the "*extraneus* group." We originally believed the subgenus *Cambarus* originated in the Kanawha basin (Jezerinac et al. 1995), but the recent discovery of a previously unknown archetypal *Cambarus* species (a description of this species and a discussion of its evolutionary significance is in development) in an isolated portion of what was once the Tennessee basin and now part of the Catawba River basin, confirms Hobbs' conclusion.

Upon entering the New River basin through interdigitating headwater streams, probably in the Burk's Garden area of Virginia, the ancestral *C. carinirostris* spread steadily through the system. *Cambarus carinirostris* probably was the first *Cambarus* to enter the upper New River system, thus having uninhibited dispersal opportunities. Access was gained to the preglacial Pittsburgh River basin in the headwaters of the Greenbrier River, again before other members of the subgenus *Cambarus.* No further dispersal occurred until postglacial times when *C. carinirostris* followed the retreating glaciers into the new Laurencian basin, where it established populations from the Gennesse River of New York in the east to the Grand River of Ohio in the west. Dispersal on the western edge of the range was thwarted by the presence of crayfish populations (presently assigned to *C. b. cavatus*) that occupied the preglacial Teays River system (Jezerinac 1983). *Cambarus b. cavatus* most likely entered the Teays basin via the Big Sandy River. The Teays River population was a stream dwelling species of the subgenus *Cambarus* that apparently had ecological preferences similar to *C. carinirostris.* In the Allegheny Plateau portion of

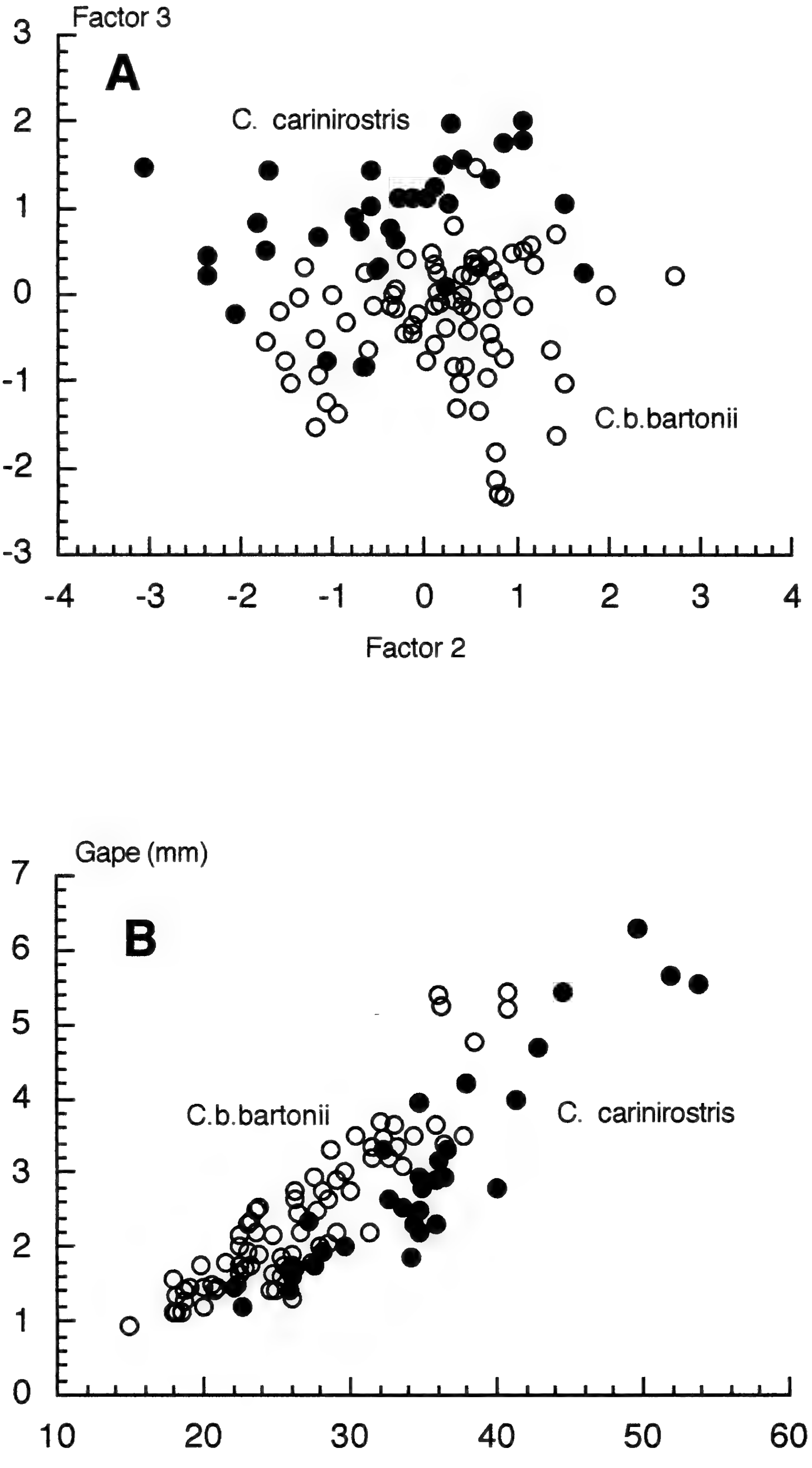

Fig. 1. A, Principal Component Analysis of *Cambarus carinirostris* (black circles, N = 33) and *C. bartonii bartonii* (open circles, N = 79) using Factors 2 and 3 (Table 1), Form I males only; B, Gape of chela fingers by length of chela for *C. carinirostris* (black circles, N = 33) and *C. b. bartonii* (open circles, N = 79), Form I males only.

Table 1.—Factor loadings for Principal Component Analysis of morphometric data of Form I male specimens of *C. b. bartonii* and *C. carinirostris.*

Measurement	Factor 2	Factor 3
Chela length	0.066	−0.044
Chela width	0.017	0.032
Chela depth	0.030	0.037
Gape of fingers	0.227	−0.326
Palm length	0.039	−0.031
Dactyl length	0.088	−0.042
Dactyl width	−0.095	0.394
Propodus finger length	0.045	−0.078
Propodus finger width	−0.076	0.120
Carapace length*	0.040	0.027
Carapace width	0.016	0.035
Areola length	0.110	0.023
Areola width	−0.667	−0.189

* Measurement includes rostrum.

the New-Kanawha River basin and those streams draining to the Ohio River downstream of the Sardis Col, *C. b. cavatus* prevailed. In the newly formed Ohio River, the two species are presently found on their respective preglacial sides of the Sardis Col, with neither having been able to advance into the other's range. To the north and to some degree to the east, the dispersal of *C. carinirostris* was inhibited by the presence of *C. b. bartonii.* It appears that the postglacial dispersal of *C. b. bartonii* (in the Atlantic slope drainage) was much more rapid than that of *C. carinirostris,* with *C. b. bartonii* effectively excluding *C. carinirostris* in those areas. Few opportunities existed for eastward dispersal of *C. carinirostris* in the Greenbrier, Monongahela, and Allegheny river basins because of physical barriers. Where potential stream piracies have been identified, no *C. carinirostris* could be found in Atlantic drainage streams. The ecological preferences of *C. carinirostris* and *C. b. bartonii* appear to be very similar.

Taxonomic distinction.—No other species in the subgenus *Cambarus* possesses the character combination of thickened ros-

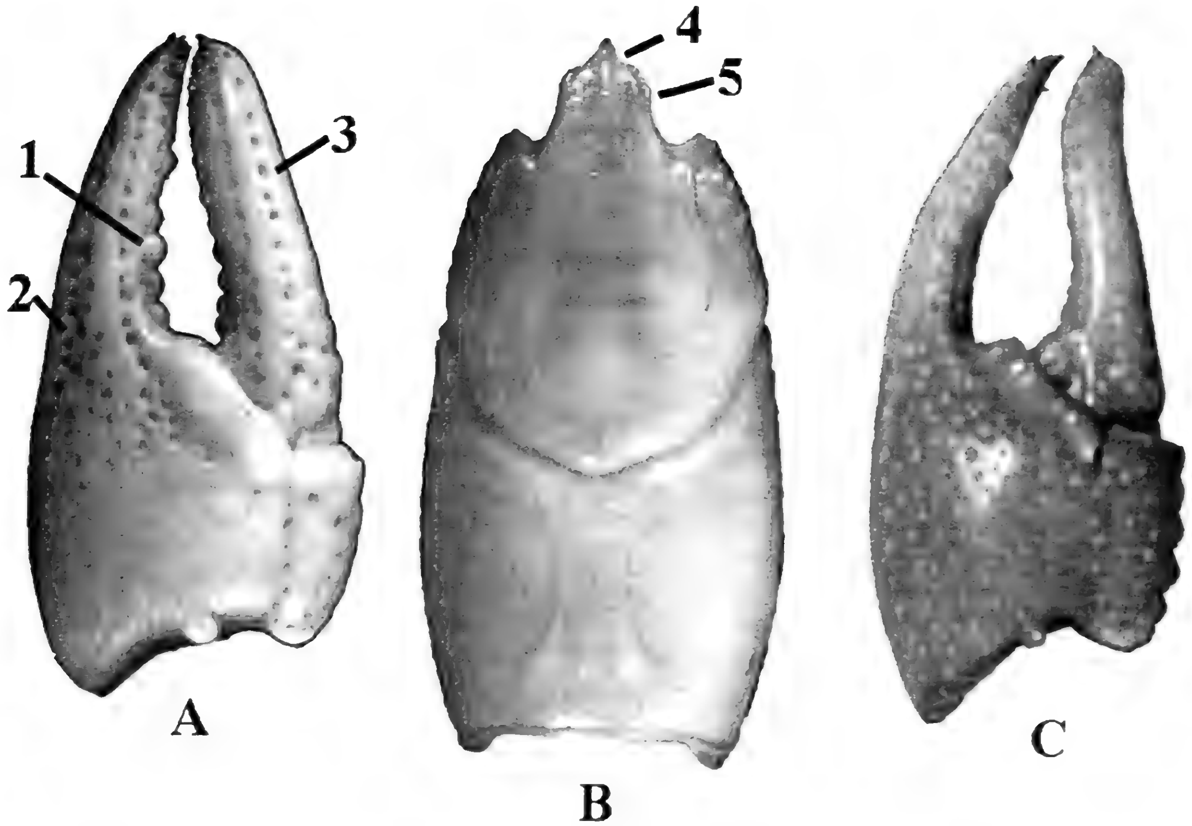

Fig. 2. A, Dorsal view of pereiopod I chela of *Cambarus carinirostris*; 1—enlarged third tubercle on mesial margin of immovable finger, 2—lateral impression, 3—dorsal ridge; B, Dorsal view of carapace of *Cambarus carinirostris*; 4—rostral carina, 5—thickened rostral margins; C, Dorsal view of pereiopod I chela of *Cambarus b. bartonii.*

tral margins, an enlarged third tubercle on the mesial margin of the opposable finger of the propodus, no enlarged tubercles on the mesial margin of the dactyl, moderate development of the lateral impression and dorsal ridges of the chela, and 1 row of palmar tubercles.

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Two new species of *Aegla* Leach (Crustacea: Decapoda: Anomura: Aeglidae) from southern Chile

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Abstract.—Two new species of the genus *Aegla* Leach from southern Chile are described. *Aegla cholchol,* new species, a medium to large sized spinulated aeglid, has the River Chol-Chol (Cautín Province) as its type locality. It is probably more related to *A. rostrata,* from subandean lakes at the Toltén and Valdivia River basins than to *A. bahamondei,* from the Tucapel River Basin on the western slope of the Nahuelbuta Coastal Cordillera. The other, *A. hueicollensis,* new species, a small to medium sized non-spinulated aeglid, has the River Pichihueicolla (Valdivia Province), on the western slope of the Pelada Coastal Cordillera, as its type-locality. *A. hueicollensis* is similar to *A. abtao* with which it shares more morphological attributes than with other non-spinulated aeglids of the same geographic region (i.e., *A. alacalufi, A. manni,* and *A. concepcionensis*).

Continental Chile is a long and narrow strip of land extending from Arica to Cape Horn, characterized by a series of climatic and biogeographical regions (see Di Castri et al. 1968). Three main topographical features, namely, the Andes Cordillera on the east, the Coastal Cordillera on the west, and the Central Valley between both ranges dominate the landscape from north to south (Börgel 1983). The central southern part of Chile, between the cities of Concepción (36°55′S) and Puerto Montt (41°28′S), harbors the highest diversity of aeglids and parastacids in the country (Bahamonde & López 1963). This diversity appears associated to the many rivers and lakes that constitute the drainage system of this area.

Aeglids are distributed along a stretch of about 2000 kilometers, from the Choapa River (31°38′S) in the north down to Madre de Dios Island (50°02′S) in the south (Bahamonde & López 1963, Jara & López 1981). At least ten species and two subspecies of *Aegla* (*A. concepcionensis* Schmitt, 1942a, *A. expansa* Jara, 1992, *A. pewenchae* Jara, 1994, *A. bahamondei* Jara, 1982, *A. spectabilis* Jara, 1986, *A. rostrata* Jara, 1977, *A. abtao* Schmitt, 1942a, *A. d. denticulata* Nicolet, 1845, *A. d. lacustris* Jara, 1989, *A. manni* Jara, 1980, *A. araucaniensis* Jara, 1980, and *A. alacalufi* Jara & López, 1981) have been described for the area between Concepción and Puerto Montt, several associated to the Coastal Cordillera. In fact, three, *A. concepcionensis, A. bahamondei,* and *A. manni,* are restricted to small basins on its western slope.

In this paper two new species of *Aegla,* both from localities in the Chilean Coastal Cordillera between Concepción and Puerto Montt, are described.

Specimens are deposited in the Crustacean Collection of the Instituto de Zoología, Universidad Austral de Chile (IZUA C), Valdivia, Chile. The size of the specimens was recorded as carapace length (CL), i.e., distance between rostral apex and posterior margin of cephalothorax.

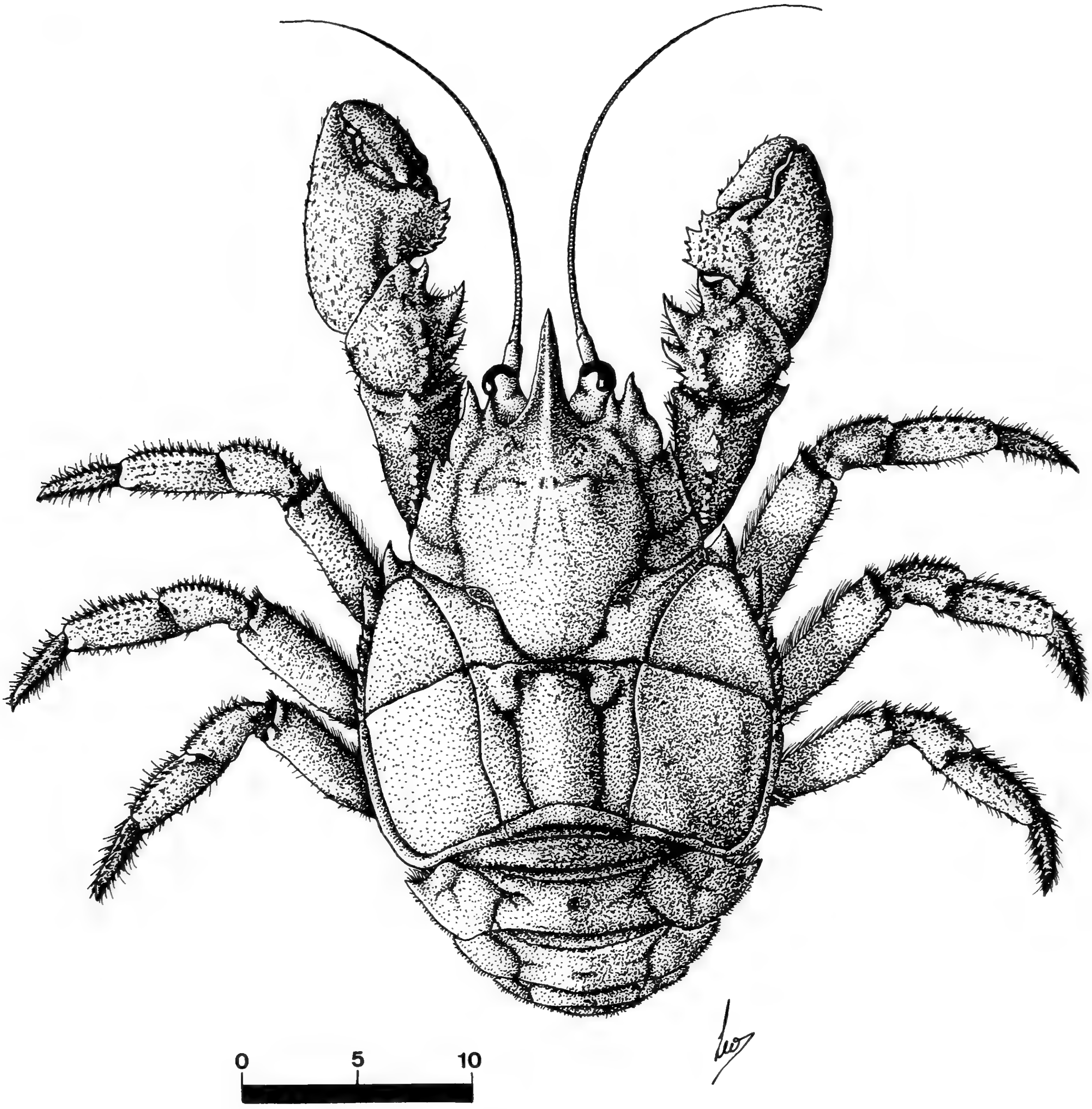

Fig. 1. *Aegla cholchol,* new species, male allotype, Chol-Chol River, IZUA C-328-B, dorsal view.

Aegla cholchol, new species

Figs. 1, 2a–i

Aegla bahamondei.—Jara, 1982:232 (in part), Fig. 1 (see Remarks).

Type locality.—Chol-Chol River, 100 m downriver from bridge in the town of Chol-Chol, 38°36′40″S, 72°51′05″W, 29 km NW of Temuco, Province of Cautín, Chile.

Type material.—Holotype: female (24.5 mm CL), C. G. Jara coll., 22 Dec 1982, IZUA C-328-B. Allotype: male (22.4 mm CL). Paratypes: 9 females (17.5–30.3 mm LC), 6 males (14.9–27.2 mm LC), same data as holotype.

Other material.—3 females (21.5–23.5 mm LC), Quepe River, 38°51′40″S, 72°37′02″W, C. A. Viviani coll., 24 Feb 1969, IZUA C-008-B. 3 males (24.3–26.1 mm LC), 2 females (23.8–25.6 mm LC), Quepe River at Boroa, 39°49′06″S, 72°53′02″W, C. G. Jara coll., 21 Dec 1982, IZUA C-297-B. 7 females (18.1–23.4 mm LC), Traiguén River, 38°14′45″S, 72°39′40″W, C. G. Jara & R. Navarro coll., 22 Dec 1982, IZUA C-316. 3 males (26.9–

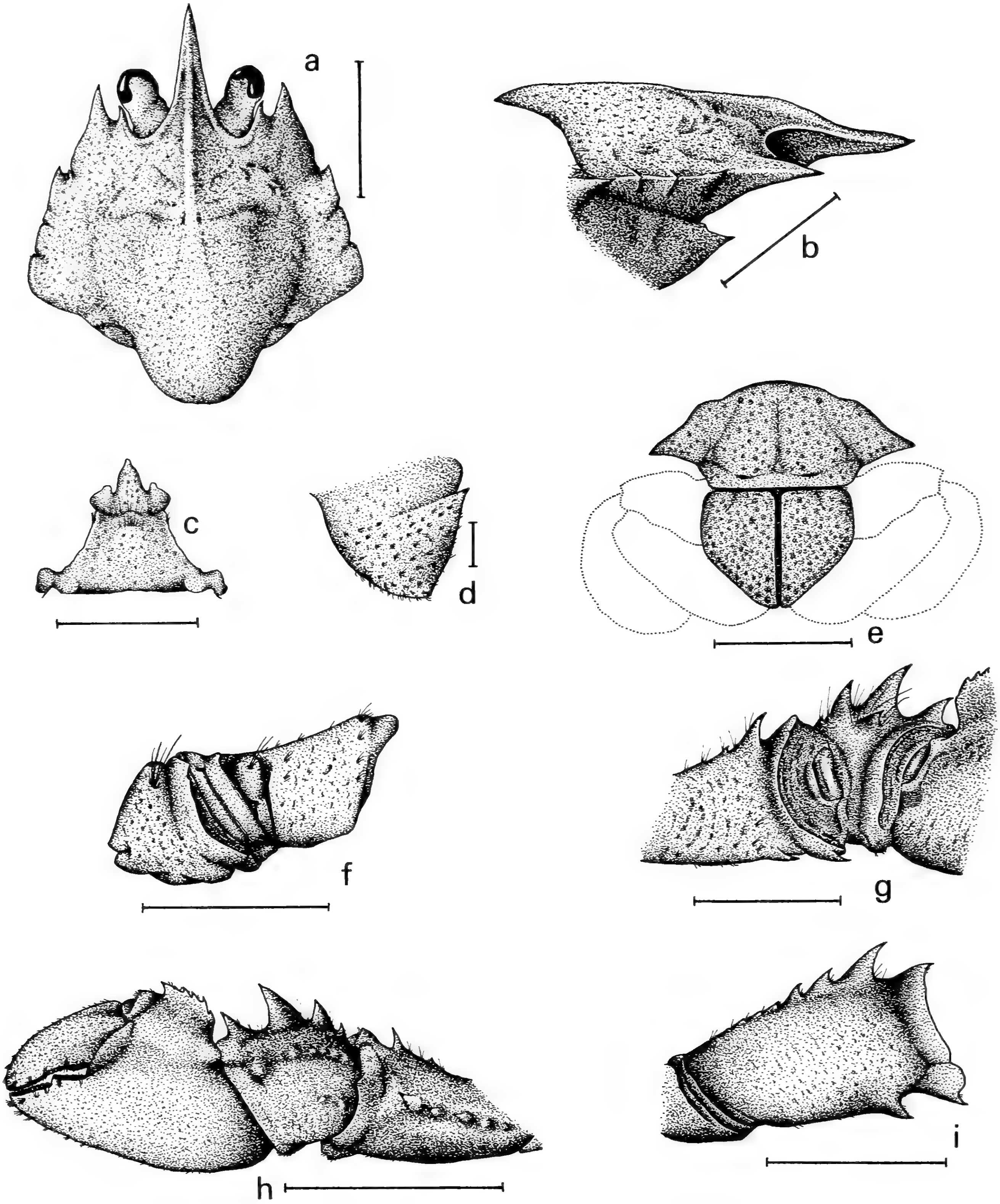

Fig. 2. *Aegla cholchol,* new species, male allotype, Chol-Chol River, IZUA C-328-B; a, anterior part of cephalothorax, dorsal view; b, anterior part of cephalothorax, lateral view; c, third and fourth sterna; d, second abdominal epimeron; e, telson plate; f, ischium of left cheliped, ventral view; g, carpus of left cheliped, ventral view; h, left cheliped, dorsal view; i, merus of cheliped, lateral view. Scales: d = 1 mm; a, b, c, e, f, g, i = 5 mm; h = 10 mm.

18.9 mm LC), 5 females (26.4–15.5 mm LC), Colpí River near Galvarino, 38°19′52″S, 72°47′10″W, C. G. Jara & R. Navarro coll., 22 Dec 1982, IZUA C-317-B. 2 males (19.3–29.3 mm LC), 6 females (23.6–26.0 mm LC), Quepe River, 38°51′40″S, 72°37′02″W, C. G. Jara & R. Navarro coll., 21 Dec 1982, IZUA C-320-A. 8 males (13.6–30.8 mm LC), 9 females (14.3–21.8 mm LC), Lumaco River at Lumaco, 38°09′46″S, 72°54′21″W, C. G. Jara & R. Navarro coll., 22 Dec 1982, IZUA C-321. 5 males (15.8–25.5 mm LC), 9 females (17.3–24.1 mm LC), Cautín River, Temuco, 38°44′30″S, 72°35′00″W, C. G. Jara & R. Navarro coll., 23 Dec 1982, IZUA C-322-B. 8 males (11.7–21.9 mm LC), 8 females (17.8–24.7 mm LC), Chol-Chol River near Galvarino, 38°36′40″S, 72°51′05″W, C. G. Jara & R. Navarro coll., 22 Dec 1982, IZUA C-324-C. 12 males (12.4–27.3 mm LC), 9 females (12.5–21.2 mm LC), Lumaco River at Pellahuén, 38°25′40″S, 72°56′00″W, C. G. Jara & R. Navarro coll., 22 Dec 1982, IZUA C-326-A. 1 juvenile (5.6 mm LC), Pichicautín River near Lumaco, 38°09′25″S, 72°54′15″W, T. Gonser coll., 16 Jan 1983, IZUA C-424.

Diagnosis.—Carapace slightly longer than wide, sparsely setose, moderately expanded at branchial level. Rostrum long, subtriangular, acute, styliform at distal half. Orbital spine prominent; extraorbital sinus wide, U-shaped. Anterolateral angle of first hepatic lobe spiniform. Anterior branchial margin subdenticulated; posterior finely serrated, dorsally upturned. Anterolateral angle of second abdominal epimeron spiniform. Fourth thoracic sternum with blunt medial tubercle, occasionally with 1 or 2 scales on frontal border. Telson divided. Adult males markedly heterochelous; females weakly so. Chelae robust; propodus inflated though dorso-ventrally flattened; dactylar lobe blunt; palmar crest subrectangular or arcuate, expanded, dentated; palmar lobe low, blunt, with scales only on frontal edge; medial scale largest; carpal lobe with prominent conical acute spine. Middorsal carpal ridge tubercles blunt.

Description.—Carapace slightly longer than wide, somewhat setose especially on branchiostegal and pterygostomial areas. Abdominal terga and middorsal line of merus of second to fourth pereopods also setose. Precervical portion narrower than postcervical; apex of acute pyramidal branchial lobe separated from margin of third hepatic lobe by wide notch. Rostrum long, acute, narrow, styliform, slightly expanded at its proximal ⅘th but conical and somewhat flattened on distal ⅕th, gently recurved. Rostral tip with acute scale. Rostral borders scarcely marginated, bearing minute scales along ⅘th of rostrum length, naked distally. Rostral carina prominent and scaly on proximal half of rostrum length, absent on distal half; scales small, buttonlike, in 2 subparallel rows. Epigastric prominences forming low, smooth, arcuate ridge, broadest just behind deepest point of orbital sinus. Protogastric prominences forming low tuberculiform area bearing short oblique row of tiny stud-like scales. Anterolateral lobe of carapace and hepatic lobes well defined; former elongated as straight conical spine reaching up to middle of adjacent cornea. Gastric area broad, posterior more protuberant. Anterolateral angle of first hepatic lobe spiniform; spine pointing straight forward. Branchial lobe pyramidal, elongated, acutely tipped, well detached from margin of third hepatic lobe and from anterolateral angle of anterior branchial area; with single irregular row of acute scales on outer border. Branchial margins moderately expanded; anterior subdenticulated, posterior finely serrated; denticles on anterior margin short, ill-defined, except anteriormost which is as large as branchial lobe; each denticle carrying 3 to 4 tiny acute scales, mingled with short stiff setae. Dorsum of anterior branchial area flat to slightly concave; posterior branchial area and adjacent marginal cardial area dome shaped; free border of posterior branchial area recurved and upturned. Anterolateral angle of second abdominal epimeron spiniform; spine apex scarcely detached from and at level with posterior branchial margin. Lateral angle of third to fifth abdominal epimera spiniform. Fourth thoracic sternum with blunt median tubercle, occasionally carrying 1 or 2 scales on frontal border. Telson longitudinally articulated. Chelae robust; propodus inflated though dorso-ventrally flattened. Dactylar lobe, at proximodorsal end of dactylus, blunt, with 1 to 4 tiny scales in a row along apex. Palmar crest subrectangular or arcuate, moderately expanded, border coarsely dentated; teeth subtriangular, recurved, apices point front-dorsally, especially the most distal. Palmar lobe, just behind dactylus-propodus joint, blunt, low, with acute scales only on frontal edge, its medial scale generally largest; frontal border of palmar crest overhanging palmar lobe, separated by deep notch. Carpal lobe prominent, massive, supporting robust, conical, acute, somewhat recurved spine. Dorsointernal border of carpus, behind carpal lobe, with neat row of 2 to 3 large conical acute spines, decreasing in size towards rear. Carpal ridge as arcuate row of blunt knob-like tubercles topped by minute scale and/or short setae. Carpus ventral face with robust conical spine. Merus of cheliped with row of blunt to spiniform tubercles, distalmost largest; dorsodistal angle of merus tuberculiform, bearing group of short stiff setae, and 2 to 4 scales of which median is largest.

Color.—Live, with dorsum of carapace and abdomen olive green; sternal surface and ventral face of pereopods creamy white. Dorsum of pereopods with alternating yellow green and dark green bars. Tip of largest spines pale yellow to creamy, darkening to green at their base. Joints of pereopods bright red, minutely spotted white. In alcohol, carapace and abdomen smoky tan to creamy white.

Geographic range (Fig. 3).—Found on the Chol-Chol River basin, from Lumaco to Chol-Chol; also in the Cautín River, in front of Temuco, and in the Quepe River near Quepe; all these are tributaries of the Imperial River basin which discharge into the Pacific Ocean, at Puerto Saavedra.

Habitat.—*Aegla cholchol* is found in medium sized rivers (order 2 to 3, after Strahler, 1957) with coarse gravel and boulder substrates where water current velocity varies between 0.1 to 0.7 m/sec. As a consequence of intensive agricultural activity, the fluvial environment of some stretches of the Chol-Chol River basin have undergone severe alterations; the riparian vegetation, mostly non-native species, is in a heterogeneous state of conservation. At these sites, specimens of *A. cholchol,* new species, were collected on coarse gravel to fine quartzitic micaceous sand, sharing the biotope with *A. spectabilis.*

Etymology.—The specific name is derived from the name of the type locality, as a latinized noun used in apposition. It is treated as indeclinable, for the purposes of Article 31b of the International Code of Zoological Nomenclature (International Trust for Zoological Nomenclature 1985).

Affinities.—*Aegla cholchol,* new species, *A. rostrata,* and *A. bahamondei* are similar in appearance but the new species is more similar to *A. rostrata* than to *A. bahamondei.* Common to the three species is a wide carapace with expanded branchial areas and denticulated or subdenticulated branchial borders; steep inward downward inclination of the branchiostegal surface; dorsum of anterior branchial area subconcave; well defined branchial lobe; protuberant gastric and cardiac areas with elevated middorsal line but non-keeled as in *A. denticulata*; acute first hepatic angle and anterolateral angle of carapace; ample front and orbital sinuses limited by acute orbital spines, one on the plane of the orbital border and one just below the former, usually not visible from above; narrow, slightly troughed, elongated and conically tipped rostrum. In each of the three species, the appendages, especially the chelipeds, present a basic morphological pattern with proper modifications. The new species differs from *A. rostrata* in hav-

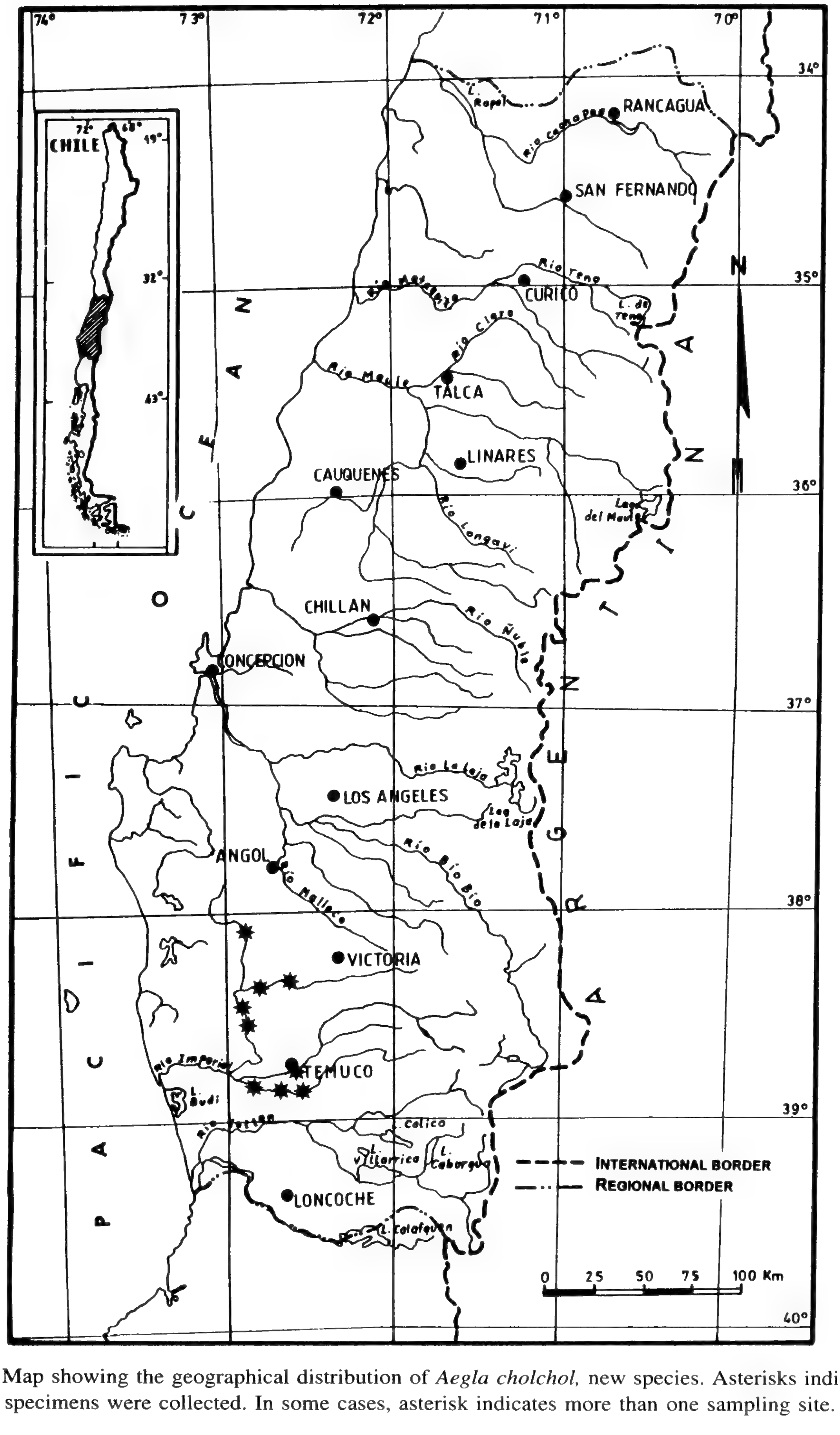

Fig. 3. Map showing the geographical distribution of *Aegla cholchol,* new species. Asterisks indicate localities where specimens were collected. In some cases, asterisk indicates more than one sampling site.

ing: blunt tubercles on the carpal ridge; dorsodistal angle of merus of chelipeds, second, and third pereopods blunt, or at most, with small round tubercle tipped by minute scales and/or setae; dactylar or palmar lobes not spiniform; edge of the anterior branchial area subdenticulated, teeth apressed non spine-like; fourth thoracic sternum with median tubercle. *Aegla cholchol,* new species, differs from *A. bahamondei* by having: epibranchial lobe monocuspidate; dactylar lobe low and blunt; protogastric prominences little protuberant; tubercle on fourth thoracic sternum acute but non-spiniform; posteroventral edge of merus of second to fourth pereopods smooth, non-denticulated; surface of carapace and chelae with few minute scales.

Remarks.—*A. cholchol,* new species, *A. rostrata,* and *A. bahamondei* share a series of complex characters. In particular, a tendency to have every protruding angle of the carapace, abdomen, and appendages, as a pointed conical tubercle or spine. However, the spines and spiniform tubercles are certainly more developed in *A. rostrata* than in *A. cholchol,* new species, and *A. bahamondei.* In the latter, the angles of the carapace are acute but never spiniform. Jara (1986:40) argued that "the trend toward profuse spinulation seems correlated with living in lentic environments." In this context, both *A. cholchol,* new species, and *A. bahamondei* are restricted to rivers while *A. rostrata* is found mostly in lakes. Jara (1982:237) indicated that "some specimens . . . found in Quepe River near Temuco . . . could prove to be conspecific with . . . [*A. bahamondei*]". On reexamination, those specimens proved to be *A. cholchol,* new species (IZUA C-008-B, formerly C-328).

Aegla hueicollensis, new species
Figs. 4, 5a–i

Type locality.— Pichihueicolla River, 0.5 km SE from its outlet into the Pacific Ocean (40°10′S, 73°40′W), on the western slope of Cordillera Pelada (Coastal Range), Province of Valdivia, Chile.

Type series.—Holotype: male (16.5 mm CL), 26 Jan 1983, C. G. Jara coll., IZUA C-245. Allotype: female (16.5 mm CL). Paratypes: 7 males (10.9–19.7 mm LC), 3 females (14.1–14.6 mm LC), 2 juveniles (7.3–7.7 mm LC), same data as holotype.

Other material.—3 males (10.7–14.1 mm LC), 3 females (19.3–20.7 mm LC), Chivería, Cordillera Pelada, 40°04′50″S, 73°10′50″W, R. Formas coll., 14 Jan 1971, IZUA C-025. 5 females (12.1–18.1 mm LC), Hueicolla River, 40°08′30″S, 73°37′42″W, R. Formas coll., 1974, IZUA C-026. 14 males (8.9–18.3 mm LC), 7 females (11.7–16.4 mm LC), Amargos Creek, Corral, Valdivia, 39°52′24″S, 72°26′25″W, C. G. Jara coll., 19 Mar 1974, IZUA C-042. 1 male (13.4 mm LC), 3 females (6.8–13.2 mm LC), Trainel River, Lago Huillinco, Chiloé, H. J. Wetzlar coll, 07 Oct 1975, IZUA C-131. 20 males (10.1–24.8 mm LC), 11 females (7.8–21.3 mm LC), San Carlos Creek, San Carlos, Corral, Valdivia, 39°51′40″S, 73°26′25″W, C. G. Jara coll, 20 Mar 1976, IZUA C-175. 9 males (11.7–24.2 mm LC), 4 females (18.3–19.9 mm LC), Chivería, Cordillera Pelada, 40°04′20″S, 73°10′30″W, R. P. Schlatter coll., 21 Jan 1977, IZUA C-184. 3 males, (12.3–18.3 mm LC), 9 females (10.9–17.6 mm LC), Hueicolla River, 40°08′30″S, 73°39′05″W, R. P. Schlatter coll., 22 Jan 1977, IZUA C-185. 18 males (10.5–16.8 mm LC), 8 females (10.2–14.6 mm LC), Manzano River, Todos los Santos Lake, Llanquihue, 41°07′20″S, 72°24′50″W, G. Milhe coll., 26 Apr 1974, IZUA C-196. 3 males (11.3–14.6 mm LC), 4 females (11.3–15.9 mm LC), Refugio River, Chiloé, R. P. Schlatter coll., 11 Oct 1977, IZUA C-197. 2 males (8.3–23.6 mm LC), 1 female (26.4 mm LC), Roblental Creek, eastern slope of Cordillera Pelada, 40°16′S, 73°12′W, C. G. Jara coll., 12 Feb 1978, IZUA C-206. 1 male (14.8 mm LC), 3 females (15.7–21.4 mm LC), Pichihueicolla River, 40°09′40″S, 73°39′50″W, C. G. Jara

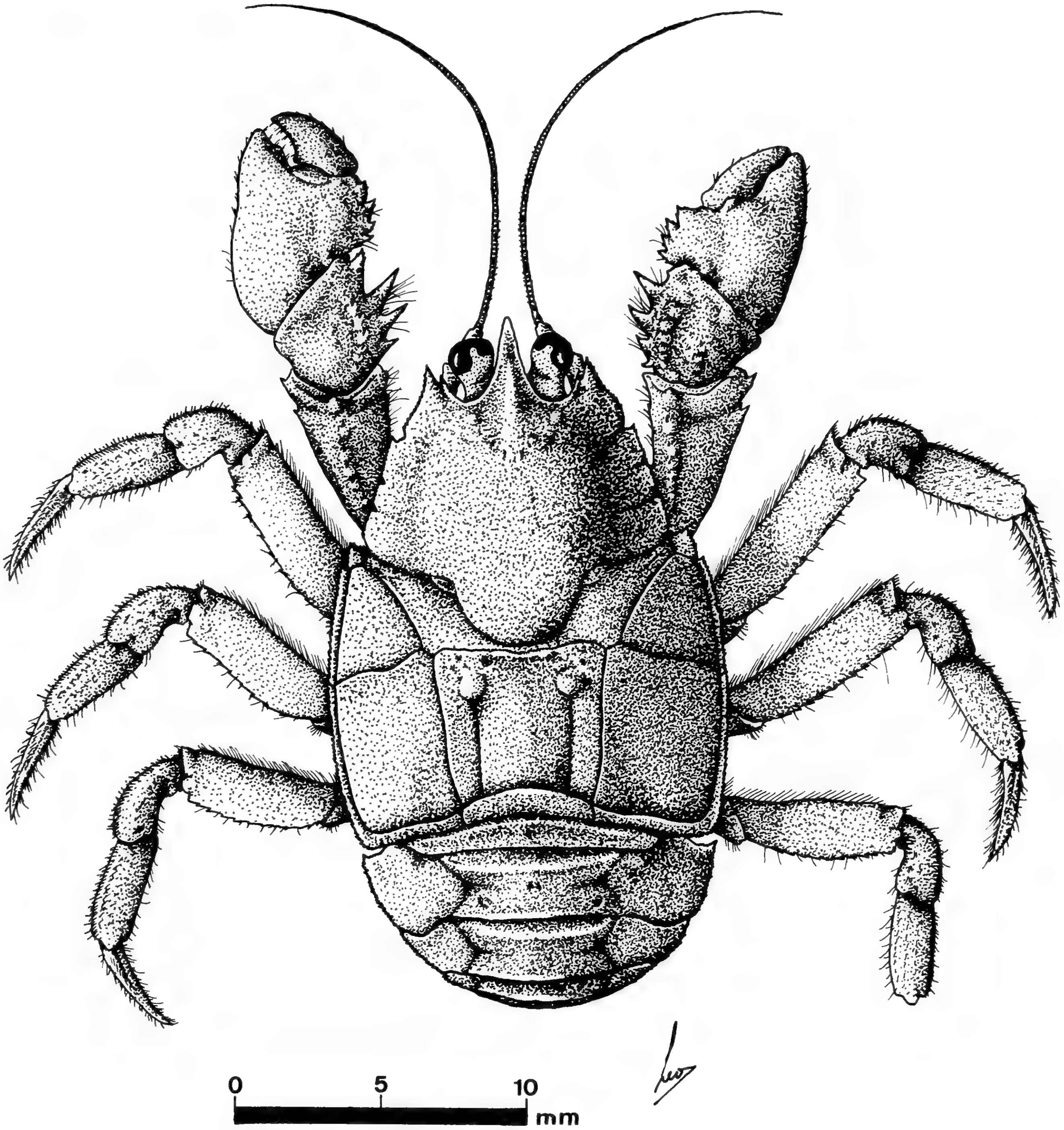

Fig. 4. *Aegla hueicollensis,* new species, male holotype, Pichihueicolla River, IZUA C-245, dorsal view.

coll., 26 Jan 1982, IZUA C-246. 27 males (4.5–15.9 mm LC), 22 females (7.9–17.6 mm LC), Hueicolla River, 40°09′07″S, 73°38′25″W, C. G. Jara coll., 27 Jan 1982, IZUA C-247. 5 males (10.3–19.7 mm LC), 9 females (10.1–22.1 mm LC), Chaihuín River, 40°05′07″S, 73°21′51″W, C. G. Jara coll., 15 Feb 1984, IZUA C-363. 10 males (4.2–27.2 mm LC), 22 females (6.9–26.3 mm LC), Colún River, 40°02′31″S, 73°31′26″W, C. G. Jara coll., 15 Feb 1984, IZUA C-364. 6 males (7.0–17.2 mm LC), 6 females (8.5–15.1 mm LC), Hueicolla River, 40°08′30″S, 73°31′38″W, H. F. Jara coll, 07 Feb 1992, IZUA C-507. 6 males (9.6–16.7 mm LC), 1 female (13.9 mm LC), Hueicolla River, 40°08′27″S, 73°30′39″W, H. F. Jara coll, 08 Feb 1992, IZUA C-508.

Diagnosis.—Carapace ovoidal, not expanded at branchial areas. Epibranchial lobe pyramidal, acute, borders scaly. Ros-

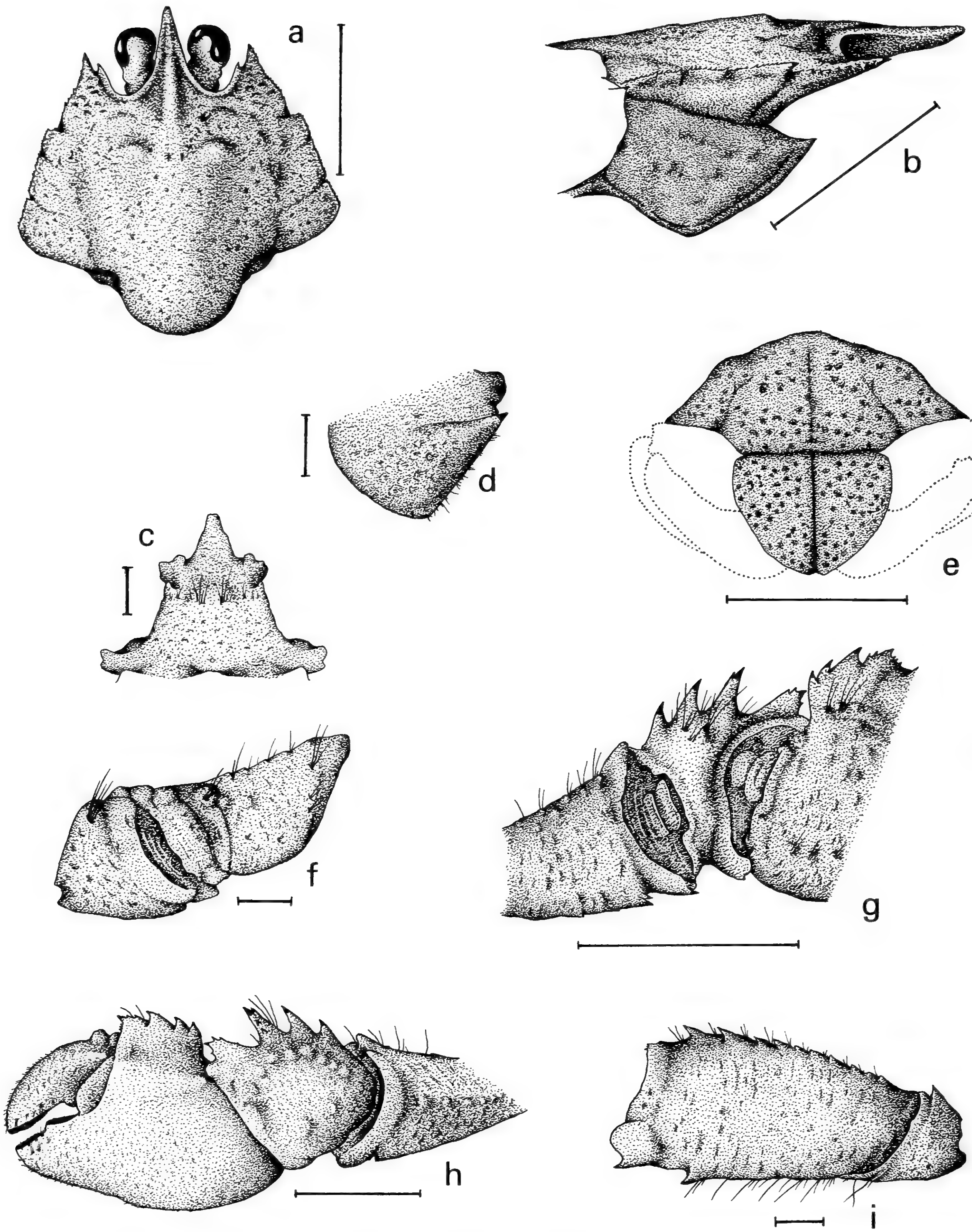

Fig. 5. *Aegla hueicollensis,* new species, male holotype Pichihueicolla River, IZUA C-245; a, anterior part of cephalothorax, dorsal view; b, anterior part of cephalothorax, lateral view; c, third and fourth sterna; d, second abdominal epimeron; e, telson plate; f, ischium of left cheliped, ventral view; g, carpus of left cheliped, ventral view; h, left cheliped, dorsal view; i, merus of cheliped, lateral view. Scales: c, d, f, i = 1 mm; a, b, e, g, h = 5 mm.

trum short, wide at base, neatly triangular, both sides of low-profiled carina barely troughed, conical at apex, acute. First hepatic lobe blunt. Orbital and extraorbital sinus present. Branchial margin smooth, slightly nodulated. Second abdominal epimeron acute but not spiniform. Telson divided. Fourth thoracic sternum smooth. Male chelae elongated, pyriform, inflated at propodus; palmar crest flabelliform, subrectangular, dentate; dactylar lobe subspiniform; carpal lobe spiniform, apex markedly displaced towards distal end of article, frontal edge with row of tufts of short setae mingled with scales; tubercles of carpal ridge blunt, low, topped by transversal row of scales and setae. Tubercles on dorsal edge of merus of chelipeds blunt, tipped by 2 to 4 scales roughly ordered in transversal oblique row. Ventroexternal border of ischium, ventral face of carpus, and ventral borders of chelae with tufts of long setae in row.

Description.—Carapace surface finely punctated, each pit with a minute scale and 1 or 2 short stiff setae; highest density of setae on abdominal epimera. Precervical carapace almost as wide as postcervical. Epibranchial lobe pyramidal, acute, its edges lined with short acute stout scales; similar scales along outer borders of carapace except for posterior border and external half of orbital sinus. Rostrum short, wide at base, neatly triangular, barely troughed; low-profiled carina merges into rostrum body at proximal half; rostral apex conical, with stout acute apical scale encircled at base by 3 to 4 minor scales; dorsum of carina with double row of tiny scales proximally, and single unordered row distally; ventral carina not particularly prominent, its deepest point at base. Epigastric prominences nodular, blunt, topped with 3 to 4 scales in transverse row; protogastric prominences barely discernible, marked by small field of button-like scales mingled with stiff setae. Anterolateral lobe of carapace laterally expanded, flattened proximally, its external border slightly sinuose; anterolateral angle of carapace short, acute, its apex reaching up to proximal third of adjacent cornea. Orbital sinus wide, delimited by an inconstantly present orbital spine; extraorbital sinus variable in depth and width, generally narrowly V-shaped. First hepatic lobe blunt, well separated from base of anterolateral lobe; second and third lobes scarcely defined, separated by shallow notches interrupting marginal row of scales. Branchial margin narrow, smooth, slightly nodulated; posterior slightly upturned. Areola broad, convex, elevated over remaining cardial area. Thoracic sterna flat; fourth sternum with frontal fringe of long stiff setae; seldom with low, blunt, median tubercle, carrying 1 or 2 scales. Anterolateral angle of second abdominal epimeron acute, dorsum subcarinate behind anterolateral angle; lateroventral face of epimeron deeply concave, profusely covered by short stiff setae; free ventral border with dense row of long plumose setae, also present over posterior branchiostegal surface, edge of remaining abdominal epimera, and borders of uropods and telson. Telson longitudinally articulated.

Males heterochelous; left hand largest. Chelae robust but not particularly massive, subovoidal in outline, surface microtuberculate; each tubercle carrying a minute acute scale and 2 short stiff microsetae, most evident on distal half of propodus and dactylus. Molar process well developed on cutting edge of fixed finger and dactylus of left chela but negligible or absent on right one. Dorsum of dactylus with robust spiniform lobe on proximal end. Ventral face of chelae with prominent ridge along ventroexternal border of propodus, marked by row of pits and tufts of long setae; pits more numerous along dactylus and fixed finger. Base of palmar crest on ventral side of chelae parallel to short tuberculate ridge with large pits and tufts of setae. Central part of ventral face of chelae broadly convex, forming longitudinal ridge between center of propodus-carpus joint and distalmost dactylus-propodus joint, marked by large pits and setae. Palmar crest prominent, thick, its border denticulated with scattered small acute scales between contiguous larger denticles. Distal end of palmar crest separated from predactylar lobe of carpus by almost right-angled deep notch; predactylar lobe elevated, its free border with irregular row of short acute scales; largest scale at anterodorsal angle. Carpus robust, with two dorsal ridges; outermost lower, distinguishable as slightly arcuate row of broad low tubercles; apex of tubercles with row of 3 to 6 short stiff setae mingled with minute scales; innermost prominent, formed by row of blunt tubercles topped by tranverse row of 3 to 5 acute scales and setae. Carpal lobe spiniform, asymetrically subtriangular, apex leveled with frontal border of same lobe. Inner border of carpus with row of 3 large spines proximally decreasing in size. Dorsum of anteriormost spine with 2 to 3 scales or setae protruding from large pits in a row along spine axis. Same arrangement on minor spines or at least, 1 pit and setae present. Ventral surface of carpus with robust conical spine; between it and inner border of carpus several thick, long, simple setae, uneven in size. Dorsal edge of merus with row of subacute tubercles tipped by 1 or 2 scales, 3 or 4 on distalmost tubercle; frontal side of tubercles with tufts of long simple setae; frontodorsal angle blunt, thick, little prominent, with patch of short stiff setae and scales; ventral borders with row of tubercles tipped with scale and/or seta; distal angles as short conical spine. Dorsal edge of merus of second, third and fourth pereopods with fringe of long plumose setae covering minute spiniform tubercles; carpus, propodus and dactylus with fringe of short stiff simple setae. Posteroventral edge of merus scabrous, subserrated, with narrow band of setae and scales.

Color.—Not observed live. In alcohol, carapace, abdomen, and appendages uniformly smoky-tan to creamy white.

Geographic range (Fig. 6). Small streams and creeks flowing from east to west on the western slope of Cordillera Pelada (Coastal Range between Corral to the north and the outlet of the Bueno River to the south). Specimens collected are from: Amargos Creek (Corral, Valdivia), Colún, Chaihuín, Hueicolla, and Pichihueicolla rivers. Also found in Manzano River, at Todos Los Santos Lake, in the Andean district of the Llanquihue province.

Habitat.—Small rivers and fast flowing streams on moderate to steep slopes, covered or surrounded by cold-temperate Valdivian rain forest. Specimens are found among pebbles and boulders on the stream bottom, at sites where a heterogeneous mass of vegetal detritus accumulates serving as shelter for the crabs.

Etymology.—The specific name derives from Hueicolla, a small town on the Pacific coast about 40 km to the south from Corral, where the rivers Hueicolla and Pichihueicolla discharge into the Pacific Ocean.

Affinities.—Aegla hueicollensis, new species, shares a series of features with other species of *Aegla.* In general, the new species closely resembles *A. abtao.* Several morphological similarities suggest a close ancestral relationship between the two. *A. hueicollensis,* new species, also displays morphological similarity to *A. alacalufi.* Both share the almond-shaped outline of the carapace, the short triangular acute rostrum, and the pronounced distalward displacement of the apex of the carpal lobe. However, *A. alacalufi* has an undivided telson plate, and lacks minute scales on the carapace surface. The new species also shares features with *A. manni* and *A. neuquensis* Schmitt, 1942b, such as: the irregular row of scales and/or setae along the dorsal axis of the larger spines on the inner border of carpus of chelipeds and the transverse row of scales on the tubercles of the carpal ridge of chelae. The new species differs from *A. manni* in having the rostral carina and rostral margins scaly; from *A. neuquensis* by having the anterolateral angle of second abdominal epimeron subspinose. The low, somewhat concave, profile of the rostral carina and the protuberant gastric

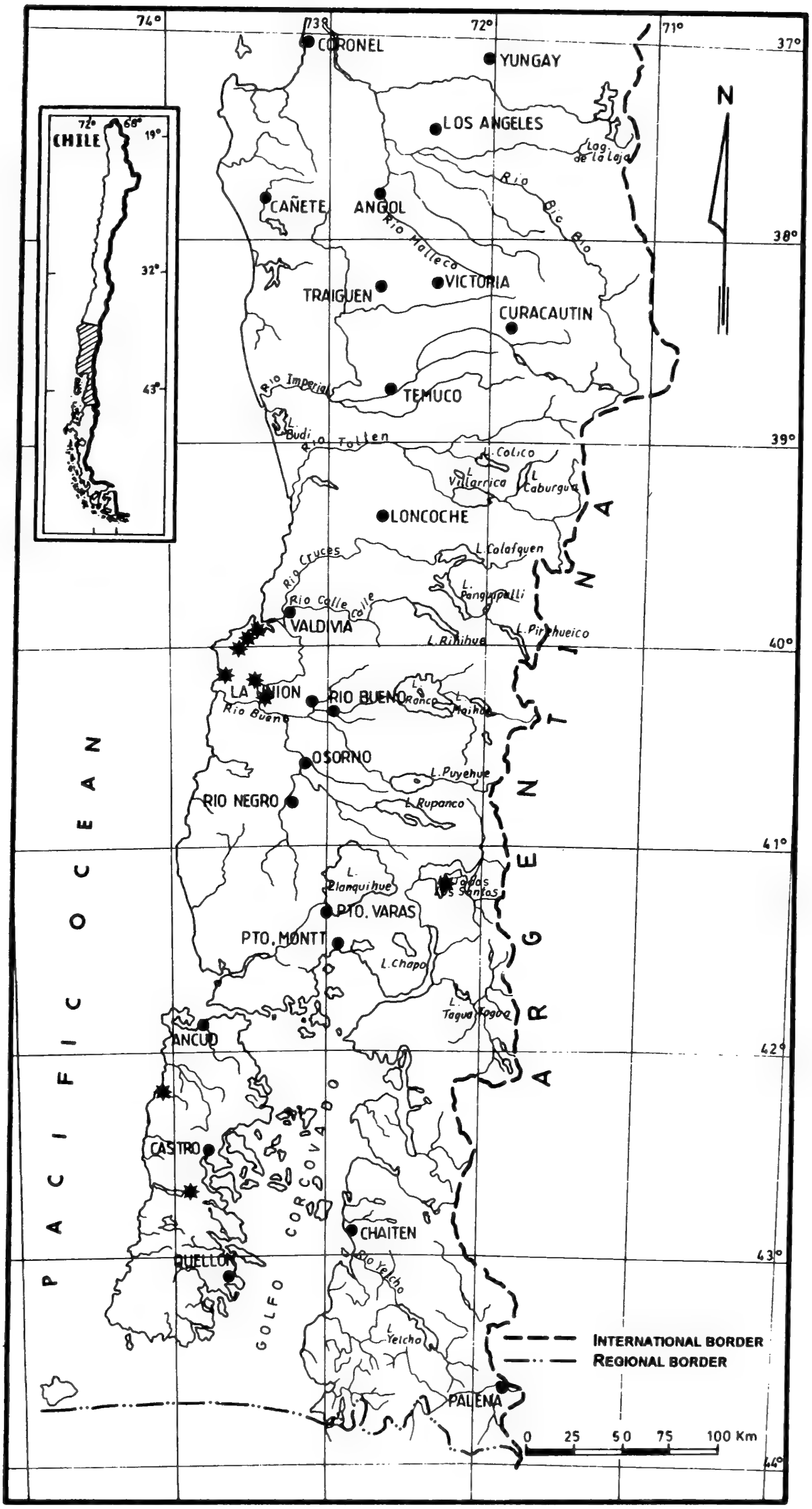

Fig. 6. Map showing the geographical distribution of *Aegla hueicollensis*, new species. Asterisks indicate localities where specimens were collected. In some cases, asterisk indicates more than one sampling site.

area of *A. hueicollensis,* new species, resemble those of *A. concepcionensis.* These similarities led Schmitt (1942b:504) to report specimens of *Aegla* from Corral (northern limit of Cordillera Pelada) as *A. concepcionensis.* Similarly, Haig (1955: 504) classified as *A. concepcionensis* specimens from Ancud (230 km to the south of Corral), Chiloé Island. To determine if these specimens are conspecific with *A. hueicollensis,* new species, they would have to be re-examined.

Remarks.—The geographic range of *A. hueicollensis,* new species, includes a series of localities on the western slope of the Coastal Cordillera and one locality (Manzano River) on the western slope of the Andes Cordillera, about 100 km southeast of the type locality. There is no hydrological connection between these areas at present. This fact leads to the assumption that, in the past, the geographic range of the new species must have been broader, enclosing localities on the intervening territory between the Andean and the Coastal ranges. Connected to this is the fact that southern Chile, from paralell 38°S southward, was severely affected by Quaternary glaciations. Illies (1960) found evidence that during glaciations the ice-sheet front advanced west from the Andean highlands completely covering the Central Valley; the ice front pushed upon the eastern slope of the Coastal Range but never surmounted it. The western slope of the Coastal Range which was never completely covered by ice (Illies 1960) could have served as a refugial area for *A. hueicollensis,* new species. Its presence in the small Manzano River basin, amid the Andean massif, presumes that somehow the site was unaffected by destructive glacial effects, thus preserving the preexisting population.

Acknowledgments

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The Hawaiian parthenopid crabs of the genera *Garthambrus* Ng, 1996, and *Dairoides* Stebbing, 1920 (Crustacea: Decapoda: Brachyura)

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Abstract.—The taxonomy of four species of deep-water parthenopid crabs, *Garthambrus stellata* (Rathbun, 1906), *G. lacunosa* (Rathbun, 1906), *G. complanata* (Rathbun, 1906) and *Dairoides kusei* (Sakai, 1938) from Hawaii is treated. *Dairoides kusei* is recorded from Hawaii for the first time. The identities of *G. stellata, G. lacunosa* and *G. complanata* are clarified, with detailed comparisons and figures provided. Despite earlier reports, there are no intermediates between these three species. A key to the genus *Garthambrus* is provided.

Rathbun (1906), in her treatment of the Hawaiian Brachyura, had originally recognized eight parthenopid species from these islands. One species, *Harrovia truncata* Rathbun, 1906, was transferred to a separate genus (*Cyrtocarcinus* Ng & Chia, 1994) in the Xanthidae by Ng & Chia (1994). Another species, *Parthenope* (*Platylambrus*) *stellata* Rathbun, 1906, was originally established with three subspecies, *P.* (*P.*) *stellata stellata, P.* (*P.*) *stellata lacunosa* Rathbun, 1906, and *P.* (*P.*) *stellata complanata* Rathbun, 1906. Garth (1993) reappraised the validity of these three taxa and regarded them as distinct species. He briefly commented that the features used by Rathbun (1906) to separate the three varieties were good species characters. Although Garth examined the type series of all three taxa, he did not comment much about them or figure any of the types. This despite the fact that one taxon, *P.* (*P.*) *complanata,* had never been figured before. Nor did he comment on specimens which Rathbun (1906) had regarded as being intermediate between the three species. In describing a new species (*Parthenope cidaris*) from Australia, Garth & Davie (1995) provided photographs of the types of *P.* (*P.*) *stellata, P.* (*P.*) *lacunosa* and *P.* (*P.*) *complanata* but did not make any additional comments other than again stating briefly that all three taxa were good species.

Sakai (1938, 1976) had commented that *P.* (*P.*) *lacunosa* (as a subspecies) was a junior synonym of *Lambrus* (*Parthenopoides*) *pteromerus* Ortmann, 1893, a species which he transferred to the genus *Tutankhamen* Rathbun, 1925. Garth (1993), however, disagreed, commenting that *P.* (*P.*) *lacunosa* lacked the lamellar ridges lining the afferent channels on the carapace found on *Tutankhamen cristatipes* (A. Milne Edwards, 1880), the type and only species of the genus. On the basis of Garth's (1993) redescription of *P.* (*P.*) *stellata* and his comments on *P.* (*P.*) *lacunosa* and *P.* (*P.*) *complanata,* Ng (1996) subsequently transferred all three species to the genus *Garthambrus* Ng, 1996.

Nine species of Parthenopidae are currently known from the Hawaiian islands, *Garthambrus stellata* (Rathbun, 1906), *G. lacunosa* (Rathbun, 1906), *G. complanata* (Rathbun, 1906), *Platylambrus nummifera* (Rathbun, 1906), *Rhinolambrus lamelligera*

(White, 1847), *Aulacolambrus hoplonotus* (Adams & White, 1848), *Aulacolambrus whitei* (A. Milne Edwards, 1878), *Pseudolambrus calappoides* (Adams & White, 1848), and *Daldorfia horrida* (Linnaeus, 1758). The generic classification used here follows that proposed by Ng & Rodríguez (1986) and Ng (1996).

The present paper reports on the deep-water Parthenopidae from Hawaii primarily based on material deposited in the Bernice P. Bishop Museum, Honolulu; and National Museum of Natural History, Smithsonian Institution, Washington, D.C. *Garthambrus stellata, G. lacunosa* and *G. complanata* are rediagnosed, and detailed figures of their diagnostic characters provided for the first time. Using new characters identified in this study, the "intermediates" reported by Rathbun (1906) can easily be assigned to the three species. A key to the genus *Garthambrus* is provided. The unusual deep-water species, *Dairoides kusei* (Sakai, 1938), previously known only from Japan, is also reported from Hawaii for the first time.

The terms used here essentially follow those used by Garth (1958, 1993). The abbreviations cw and cl are for the carapace width and length, and G1 and G2 are for the male first and second pleopods respectively. Specimens are deposited in the Bernice P. Bishop Museum, Honolulu (BPBM); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Nationaal Naturhistorish Museum, Leiden (ex Rijksmuseum van Natuurlijke Historie, RMNH); and the Zoological Reference Collection, National University of Singapore (ZRC).

Systematic Account

Genus *Garthambrus* Ng, 1996

Garthambrus Ng, 1996: 156 (type species: *Garthambrus posidon* Ng, 1996, by original designation).

Diagnosis.—Carapace subtriangular in shape, broader than long; angle between antero- and posterolateral margins strongly produced; dorsal surfaces granulose, spinose or rugose; progastric, mesogastric, metagastric, mesobranchial, metabranchial, cardiac and intestinal regions strongly inflated; gastric and branchial regions separated by deep grooves. Median lobe of rostrum prominent, sub-spatulate, deflexed downwards. Hepatic region and margin separated from anterolateral margin by cleft, notch or large tubercle. Posterolateral margin and metabranchial regions without long or prominent teeth or spines. Chelipeds at least 2.5 times carapace length. G1 relatively stout, not armed with long spines or stiff hairs. Distal segment of G2 elongate, subequal to or distinctly longer than basal segment (modified from Ng 1996: 156).

Remarks.—Ng (1996) removed a number of species previously assigned to *Parthenope, Platylambrus* or *Parthenope* (*Platylambrus*) to a separate genus which he characterised by their triangular carapaces and long distal segment of the second male pleopod. All eight species (see key) currently placed in *Garthambrus* are essentially deep-water species.

One unusual species which requires mention is the Japanese species *Parthenope pteromerus* (Ortmann, 1893). It is very similar in appearance to *G. lacunosa,* which Sakai (1976) synonymised under *P. pteromerus.* Sakai (1976) also transferred *P. pteromerus* to the genus *Tutankhamen* Rathbun, 1925, arguing that the afferent respiratory channels on its carapace are lined with lamellar ridges. Garth (1993) refuted this synonymy because *G. lacunosa* and all *Garthambrus* species do not have such lamellar ridges. Subsequently, Ng (1996) suggested that *P. pteromerus* was not assignable to *Tutankhamen,* and probably belonged in a separate genus. While *P. pteromerus* resembles many *Garthambrus* species superficially, the possession of lamellar ridges lining the afferent respiratory channels on its carapace argues against its inclusion in *Garthambrus* as presently defined. *Parthenope pteromerus* is also a relatively shallow-water species compared to known species of *Garthambrus* (unpublished data).

Key to *Garthambrus* species

1a. Carapace and legs covered with numerous long, sharp spines; margin of branchial region with deep, distinct cleft . . . . *G. mironovoi*
1b. Carapace and legs not covered with numerous long, sharp spines; margin of branchial region entire or almost so . . 2
2a. Granules on branchial, cardiac and gastric regions of carapace fused to various degrees forming distinct granular patches . . . . *G. allisoni*
2b. Carapace dorsal surface almost smooth or if granules present, those on branchial, cardiac and gastric regions never distinctly fused 3
3a. Margins of ambulatory meri distinctly cristate . . . . *G. lacunosa*
3b. Margins of ambulatory meri not distinctly cristate, but lined with spines, teeth or granules 4
4a. Carapace and cheliped surfaces without pits or lacunae . . . . *G. complanata*
4b. Carapace and cheliped surfaces with distinct pits and/or lacunae 5
5a. Margins of ambulatory meri with prominent rounded granules 6
5b. Margins of ambulatory meri with uneven granules, tubercles or small spines 7
6a. Median protuberance of rostrum large, margins of ambulatory propodi and carpi distinctly granulated . . . . . . *G. poupini*
6b. Median protuberance of rostrum small, margins of ambulatory propodi and carpi smooth, unarmed . . . . *G. posidon*
7a. Dorsal surface of carapace densely granulated all over; metabranchial regions strongly swollen, appears peak-like from frontal view . . . . *G. stellata*
7b. Dorsal surface of carapace with rugae and granules but never densely packed; metabranchial regions high but not very swollen, not peak-like from frontal view . . . . *G. cidaris*

Garthambrus stellata (Rathbun, 1906)
(Figs. 1A–D, 6A–C)

Parthenope (*Platylambrus*) *stellata* Rathbun, 1906:884 (part), pl. 15 Figs. 1, 2.—Garth, 1993:786, Figs. 3, 4.
Parthenope (*Platylambrus*) *stellatus.*—Serène, 1968:60.
Parthenope stellata.—Garth & Davie, 1995:225, Fig. 2B.
Garthambrus stellata.—Ng, 1996:158.

Material examined.—Holotype, 1 male, cw 48.6 mm, cl 32.8 mm (USNM 29839), south coast of Oahu Island, Hawaii, 435–461 m, station 3811, coll. Albatross Expedition, 27 Mar 1902. Paratype, 1 male, cw 32.9 mm, cl 23.1 mm (USNM 29840), Kawaihae, Hawaii Island, Hawaii, 20°01′45″N 155°54′15″W, 269–362 m, station 4045, 8 hemp tangles gear, coll. Albatross Expedition, 11 Jul 1902. Others—1 female (USNM 239148), Pearl Harbor, Mamala Bay, Oahu Island, Hawaii, disposal site, 21°16′48″N 157°56′30″W, 366 m, coll. R/V Hurl, 30 Apr 1983. 1 male, cw 70.2 mm, cl 45.6 mm (ZRC 1997.441), Off Pearl Harbor, Oahu Island, Hawaii, station 82-105, in dredge spoil site, on sediment bottom in vicinty of outcrop, 366 m, coll. R/V Hurl, Makali'i Dive, D. M. Devaney & B. Bartko, 1 Sep 1982. 1 female (carapace only) (BPBM 1978.417), Off Makupuu Point, Molokai Channel, Hawaii, 12 km straight cast, 21°02′N 157°32′W, coll. Valkryrien, Capt. S. Rayner, 20 May 1967. 1 male, ca. cw 65.5 mm, cl 43.4 mm (left edge of carapace broken) (BPBM 1976.259), Entrance to Pearl Harbor, Oahu Island, Hawaii, 2.5 km off buoy 1,338 m, coll. in shrimp traps, Easy Rider, E. H. Chave, 27 Sep 1976. 2 females, cw 21.6 mm, cl 16.5 mm, ca. cw 16.0 mm, cl 12.5 mm (right side of carapace crushed) (BPBM 5508), Oahu Island, 1.9 km off Kahala, Hawaii, 46 m, coll. Brock, 14 Apr 1949.

Diagnosis.—Surface of carapace densely and granulated uniformly throughout, including grooves and depressions; metabranchial regions strongly swollen, appearing

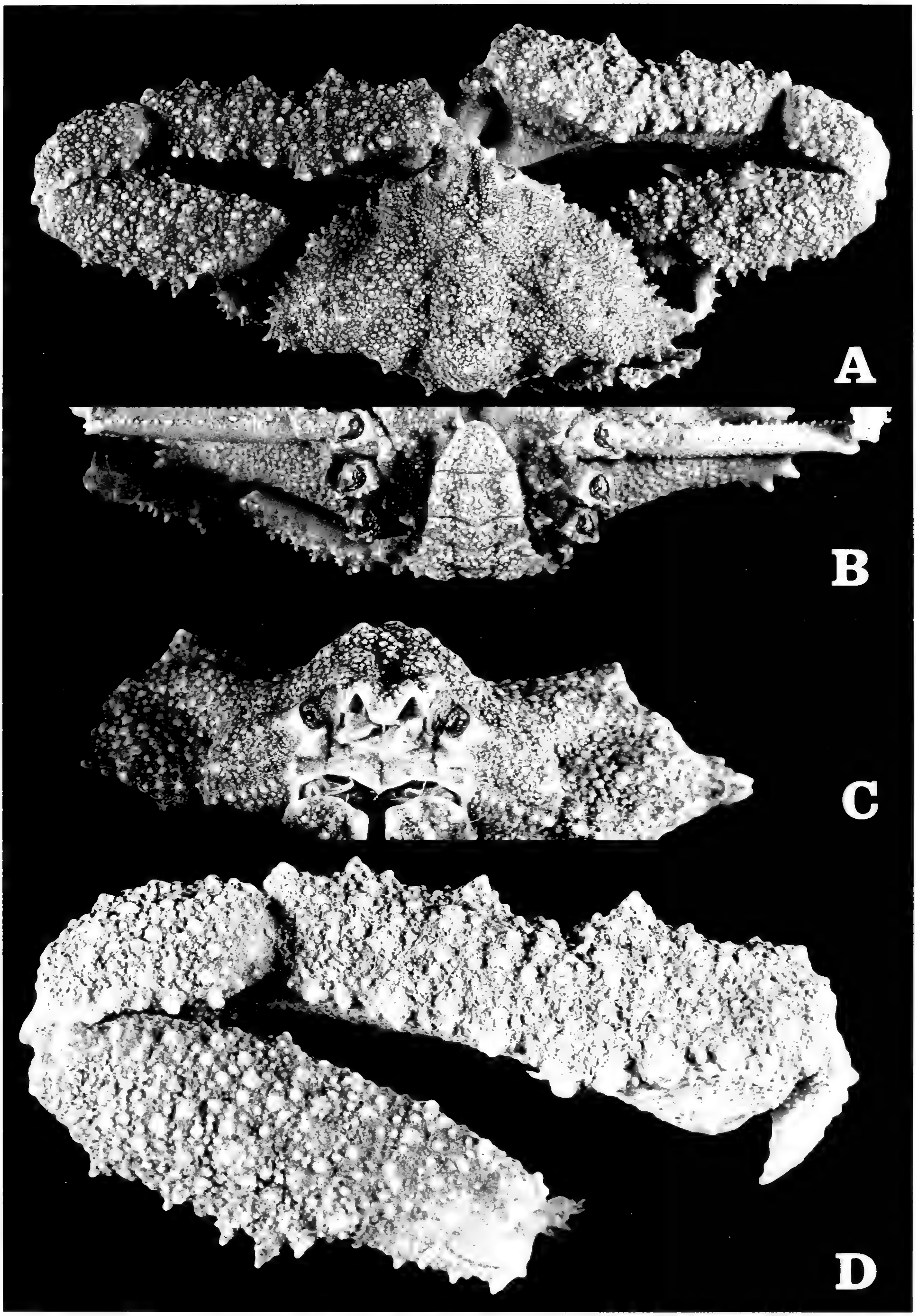

Fig. 1. *Garthambrus stellata* (Rathbun, 1906). Holotype male (48.6 by 32.8 mm) (USNM 29839). A, Carapace; B, Abdomen; C, Front; D, Left chela.

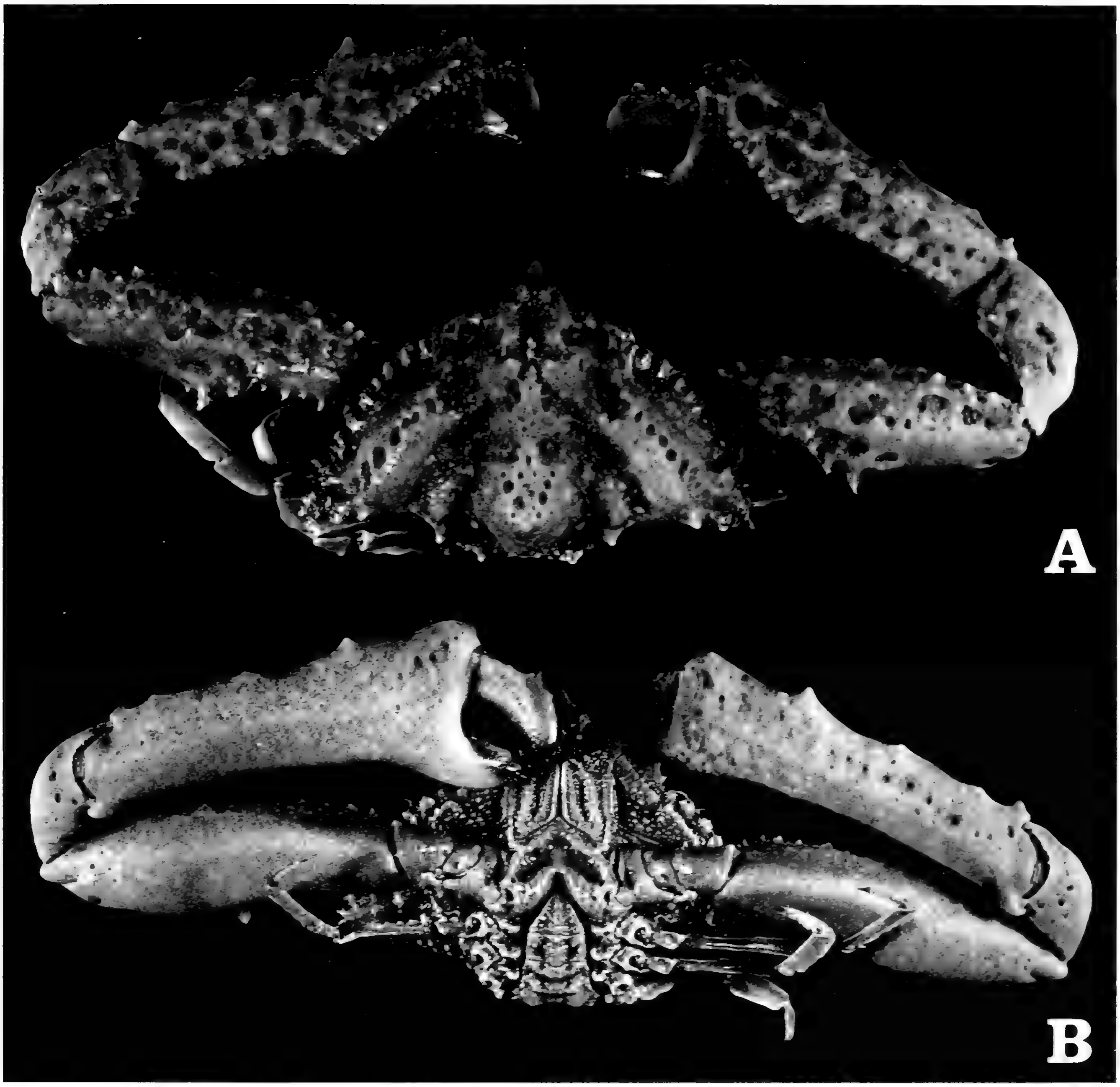

Fig. 2. *Garthambrus lacunosa* (Rathbun, 1906). Holotype male (30.9 by 21.8 mm) (USNM 29842). A, Carapace; B, Abdomen.

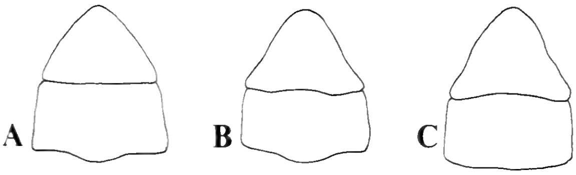

Fig. 3. Male telson and sixth abdominal segment. A, *Garthambrus stellata*, holotype male (USNM 29839); B, *Garthambrus lacunosa*, holotype male (USNM 29842). C, *Garthambrus lacunosa*, male (USNM 29842b).

peak-like in frontal view (Fig. 1C), highest point with sharp granule; sub-branchial, suborbital, subhepatic and branchiostegal regions distinct, densely covered with distinct small granules. Anterolateral margin with sharp, acutely triangular teeth, lateral margins of teeth with numerous accessory spinules and/or small, sharp granules. Cheliped surfaces (especially merus, carpus, propodus and dactylus) with well developed sharp spines, spinules and granules (Fig. 1D); merus with oblique ridge of strong spines about ⅓ from proximal end;

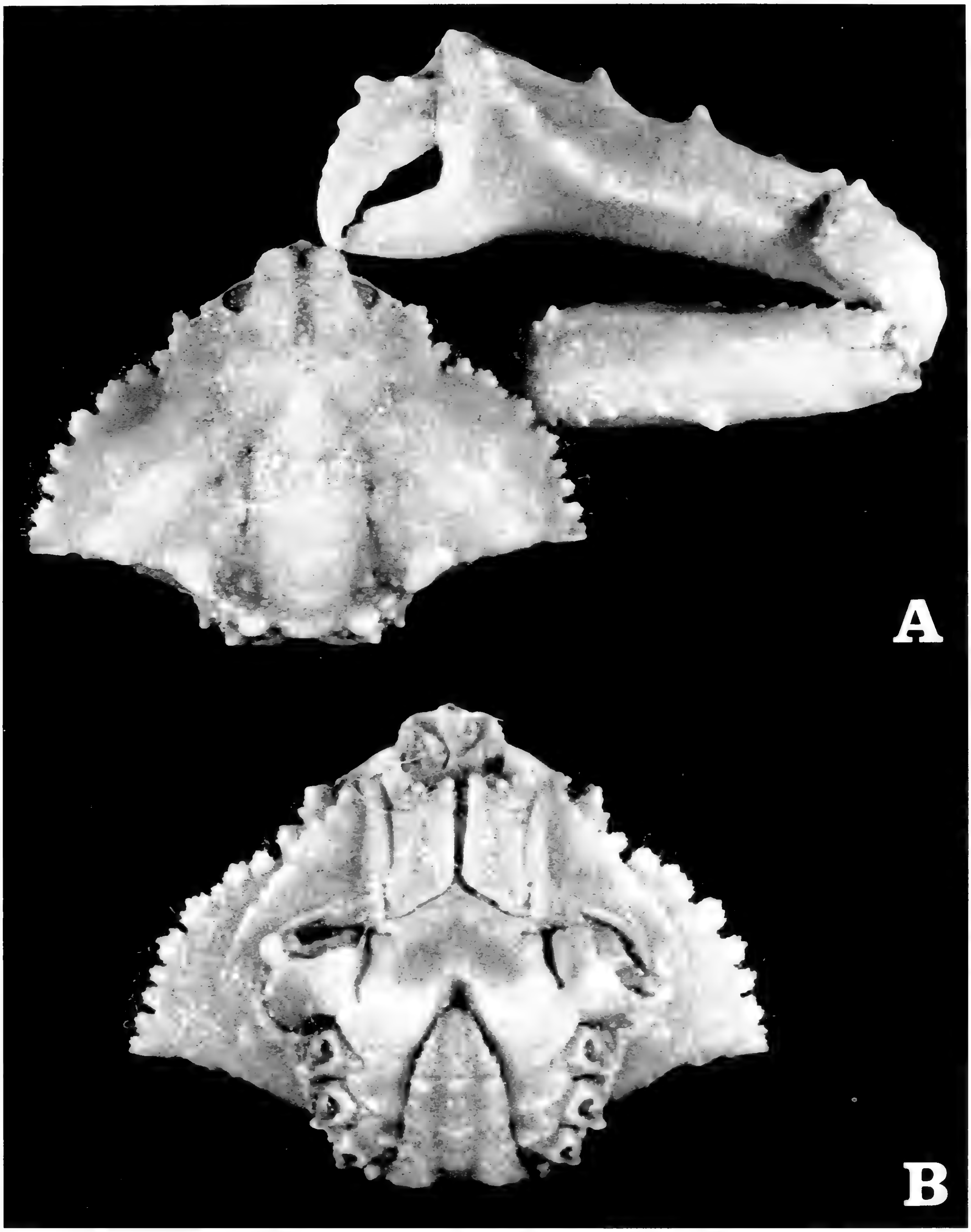

Fig. 4. *Garthambrus complanata* (Rathbun, 1906). Lectotype male (17.3 by 12.7 mm) (USNM 29845a). A, Carapace; B, Abdomen.

surfaces never with pits or lacunae. Margins of ambulatory legs unevenly cristate to dentate, with numerous accessory spinules; surfaces densely covered with small granules, never with pits or lacunae. Anterior thoracic sternites densely covered with small granules, without pits or lacunae (Fig. 1B). Abdominal surfaces densely covered with small granules, never with pits or lacunae; lateral margins of male telson gently convex. G1 relatively slender, tip distinctly turned inwards towards median part of thoracic sternum.

Remarks.—Rathbun (1906) described *Parthenope stellata* on the basis of ten specimens from various parts of Hawaii. In her discusion on variation within the species, however, she noted that only two specimens conformed with *P. stellata* sensu stricto, and the other eight specimens appeared to belong to two other varieties or were intermediate in form (see discussion for next two species). One specimen (USNM 29839) was designated as the "type" (= holotype) of *P. stellata.* However, Rathbun (1906:884), noted that the smaller specimen (USNM 29840) "... shows the tubercles and spines all sharp instead of blunt pointed, and lacks the hair near the ends of the legs." She regarded this smaller specimen as belonging to the "sharp-spined variety" of *P. stellata* sensu stricto, but did not apply any name. Examination of a relatively good series of specimens has shown that differences noted by Rathbun (1906) between her two type specimens can easily be accounted for by infraspecific variation. Edmondson (1951: 213) had reported two small specimens from shallow waters in Hawaii and Ng (1996:159) commented that "... his specimens are probably misidentified" as the carapace proportions were different, the rostrum was not trifid and the ambulatory dactylus was more styliform. We have reexamined these two specimens (BPBM 5508), and they are clearly juvenile *G. stellata.* The differences in carapace proportions are almost certainly due to their small size and the ambulatory dactylus is actually not as styliform as depicted in Edmondson's (1951:Fig. 18d) illustration. The bifid rostrum shown for the specimen figured by Edmondson (1951:Fig. 18a) is such because the median lobe is broken. In the other specimen, the rostrum is clearly trifid.

The relatively good series of specimens of various sizes and sexes shows that the characters identified here are consistent and are useful for defining this species. The G1 shows slight variation, in that the distal part may appear slightly more flared or slightly more bent inwards (towards the median part of the thoracic sternum). The density of the granules does not change much with growth. However, with an increase in size, the individual granules do become larger, more prominent and distinctly more stellate in structure.

Garthambrus stellata is known from Hawaii, Tuamotu and Taiwan (Garth 1992, Poupin 1996:32, Tan et al. 1999). In Hawaii, the species is recorded up to depths of 461 m, although juveniles have been found in shallower waters of only about 46 m. The record from Tuamotu is of an adult from about 300 m depth. The specimen figured by Poupin (1996: pl. 15f) from Tuamotu is a dirty white overall and speckled with numerous fine brown spots, and the fingers are pigmented brown.

Garthambrus lacunosa (Rathbun, 1906)
(Figs. 2A–B, 3A–C, 6D–F)

Parthenope (Platylambrus) stellata lacunosa Rathbun, 1906:884, pl. 15 Fig. 7.
Parthenope (Platylambrus) lacunosa.—Garth, 1993:788.
Parthenope lacunosa.—Garth & Davie, 1995:226, Fig. 3A.
Garthambrus lacunosa.—Ng, 1996:158

Material examined.—Holotype, 1 male, cw 30.9 mm, cl 21.8 mm (USNM 29842), Kawaihae, west coast of Hawaii Island, Hawaii, 269–362 m, 20°01′45″N 155°54′15″W, station 4045, 8 hemp tangles gear, coll. Albatross Expedition, 11 Jul 1902. Paratypes, 1 male, cw 30.4 mm, cl 31.6 mm (USNM 29843a), Maui Island, Lipoa Point, Pailolo Channel, Hawaii, 238–276 m, 21°05′30″N 156°40′30″W, station 4100, 8 hemp tangles gear, coll. Albatross Expedition, 23 Jul 1902, (1 other paratype male specimen transferred to Stanford University according to labels, not examined). 1 female (USNM 29844), northwest coast of Oahu Island, Hawaii, 282–357 m, coll. Albatross Expedition. 1 female, cw 30.2 mm, cl 21.3 mm (USNM 29841), south coast of Molokai Island, Hawaii, off Lae-O-Ka Laau Lighthouse, 309–333 m, 64°00′N 00°13′42″W, station 3835, coll. Albatross Expedition, 3 Apr 1902. Others—1 male, cw 31.4 mm, cl 21.5 mm (USNM 29843b), Maui Island, Lipoa Point, Pailolo Channel, Hawaii, 238–276 m, 21°05′30″N 156°40′30″W, station 4100, 8 hemp tangles gear, coll. Albatross Expedition, 23 Jul 1902.

Diagnosis.—Surface of carapace slightly rugose, with scattered to relatively numerous granules; metabranchial regions moderately raised but not strongly swollen, not peak-like from frontal view, highest point unarmed; sub-branchial, suborbital, subhepatic and branchiostegal regions distinct, covered with numerous but scattered small granules. Anterolateral margin with lobiform to truncate teeth, lateral margins of teeth lined with numerous accessory spinules or small, sharp granules especially along anterior margin. Outer surfaces of chelipeds (especially merus, carpus, propodus and dactylus) with well developed spines, spinules and granules; merus with oblique ridge of strong spines about ⅓ from proximal end; outer surfaces with numerous pits, often with well developed lacunae. Margins of ambulatory legs distinctly cristate, entire to uneven; surfaces almost smooth or with very small, scattered granules, usually with distinct pits and/or lacunae. Anterior thoracic sternites with numerous scattered small granules and pits, often with lacunae. Abdominal surfaces covered with numerous scattered small granules and pits, often with lacunae; lateral margins of male telson concave. G1 relatively slender, tip turning slightly inwards towards median part of thoracic sternum.

Remarks.—Rathbun (1906) regarded five specimens of the original nine specimens of *Parthenope* (*Platylambrus*) *stellata* belonging to a separate variety *P.* (*P.*) *stellata lacunosa.* She has also mentioned that the differences of these five specimens are so different from the type specimen of *G. stellata,* that they could be a different species altogether and she mentioned several characters: "The branchio-cardiac depression is deep, and another depression runs along the outer side of the branchial region, adjacent to the marginal teeth. The elevated part of this region has a row of large pits through its middle, and similar line of pits dividing the gastric region in three and roughening the chelipeds. The granules are in large part confluent and thus obliterated, especially on the higher parts of the carapace and the chelipeds. The legs have smooth surfaces, thin cristate margins which are somewhat crenate or dentate in the merus and are destitute of long hair. Along with two of this variety from station 4100 is one which is intermediate between the typical (*P. stellata stellata*) and varietal form (*P. stellata lacunosa*), the stellate granules being everywhere fairly well shown, and also the lines of pits." (Rathbun, 1906:884).

One of the original nine type specimens of *Garthambrus stellata* was considered as intermediate between *P. stellata* and *P. lacunosa.* This specimen (USNM 29843b) is similar to *P. stellata* sensu stricto in having smaller granules overall, even on the carapace depressions and grooves, compared to typical *P. lacunosa.* The lacunae on the carapace and chelipeds are also smaller and less developed. A close examination of this supposedly intermediate specimen, however, shows that it only represents the extreme end of the variation in *P. lacunosa.* In the presence of lacunae on the carapace and chelipeds, truncate anterolateral teeth, distinctly cristate ambulatory meri, low, non-peaked metabranchial regions which lack a sharp median granule and gently concave male telson (Fig. 3C), the specimen clearly represents *P. lacunosa.* Even though this specimen is more granulated than typical *P. lacunosa,* it is still much less granulated overall compared to any specimen of *P. stellata* sensu stricto we have examined, even specimens of similar sizes.

Rathbun (1906) identified one specimen

(USNM 29842) as the "type" (= holotype) of *Garthambrus lacunosa*. The other four specimens listed by Rathbun (1906) are thus paratypes. The supposedly intermediate specimen (USNM 29843b) was not regarded as belonging to *P.* (*P.*) *stellata lacunosa* by Rathbun (1906) when she originally named the taxon, and thus, is not part of the type series.

Garthambrus complanata (Rathbun, 1906)
(Figs. 4A–B, 6G–I)

Parthenope (*Platylambrus*) *stellata complanata* Rathbun, 1906:884.
Parthenope (*Platylambrus*) *stellata complanataus* Serène, 1968:60.
Parthenope (*Platylambrus*) *complanata*.—Garth, 1993:789.
Parthenope complanata.—Garth & Davie, 1995:226, Fig. 3B.
Garthambrus complanata.—Ng, 1996:158.

Material examined.—Lectotype, herein designated, 1 male, cw 17.3, cl 12.7 mm (USNM 29845a), Hanamaulu Bay, Kauai Island, Hawaii, 470–570 m, 22°01′30″N 150°21′10″W, station 4132, 8 foot Blake Beam trawl gear, coll. Albatross Expedition, 1 Aug 1902. Paralectotype, 1 male (USNM 29845b), same data as lectotype.

Diagnosis.—Surface of carapace smooth to gently rugose, not granulated; metabranchial regions raised but not strongly swollen, not peak-like from frontal view, highest point unarmed; sub-branchial, suborbital, subhepatic and branchiostegal regions distinct but almost smooth except for a few scattered granules. Anterolateral margin with liboform to truncate teeth, lateral margins of teeth lined with scattered accessory spinules or small, sharp granules especially along anterior margin. Surface of chelipeds (especially merus, carpus, propodus and dactylus) with few, scattered granules, but with distinct simple spines; merus without distinct oblique ridge of spines; surfaces with few, scattered simple granules. Margins of ambulatory legs smooth, not cristate but with well spaced spines and/or teeth; surfaces smooth, without lacunae. Anterior thoracic sternites almost smooth, without pits or lacunae. Abdominal surfaces almost smooth, without pits or lacunae; lateral margins of male telson concave. G1 relatively stout, straight.

Remarks.—For her third variety of *P.* (*P.*) *stellata*, Rathbun (1906:884) noted that "Still a third type seems worthy of a distinguishing name, *P.* (*P.*) *stellata complanata*. It differs from the type of *P.* (*P.*) *stellata stellata* in the surface of carapace and chelipeds being smooth to the naked eye, though under the lens finely punctate and roughened; the tubercle or spine at the inner third of the postero-lateral margin is represented by a triangular nodule; tubercle at each end of posterior margin large and round; antero-lateral teeth broader and more dentiform than in other forms; no teeth nor spines at outer end of postero-lateral margin, but a nodule on the dorsal surface at that point may represent them; marginal spines of chelipeds inclining to sharp; legs approaching the type in roughness; margins prominently spinate, without long hair." Most of these differences are valid, and *G. complanata* can easily be separated from congeners by the carapace sculpturation, armature of the antero-lateral margin, absence of an oblique ridge on the relatively smooth merus of the cheliped, structure of the ambulatory merus, and form of the thoracic sternites and abdominal surface.

Garth & Davie (1995:Fig. 3B) provided a photograph of the "holotype" of this species, but no measurements were provided. However, Rathbun (1906) listed two male specimens (USNM 29845a) only as "types" without designating a holotype; thus, both are syntypes. Garth (1993) had earlier examined both specimens and listed them as syntypes. The larger specimen (17.3 by 12.7 mm) (USNM 29845a) in better condition, is here designated as the lectotype. It is the same specimen figured by Garth & Davie (1995).

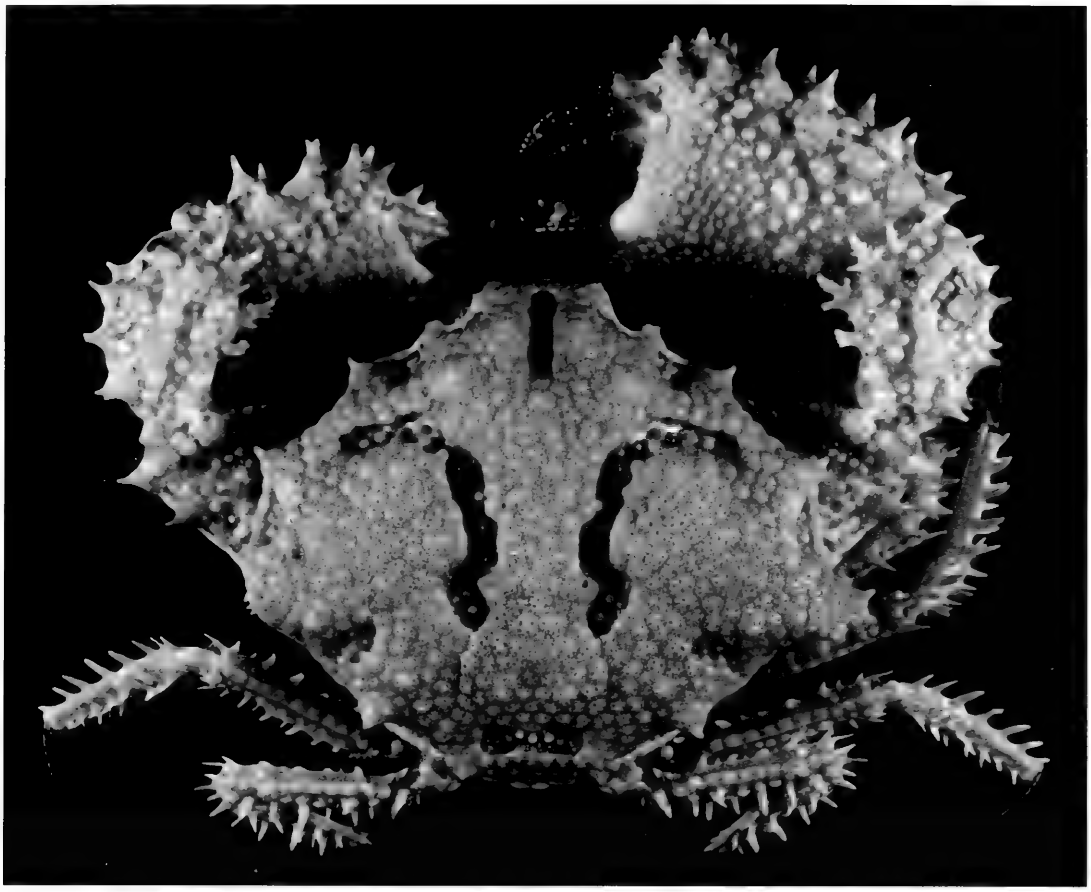

Fig. 5. *Dairoides kusei* (Sakai, 1938). 1 male (52.2 by 47.3 mm) (ZRC 1997.447).

Genus *Dairoides* Stebbing, 1920

Dairoides Stebbing, 1920:233 (type species: *Dairoides margaritus* Stebbing, 1920, by monotypy).

Astherolambrus Sakai, 1938:341 (type species: *Astherolambrus kusei* Sakai, 1938, by monotypy).

Remarks.—Sakai (1938) established *Astherolambrus* for a new species from Japan, *A. kusei.* Sakai (1965) later synonymised *Astherolambrus* under *Dairoides* Stebbing, 1920, which had been established for *D. margaritus* Stebbing, 1920, a species known only from South Africa. Takeda & Ananpongsuk (1991) subsequently described a third species, *D. seafdeci,* from the Andaman Sea in the Indian Ocean.

Dairoides kusei (Sakai, 1938)
(Figs. 5, 6 J–L)

Astherolambrus kusei Sakai, 1938:341, pl. 41 Figs. 5, 6.

Dairoides kusei.—Sakai, 1965:99, pl. 45 Fig. 2.—Sakai, 1976:288, pl. 97 Figs. 1, 2.

Material examined.—1 male, 2 females (BPBM 1980.194), Oahu Island, off Barber's Point, Hawaii, 117–128 m, trapped by gill nets laid overnight, coll. Teritu, T. Clarke, 19-20 Apr 1971. 1 male, cw 52.2 mm, cl 47.3 mm (ZRC 1997.447), Hawaii, coll. E. Bilderback, 17 Jan 1979. 1 male (dried), cw 54.8 mm, cl 44.6 mm (RMNH), Wagu, Kii Peninsula, Mie Prefecture, Japan, coll. N. Yamashita, 1978–79. 2 males, 1 female (RMNH 32004), Wagu, Kii Peninsula, Mie Prefecture, Japan, coll. N. Yamashita, 1978–79.

Remarks.—Dairoides kusei had previously been reported only from Japanese waters. The specimens reported here agree well with the descriptions and figures of this species by Sakai (1938, 1965, 1976). We have also examined four specimens of *D. kusei* from Japan in the RMNH donated

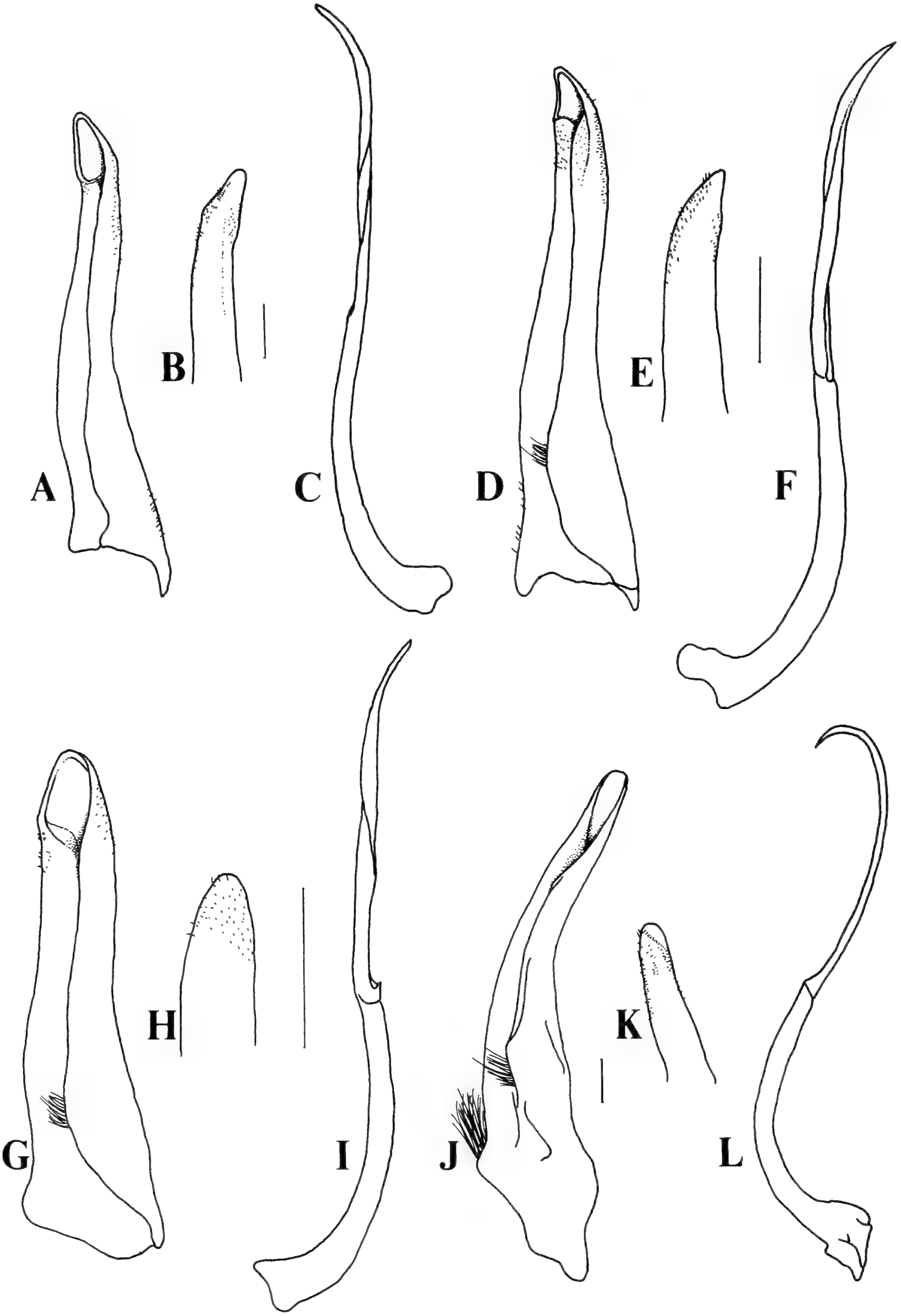

Fig. 6. G1s. A–C, *Garthambrus stellata* (Rathbun, 1906), holotype male (48.6 by 32.8 mm) (USNM 29839); D–F, *G. lacunosa* (Rathbun, 1906), holotype male (30.9 by 21.8 mm) (USNM 29842); G–I, *G. complanata* (Rathbun, 1906), lectotype male (17.3 by 12.7 mm) (USNM 29845a); J–L, *Dairoides kusei* (Sakai, 1938), 1 male (52.2 by 47.3 mm) (ZRC 1997.447).

by the late Tune Sakai. They agree with the specimens from Hawaii in all major aspects, including the structures of their gonopods.

Acknowledgments

The first author is most grateful to Lu Eldredge for his excellent hospitality during his visit to the BPBM. Thanks are also due to Rafael Lemaitre and Lipke Holthuis for their kind assistance in examining the specimens in the USNM and RMNH respectively. This study has been partially supported by grant RP 3972371 of the National University of Singapore to the first author.

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Reinstatement and further description of *Eualus subtilis* Carvacho & Olson, and comparison with *E. lineatus* Wicksten & Butler (Crustacea: Decapoda: Hippolytidae)

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Abstract.—*Eualus subtilis* Carvacho & Olson 1984 is presently considered a synonym of *E. lineatus* Wicksten & Butler 1983. Comparisons of the two forms revealed differences in the armature of the antennular peduncle, stylocerite, and pereopods, as well as differences in color and maximum size, indicating that *E. subtilis* is a valid species. Furthermore, *E. subtilis,* unlike *E. lineatus,* exhibits marked sexual dimorphism, and characteristics of the previously undescribed, diminutive males of this species are provided.

The genus *Eualus* Thallwitz, 1891 is comprised of relatively small caridean shrimps that occur primarily in the higher latitudes. Butler (1980) illustrated a small, striped shrimp as *E. herdmani* (Walker, 1898), and mentioned that it could be trawled in small numbers in Departure Bay, Canada. However, subsequent examination of the holotype and only known specimen of *E. herdmani* by Wicksten & Butler (1983) revealed that *E. herdmani* belonged in the genus *Heptacarpus* (Holmes, 1900) and the specimens illustrated by Butler (1980) were described as a new species, *E. lineatus* Wicksten & Butler, 1983. One of the characters distinguishing *E. lineatus* was the presence of three moderate dorsodistal spines on the first article of the antennular peduncle (hereafter referred to as "antennular spines").

A second description of a small eualid, *E. subtilis* Carvacho & Olson, 1984 was published based on a single specimen trawled off Baja California. As Carvacho & Olson did not mention *E. lineatus,* and still referred to "*E. herdmani*", they were evidently unaware of Wicksten & Butler's (1983) paper. *Eualus subtilis* strongly resembled *E. lineatus* in the size and armature of the rostrum, but had only a single, stout, dorsolateral antennular spine. Wicksten (1988) considered *E. subtilis* to fall within the range of variation of *E. lineatus* and thus a junior synonym, and used the record as a southern range extension for *E. lineatus.*

Subtidal sampling in the Puget Sound region revealed an extremely abundant small eualid that matched the description of *E. subtilis.* However, out of hundreds of specimens examined, all had a single antennular spine. Based on the length of the rostrum some of these specimens keyed out to *E. pusiolus* (Krøyer, 1841), yet they bore several strong, distal spines on the merus of the walking legs while *E. pusiolus* has only a single spine (Squires 1990). Furthermore, this species exhibited marked sexual dimorphism, whereas there is no distinct differences between sexes in *E. pusiolus* (Greve 1963). In view of these observations, a study was undertaken to determine if *E. subtilis* is distinct from *E. lineatus,* and provide information about the unusual, small males.

Materials and Methods

Due in part to the ambiguity of existing keys, museum specimens of these shrimps have been variously cataloged under the names *E. herdmani, E. pusiolus,* or *E. lineatus.* These specimens needed to be reexamined. Sixty-one specimens from the British Columbia Provincial Museum collection were examined, as was the holotype of *E. lineatus* (AHF 4129) deposited in the Natural History Museum of Los Angeles County and the paratype from the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). The two paratypes reportedly deposited in the National Museum of Canada were not sent at the time *E. lineatus* was described and now cannot be located. Additional material was acquired from Friday Harbor Laboratories of the University of Washington (43 specimens), the California Academy of Sciences (8 specimens), and our own collections ranging from the Pribilof Islands to Puget Sound (45 specimens). Twenty-two North Atlantic specimens of *E. pusiolus* from the Royal Norwegian Society of Sciences were examined for comparison.

Live specimens having a single antennular spine were abundant in shell rubble and easily collected while diving by carefully placing dead bivalve shells in a fine-meshed bag. Hand-operated suction devices were used to sample in rock crevices.

Measurements were taken using an image analysis system (Optimus®) on a Wild MC3 dissecting microscope, with additional measurements taken using an ocular micrometer. Carapace length (cl) was measured from the posterior margin of the orbit to the middorsal posterior margin of the carapace; rostrum length, from the same position on the orbit to the tip. Sex, rostral formula, number of distal spines on the basal article of the antennular peduncle, and relative lengths of the stylocerite and rostrum were also noted, as was the number of meral spines on pereopods 3–5. Drawings were made with the aid of a camera lucida on a Wild® M5 microscope.

Results

Of the 159 shrimp measured, only 17 were found bearing multiple antennular spines, and these were compared with 93 specimens that had only a single antennular spine and multiple spines on the merus of the third pereopod. The remaining 49 specimens were identified as *E. pusiolus* based on published descriptions and comparison with the specimens from Norway.

The 17 specimens with multiple antennular spines reached substantially larger sizes than those bearing a single spine (Fig. 1a, b). Multiple antennular spines were also correlated with a reduced number of meral spines on the third pereopod. Those with multiple antennular spines typically had only one meral spine, although some specimens had a second, much reduced spine present on at least one side. Shrimp with a single antennular spine had significantly more meral spines ($\chi^2 = 81.21$; $p \ll 0.001$), the great majority bearing three strong meral spines and the remainder varying from two to five (Fig. 2).

Those with multiple antennular spines also had a curved, dorsal tooth near the base of the stylocerite not previously noted in the literature (Fig. 3); that tooth was lacking in those with a single antennular spine. A blunt suborbital carapace spine was also present in those with multiple antennular spines, and missing in those with a single antennular spine and more than one spine on the merus.

Males with a single antennular spine typically had a very thin, bifid rostrum (Fig. 4c); the largest male (2.1 mm cl) was smaller than any of the ovigerous females (2.6–3.8 mm). Unlike that of females, the propodus of pereopods 3–5 of males was distinctly broadened distally and armed with two rows of spines forming a dense comb on the flexor margin, with spines increasing in length distally (Fig. 4a); the male dactylus was also armed with an unusual series of compound spines on the flexor margin (Fig. 4b). The appendix masculina was subequal in length to the appendix interna, and tipped with two long spinules and five short ones. Males comprised only 10% of the samples.

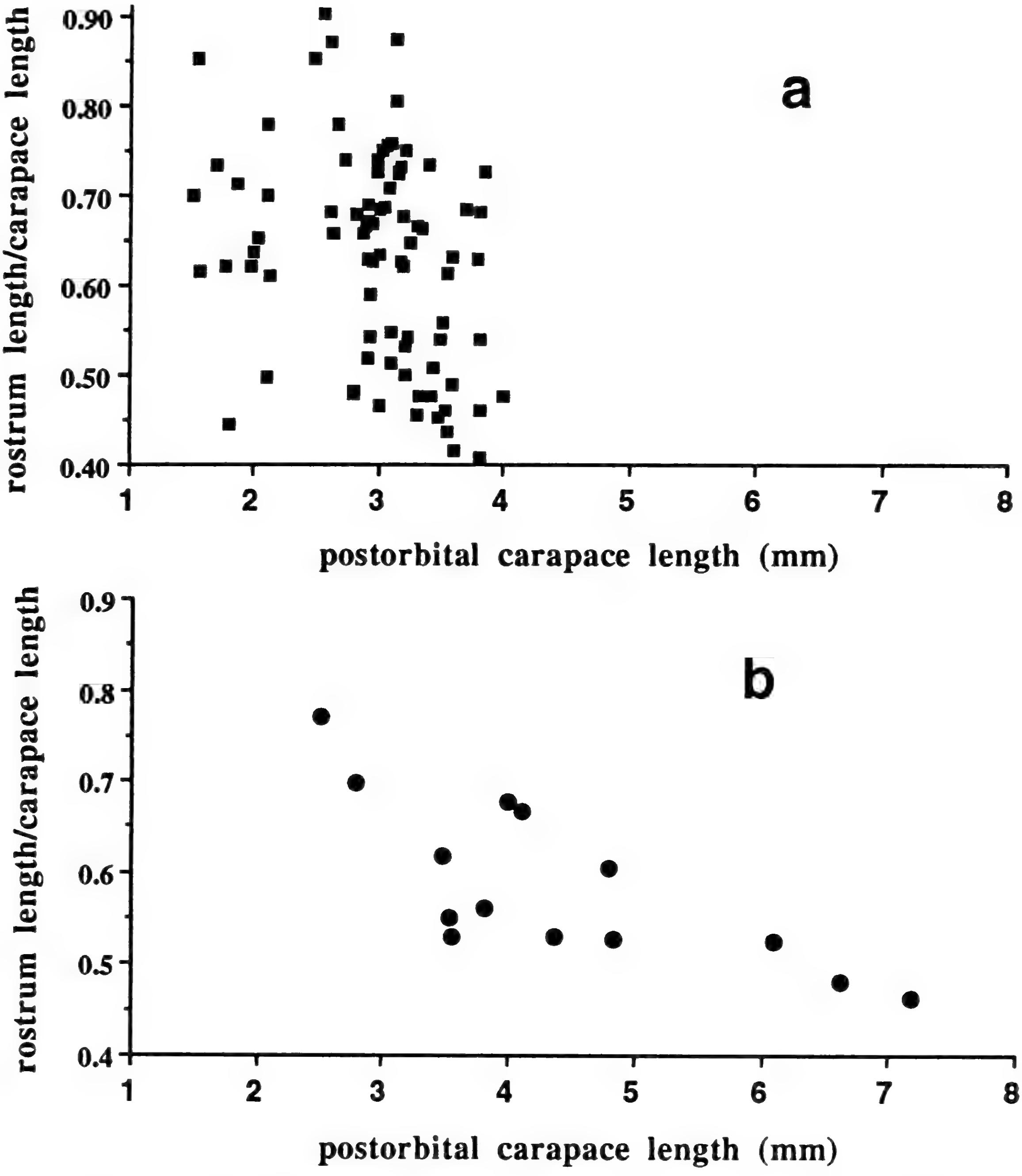

Fig. 1. Scatterplot of postorbital carapace length vs. proportional rostrum length for specimens having a single distodorsal spine on the basal article of the antennular peduncle (a), and specimens with multiple distodorsal spines on the basal article of the antennular peduncle (b).

Only two males with multiple antennular spines were available for examination, but other than the presence of an appendix masculina they did not appear to differ from females with multiple spines. The appendix masculina in these specimens was slightly more than half the length of the appendix interna and tipped with eight long spinules, as previously described (Wicksten & Butler 1983; Fig. 2d).

The form with only a single antennular spine consistently displayed the color pattern described for *E. lineatus* (Wicksten & Butler, 1983) as shown in Butler (1980: plate 1C), having thin red diagonal lines on the carapace and first two abdominal segments and red spotting on the remainder of the abdomen. In contrast, a live specimen of the form that has multiple antennal spines was boldly marked on both the car-

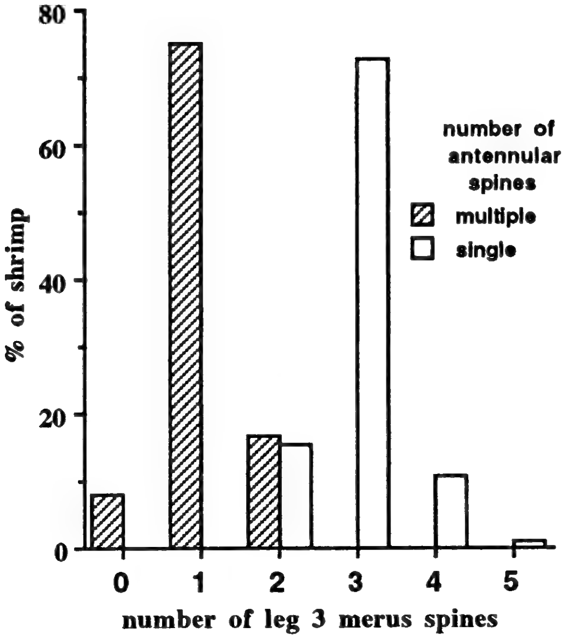

Fig. 2. Bar graph showing number of lateral spines on the merus of the third pereopod for specimens with single (n = 85) or multiple (n = 12) distodorsal spines on the first article of the antennular peduncle.

apace and abdomen with broad orange bands against a translucent background (Fig. 5).

The holotype of *E. lineatus* has multiple antennular spines, a suborbital carapace spine, dorsal tooth on the stylocerite, and two spines on the merus of the third pereopod, whereas the USNM paratype of *E. lineatus* has only a single antennular spine, no suborbital spine or stylocerite tooth, and three strong spines on the merus of the third pereopod.

Discussion

The combination of size, color and morphological differences clearly indicate that *E. subtilis* should be considered a valid species, distinctly separate from *E. lineatus. Eualus subtilis* lacks the multiple dorsodistal spines on the basal article of the antennular peduncle, the suborbital carapace spine, and the dorsal tooth on the stylocerite that are all present in *E. lineatus*. Furthermore, the largest *E. subtilis* barely exceed half the length of *E. lineatus,* and *E. subtilis* exhibits marked sexual dimorphism while *E. lineatus* does not. The number of spines on the merus of the third walking leg is usually reliable for differentiating the two species, but there is some slight overlap, with *E. subtilis* varying from 2 to 5 (usually 3) spines whereas *E. lineatus* varies from 0 to 2 (usually 1). The type series for *E. lineatus* consists of a mix of both of these species, but since the specimen designated as the holotype has multiple antennular spines and a spine on the stylocerite, this is the form that should retain the name *E. lineatus.*

Much of the confusion regarding these species is due to variability in the length of the rostrum of *E. subtilis* (Fig. 4c–f). Most keys continue to follow the pattern established by Rathbun (1904) of separating *E. pusiolus* and "*E. herdmani*" (= *E. lineatus*) solely on the basis of whether the rostrum overreaches the second article of the antennular peduncle. We found many cases where, depending on the length of the rostrum, specimens of *E. subtilis* from the same haul had been cataloged as *E. pusiolus* and *E. herdmani* or *E. lineatus.*

The presence of multiple antennular spines makes *E. lineatus* very easy to differentiate from *E. subtilis* and *E. pusiolus.* The latter two species can be reliably separated by the number of meral spines on the pereopods: *E. subtilis* has 2 to 5 strong, distal spines on the merus of the third pereopod (and normally multiple spines on the fourth), whereas *E. pusiolus* has only a single spine on each of these pereopods. *Eualus pusiolus* has a small, rounded suborbital carapace spine, while *E. subtilis* has none. In this respect *E. subtilis* resembles the South American species *E. dozei* (A. Milne Edwards, 1891), but this species also has only single meral spines (Holthuis 1952).

We found that some of the characters given by Carvacho & Olson (1984) to differentiate *E. subtilis* were not useful. The ventral spines on the abdomen (considered by these authors to be unique to this species) were present on all males and most non-ovigerous females of *E. pusiolus* and

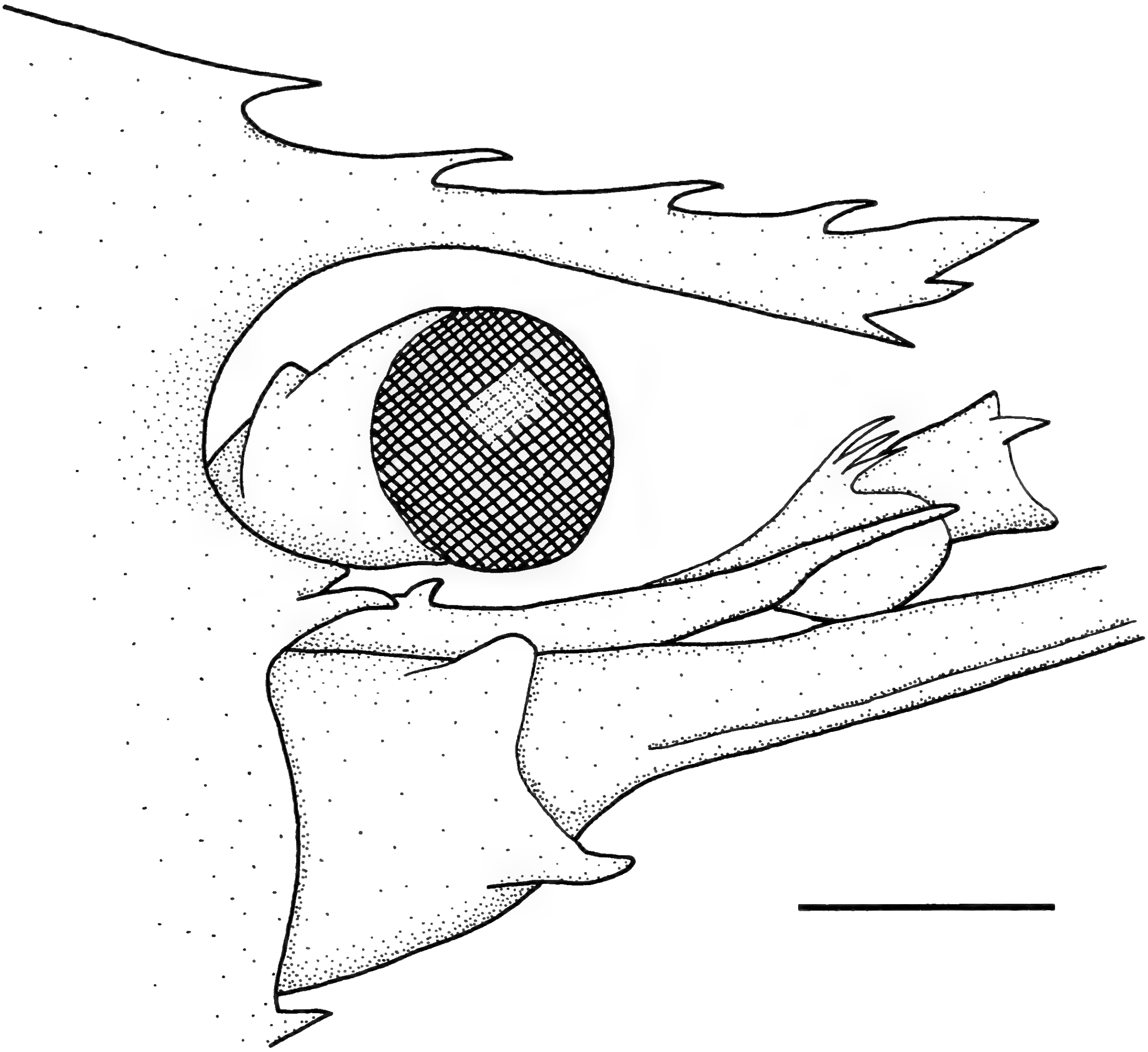

Fig. 3. *Eualus lineatus* Wicksten & Butler, 1983. Lateral view of anterior region of carapace, showing curved tooth on the base of the stylocerite and multiple spines on the basal article of the antennular peduncle. Scale bar is 1 mm.

E. lineatus. Furthermore, the basicerite of *E. pusiolus* has only one (not two) lateral spines, so this character is not useful for separating this species from *E. subtilis.*

Eualus subtilis is quite possibly the most abundant shrimp in Puget Sound, occurring subtidally on virtually any bottom type from mud to solid rock. It sometimes occurs in the low intertidal and has been collected in trawls to at least 74 m, and to date has been found from Barkley Sound, British Columbia (this study) to Bahía de Todos Santos, Punta Banda, Baja California (Carvacho & Olson 1984). Males of *E. subtilis* are fairly uncommon in collections, probably due to their very diminutive size. Although males were always much smaller than ovigerous females, the presence of small females suggests that the species is not strictly protandric. The unusual modifications to the pereopods bear some resemblance to those described by Bauer (1986) for another small hippolytid, *Thor manningi* Chace, 1972, a species that exhibits a novel reproductive strategy involving nearly equal proportions of protandric individuals and primary males.

Less is known about the habits and habitat of the much rarer *E. lineatus.* Specimens have been collected at depths of 12–

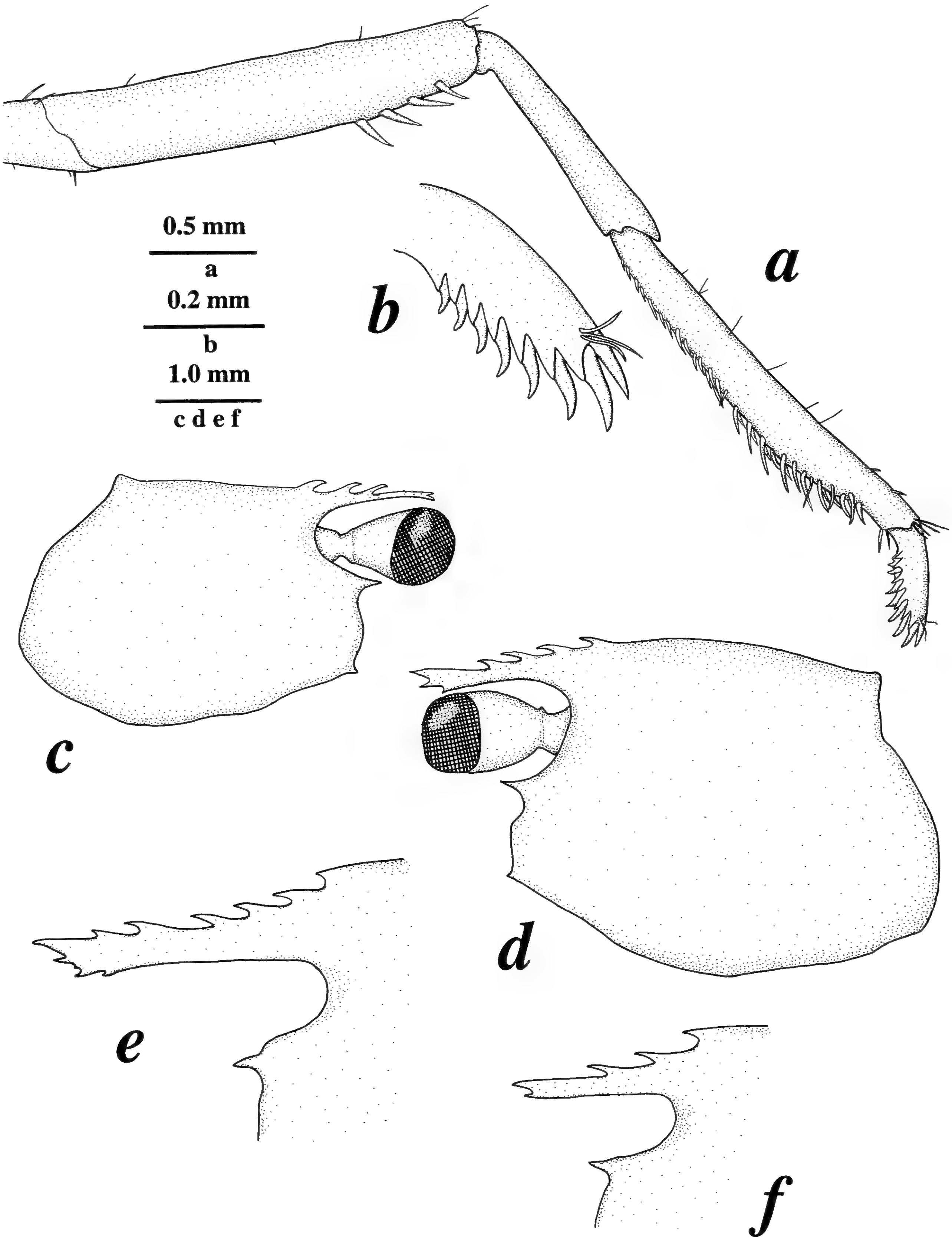

Fig. 4. *Eualus subtilis* Carvacho & Olson, 1984. a, Third pereopod of male, lateral view; b, dactyl of third pereopod of male, lateral view; c, lateral view of male carapace; d, lateral view of female carapace; e, rostrum variation, female, lateral view; f, rostrum variation, female, lateral view.

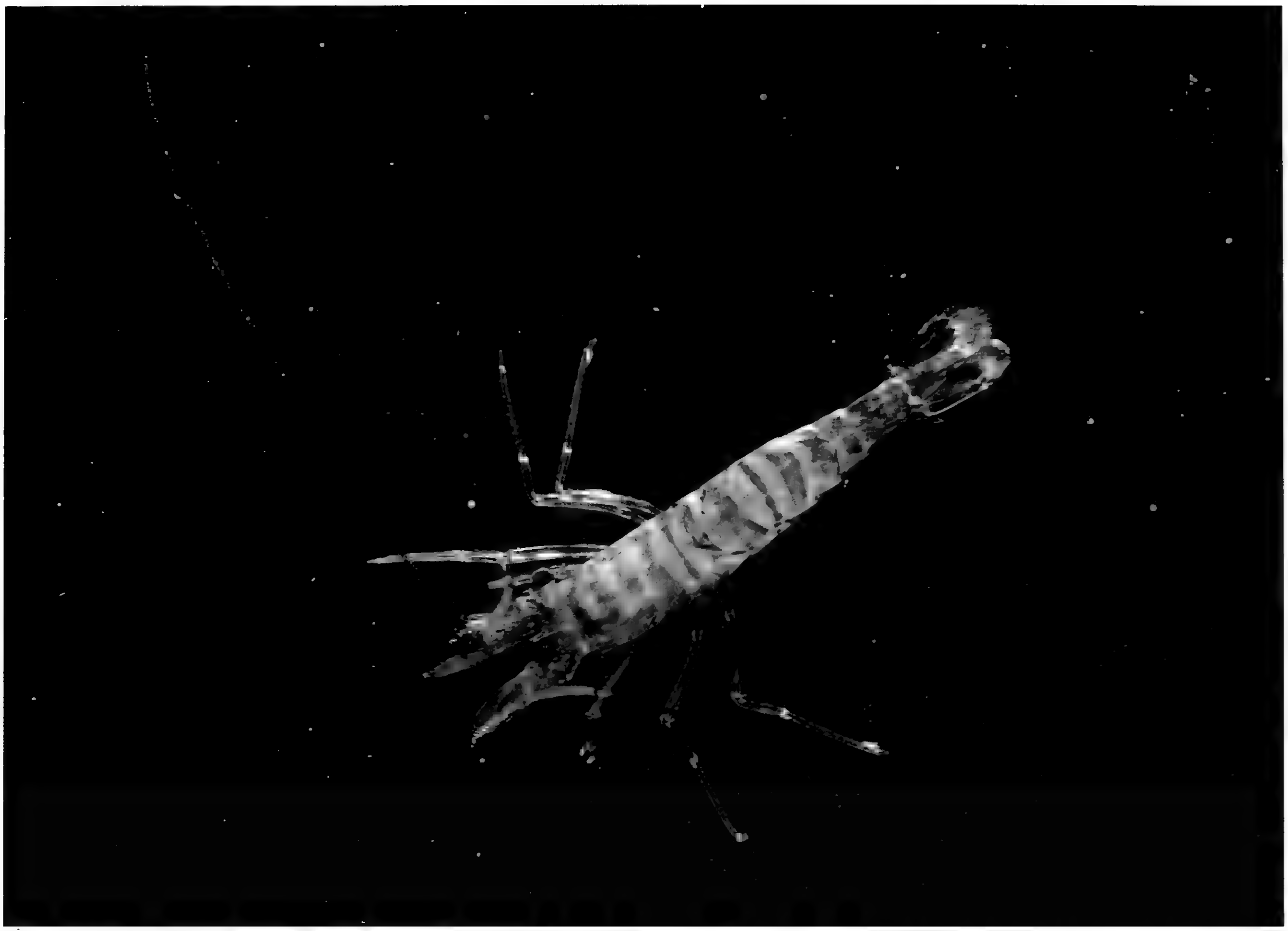

Fig. 5. *Eualus lineatus* Wicksten & Butler, 1984. Dorsal view of live specimen (male, 3.5 mm postorbital carapace length) showing pattern of broad orange bands.

120 m from Juneau, Alaska to at least Santa Cruz Island, California. This species may associate with sponges since the holotype was collected from "mud and sponge bottom," and the trawl collection records for the specimens examined often indicated that the shrimp were removed from sponge cavities, or noted the presence of sponges in the haul. The live specimen collected by one of us (GCJ) was found in a suction sampler that had been used in both crevices and small sponges on a vertical rock face, but it is not known at which point in the dive it was captured.

Given the confusion that has surrounded these species, any records should be considered suspect until the specimens have been reexamined. It is likely that at least some of the depth and range records will be revised, and perhaps new information on the habitat of *E. lineatus* will come to light.

Acknowledgments

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Deilocerus captabilis, a new species of cyclodorippid crab from southeastern Brazil (Crustacea: Decapoda: Brachyura: Cyclodorippidae)

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Abstract.—*Deilocerus captabilis,* new species, the third western Atlantic species and seventh representative of the genus is herein described based on an adult female collected on calcareous algae nodules from 50 m depth, southeastern Brazil. *Deilocerus captabilis,* new species, is the only species in the genus with three teeth on the lateral margin of the carapace.

Resumo.—*Deilocerus captabilis* nova espécie, terceira a ocorrer no Atlântico sul ocidental das sete conhecidas para o gênero, é descrita e ilustratada. A nova espécie é baseada em uma fêmea adulta coligida a 50 m de profundidade em fundos de nódulos de algas calcáreas. A nova espécie se distingue facilmente das demais espécies do gênero por ser a única a apresentar três dentes na margem lateral da carapaça.

As part of an ongoing project (REVIZEE) of the Brazilian government's department "Ministério do Meio Ambiente" to evaluate the country's marine living resources, a biological survey of the continental shelf and slope from Salvador (12°S) to Cabo de São Tomé (23°S) was conducted in 1997 onboard the "Astro Garoupa".

The samples yielded an adult female of a new species of cyclodorippid crab, *Deilocerus captabilis,* described herein.

The holotype is deposited in the Museu Nacional, Rio de Janeiro (MNRJ). Descriptive terminology follows Tavares (1991, 1996). Abbreviations: Mxp1–3, first to third maxillipeds; P2–P5, second to fifth pereopods, P1, cheliped; cl, carapace length; cw, carapace width; mm, millimeters.

Deilocerus captabilis, new species
Fig. 1

Material examined.—Brazil: Espírito Santo. "Astro Garoupa", REVIZEE Central II, st. 34C, 3 Nov 1997, 20°24′S, 39°49′W, 50 m: female holotype cl 1.7 mm, cw 2.0 mm (MNRJ 7303).

Type locality.—Brazil: Espírito Santo (20°24′S, 39°49′W, 50 m).

Description.—Carapace slightly broader than long. Dorsal surface ornamented with very fine scattered granules, denser near margins, except on smooth, shallow grooves defining gastric regions. Ventrolateral surfaces of carapace almost smooth; subhepatic region densely covered with rounded coarse granules, coarser on dorsal surface. Frontolateral tooth rounded, densely covered with small granules; exorbital tooth blunt. Hepatic and anterolateral teeth short, blunt, covered with rounded granules; anterolateral tooth smallest. Laterobranchial tooth present as low lobe. Anterolateral margin (from exorbital tooth to branchial tooth) rounded, about as long as posterolateral margin (measured from branchial tooth to posterior margin). Posterolateral margin straight, well defined by row of small granules.

Ocular peduncle covered with small rounded tubercles, anterodistal tubercles more acute; cornea pigmented. Antenna very small, hidden in dorsal view; articles

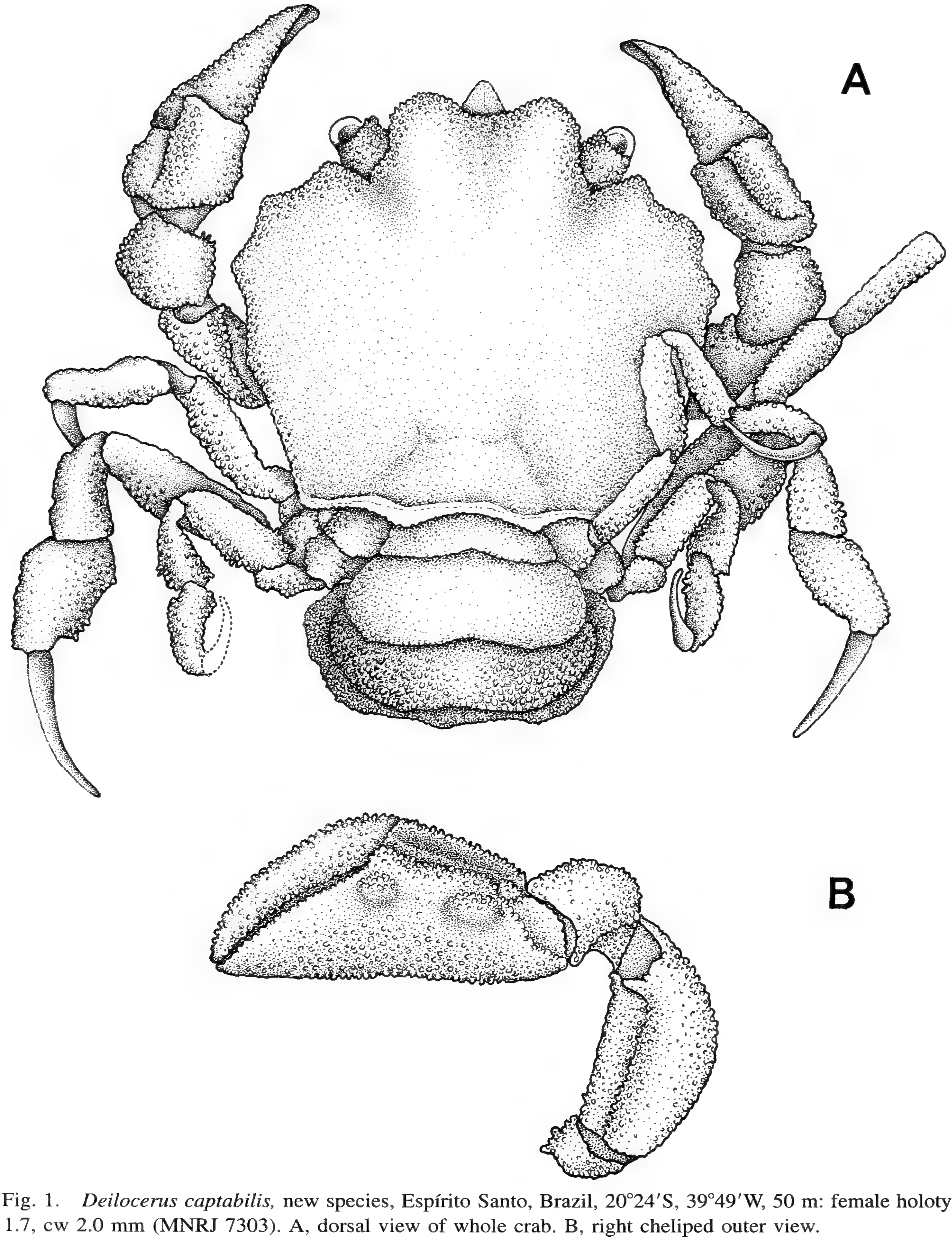

Fig. 1. *Deilocerus captabilis,* new species, Espírito Santo, Brazil, 20°24′S, 39°49′W, 50 m: female holotype cl 1.7, cw 2.0 mm (MNRJ 7303). A, dorsal view of whole crab. B, right cheliped outer view.

1–4 ornamented with small granules; second article slightly flattened; fifth article almost smooth; flagellum obsolete.

Endostomial channel visible dorsally between frontolateral teeth. Third maxilliped with ischium and merus, each more than 2 times as long as broad, with outer surfaces covered with rounded granules; palp without granules, articulated on inner surface of merus.

Chelipeds densely covered with small tubercles, much less dense and smaller on inner surfaces; inner surfaces of merus, carpus and chela forming concave surface fitting closely against walls of carapace; dorsal and ventral margins of merus, carpus, palm and fingers well defined. Fingers terminating in sharp tips, cutting edge with few small acute teeth. Dactyl smaller than palm, set obliquely relative to palm axis. Fixed finger about 2 times broader proximally than distally. Palm about 2 times longer than broad, ornamented longitudinally with 2 rounded protuberances, proximal one largest.

P2 longer than P3, otherwise similar. P2 and P3 laterally flattened; both legs with propodus, carpus, and merus densely ornamented with tubercles on dorsal and ventral margins, flanks almost smooth; dactyl cylindrical, with minute granules.

P4 and P5 generally similar, subdorsal, subcheliform, much smaller than P2 and P3; P4 with ischium about 3 times longer than in P5; dactylus and propodus short, strongly curved; propodus twisted, dactylus flexing on its lateral surface. Ornamentation on propodi, carpi and meri less pronounced on P4–5 than on P2–3.

Female abdomen with 6 segments densely covered with small tubercles diminishing in size and density from pleotelson to first segment. Pleotelson as wide as fifth segment, lateral margins broadly rounded.

Distribution.—Known only from the type-locality Espírito Santo, Brazil (20°24′S, 39°49′W, 50 m).

Etymology.—The specific name, *captabilis* (Latin, that can take), refers to the subcheliform P4 and P5.

Remarks.—The genus *Deilocerus* Tavares, 1993, is strictly American in distribution. The genus is represented in the western Atlantic by two species, and in the eastern Pacific by four (Tavares 1993, 1996). Two groups of species are recognizable. The first group includes species with only one anterolateral tooth on the margin of the carapace: *D. perpusillus* (Rathbun, 1900) and *D. analogus* (Coelho, 1973), from the western Atlantic, and *D. laminatus* (Rathbun, 1935) from the eastern Pacific. The second group is found only in the eastern Pacific and encompasses species with two teeth (one hepatic and one anterolateral), along the margin of the carapace: *D. planus* (Rathbun, 1900), *D. decorus* (Rathbun, 1933) and *D. hendrickxi* Tavares, 1993. *Deilocerus captabilis,* new species, falls into the second group and is, therefore, the first western Atlantic representative of that group. *Deilocerus captabilis,* new species is, so far, the only species in the genus with three teeth on the lateral margin of the carapace (hepatic, anterolateral, and laterobranchial): the first two teeth being well developed, and the laterobranchial represented by a low lobe. *Deilocerus captabilis,* new species, can also be readily recognized from the remaining six species of the genus by the shape and ornamentation of the fronto-orbital margin of the carapace.

Although no carrying behavior (Guinot et al. 1995) has been observed in *Deilocerus captabilis,* new species, it is possible that the crab can hold an object over its carapace using the last two pairs of legs. P4 and P5 are subchelate, with the propodus and especially the dactyl strongly curved; the propodus is twisted so the dactyl closes on the lateral surface of the propodus. This structure allows a small object, such as a piece of shell, to be held over the carapace. Carrying behavior has been observed in other species of the genus, such as *D. laminatus* (see Garth 1946, Tavares 1994) and *D. planus* (see Schmitt 1921, Wicksten 1982).

Acknowledgments

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The Albuneidae (Decapoda: Anomura: Hippoidea) of the Hawaiian Islands, with description of a new species

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Abstract.—*Albunea danai,* a new species that has been confused with *A. speciosa* Dana, is described from Oahu, Hawaii. The new species actually resembles *A. carabus* (Linnaeus) from the Mediterranean and western Africa. The discovery of this new species brings the total number of Indo-West Pacific members of the genus to eight. *Albunea speciosa* is broadly distributed in the Indo-West Pacific and is not a Hawaiian endemic as previously believed. As the identities of the two Hawaiian species have been confused, *A. speciosa* is here redescribed from new material and a neotype is selected. Both *A. danai* and *A. speciosa* are discussed using newly defined morphological characters.

Albunea speciosa Dana, 1852, is the only species of albuneid heretofore known from the Hawaiian Islands and has been considered a Hawaiian endemic (Serène 1973). In the course of examining specimens of sand crabs for a worldwide revision of the family Albuneidae, material from Hawaii was found labeled "*Albunea speciosa*" and "*Albunea symnista*" [sic] in the collections of the Western Australian Museum (WAM), but that was clearly not conspecific with *A. speciosa.* Later, additional Hawaiian specimens were obtained from the Bernice P. Bishop Museum that were labeled "*Albunea thurstoni*" that clearly are not *A. thurstoni* Henderson, 1893, but instead are the same taxon as the WAM material. Since these specimens cannot be placed in any known species of albuneid, they are described here as a new species. In addition, my examination of specimens that are referable to *A. speciosa* revealed that this species is not endemic to Hawaii, but has a broad range in the Indo-West Pacific. Because the faunal composition and biogeography of island groups has attracted much attention of late and the fact that more than one species has been repeatedly identified with *A. speciosa,* that species is redescribed from new material and a neotype is designated herein in order to fix its identity. This description of the new species brings the total number of Indo-West Pacific species of *Albunea* to eight: *A. symmysta* (Linnaeus, 1758), *A. speciosa, A. microps* Miers, 1878, *A. thurstoni, A. elioti* Benedict, 1904, *A. steinitzi* Holthuis, 1958, *A. madagascariensis* Thomassin, 1973, and *A. danai* new species.

Materials, Methods, and Morphological Terminology

Materials.—Specimens for this study came from the collections of the American Museum of Natural History, New York (AMNH), Bernice P. Bishop Museum, Honolulu, Hawaii (BPBM), California Academy of Sciences, Invertebrate Zoology, San Francisco (CASIZ), Musée Royal de l'Afrique Centrale, Tervuren, Belgium (MRAC), Queensland Museum (QM), University Museum of Zoology, Cambridge (UMZC), National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), Western Australian Museum, Perth (WAM), and Yale Peabody Museum, New Haven, Connecticut (YPM).

Methods.—Carapace length (CL), as measured from the midpoint of the anterior margin (including rostrum) to the midpoint of the posterior concavity, is provided as an indicator of specimen size. In the list of synonyms, asterisks refer to publications citing material examined during the present study. Absence of an asterisk in a specific entry does not imply that the identifications therein are in doubt, but only that it was not possible to examine the material cited in that publication.

Illustrations were created using a modified approach of Harvey & De Santo (1997). Specimen images were first captured on a Macintosh™ computer with a digital camera connected to a Wild M8 dissecting microscope. These images were then prepared using the programs Adobe Photoshop™ and Adobe Illustrator™. I attempted to record the position and size of setae in these drawings as accurately as possible, although for clarity of presentation the plumules of plumose setae were not drawn.

Morphological terminology.—During the course of this study and that of Boyko & Harvey (in press), several important diagnostic morphological features were encountered that have not been described previously for albuneids. Although these, along with other features, are discussed in Boyko & Harvey (in press), they are also considered here to facilitate a clearer understanding of the descriptive terms used in this paper.

The front of the carapace of albuneids bears a broad mat of very short, dense, simple setae. This mat, hereafter called the setal field, varies in shape and extent across genera and species, but appears to be relatively invariant within species. The carapace also possesses numerous transverse, setose grooves. Although carapace grooves (CG) have been scarcely mentioned by previous authors, 11 major grooves (numbered 1–11, Fig. 1) have been identified which can be recognized across albuneid genera. Variability in the presence and the degree of fragmentation of specific grooves, in the anterior-posterior displacement of individual fragments, and in the texture of the grooves (e.g., smooth, crenulate) tends to be conservative within species, and thus carapace grooves are useful in recognizing species.

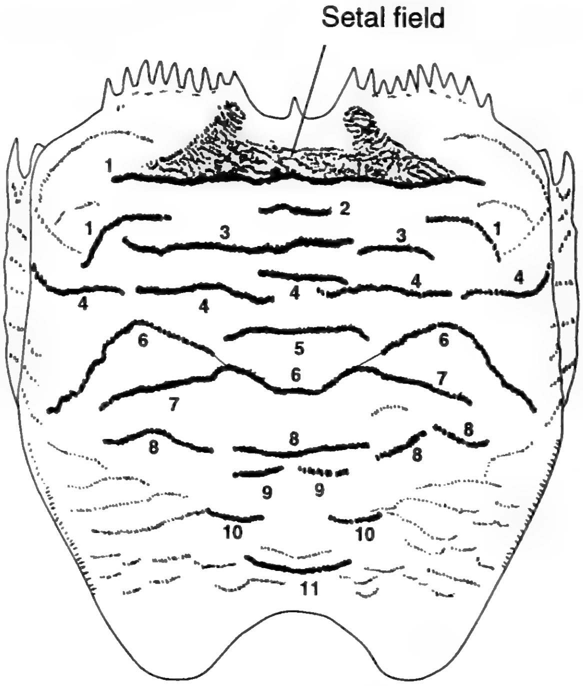

Fig. 1. Diagrammatic albuneid carapace based on *Albunea microps* Miers, 1878, showing setal field and setose carapace grooves (CG 1-11) discussed in text.

Because several of the specimens examined during this study were incorrectly sexed, brief remarks on the determination of male and female identity in albuneids are presented here. As in most decapod crustaceans, albuneid females have gonopores on the coxae of the third pereopods, whereas males have gonopores on the coxae of the fifth pereopods. However, in some albuneid genera (e.g., *Lepidopa* Stimpson, 1858 and some *Albunea,* including both species from Hawaii), males also have a small pore on the coxa of the third pereopod in a position analogous to that of the female gonopore. The precise nature and function of this pore is unknown.

In albuneids, females have well developed uniramous pleopods on abdominal so-

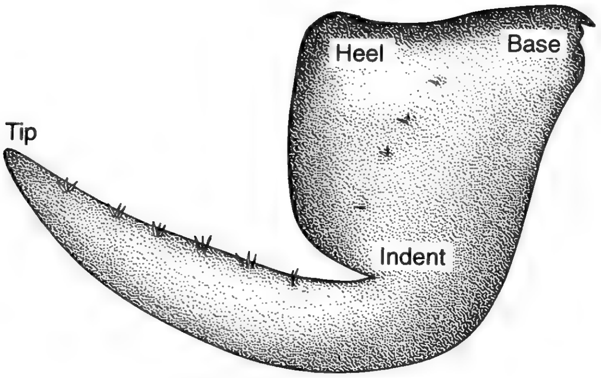

Fig. 2. Pereopod II dactyl of *Albunea* sp., lateral view, showing terms used in species accounts for landmarks on pereopod dactyli.

mites II–V. Male albuneids have traditionally been considered to lack pleopods (Efford & Haig, 1968). However, rudimentary or small pleopods were found on abdominal somites II–V of male specimens with well developed gonopores on the fifth pereopods in species of several albuneid genera (e.g., *Lepidopa*). In some *Albunea* species (e.g., *A. microps, A. speciosa*), specimens with large pores on the fifth pereopods and with small pores on the coxae of the third pereopods, show no signs of pleopod development. In those species in which the male pore occurs, it is always smaller than gonopores of same-sized females; likewise, the pleopods of females are always much more developed than those of males. Males are most reliably recognized by the presence of a gonopore on the fifth pereopod and the rudimentary degree of development of the pleopods or lack thereof. In small specimens, however, the presence or absence of the male gonopore is a more reliable indicator of sex than is pleopod development because both males and females may have small pleopod buds as juveniles.

The shape of the dactylus of the pereopods, particularly the third pereopod, has been used to distinguish among species of albuneids. To facilitate the description of the complex shape of this segment, several terms are used to refer to important landmarks (Fig. 2). The "base" of the dactylus is the ventroproximal angle; the "heel" corresponds to the dorsoproximal angle, which is often strongly produced. The dorsal margin is almost always concave, sometimes smoothly so; in most species, however, the dorsal margin has a distinct angle, the apex of which is referred to as an "indent." The dactylus terminates in a "tip," which is somewhat rounded and lacking in a corneous nail.

In some species of albuneids, certain segments of the pereopods bear a large transparent, decalcified area, hereafter called the "window," that has not been previously reported in this family. This area, when present, is most prominent on the lateral surface of the merus, where it is comparable to the "leg membranes" of porcelain crabs (Porcellanidae) discussed in detail by Stillman & Somero (1996). These windows can also be found to a lesser degree on other pereopod segments, both laterally and mesially.

Superfamily Hippoidea Latreille, 1825
Family Albuneidae Stimpson, 1858
Albunea Weber, 1795
Albunea speciosa Dana, 1852
Figs. 3, 4

Albunaea speciosa Dana, 1852: 405–406; 1855: pl. 25, figs. 6a–f.—Stimpson, 1858: 230 (list).

Albunea speciosa.—Miers, 1878: 315 (list), 331 (after Dana, 1852).—Ortmann, 1896: 223 (key), 225 (list), 239 (table).—Gordon, 1938: 187 (list).—Edmondson, 1946: 266.—Serène, 1973: 262–263, pl. 2.

"?*Albunea speciosa*".—Borradaile, 1904: 751*.

Material examined.—Neotype: Hawaii, Oahu, 27 May 1938: 1 male, 9.0 mm CL (USNM 260868); same data as neotype: 2 males, 9.5–10.4 mm CL, 1 female, 14 mm CL (USNM 287087); Kailua, Oahu, Mar 1938: 1 male, 10.1 mm CL (BPBM S11781); Honolulu Harbor, Oahu, coll. E. M. Ehrhon, Dec 1916: 2 males, 6.4–9.9 mm CL, 1 female, 7.3 mm CL (CASIZ 109240); Halonu Blow Hole dive site, south shore, Oahu, coll. R. Holcom, 3 Aug 1997: 1 fe-

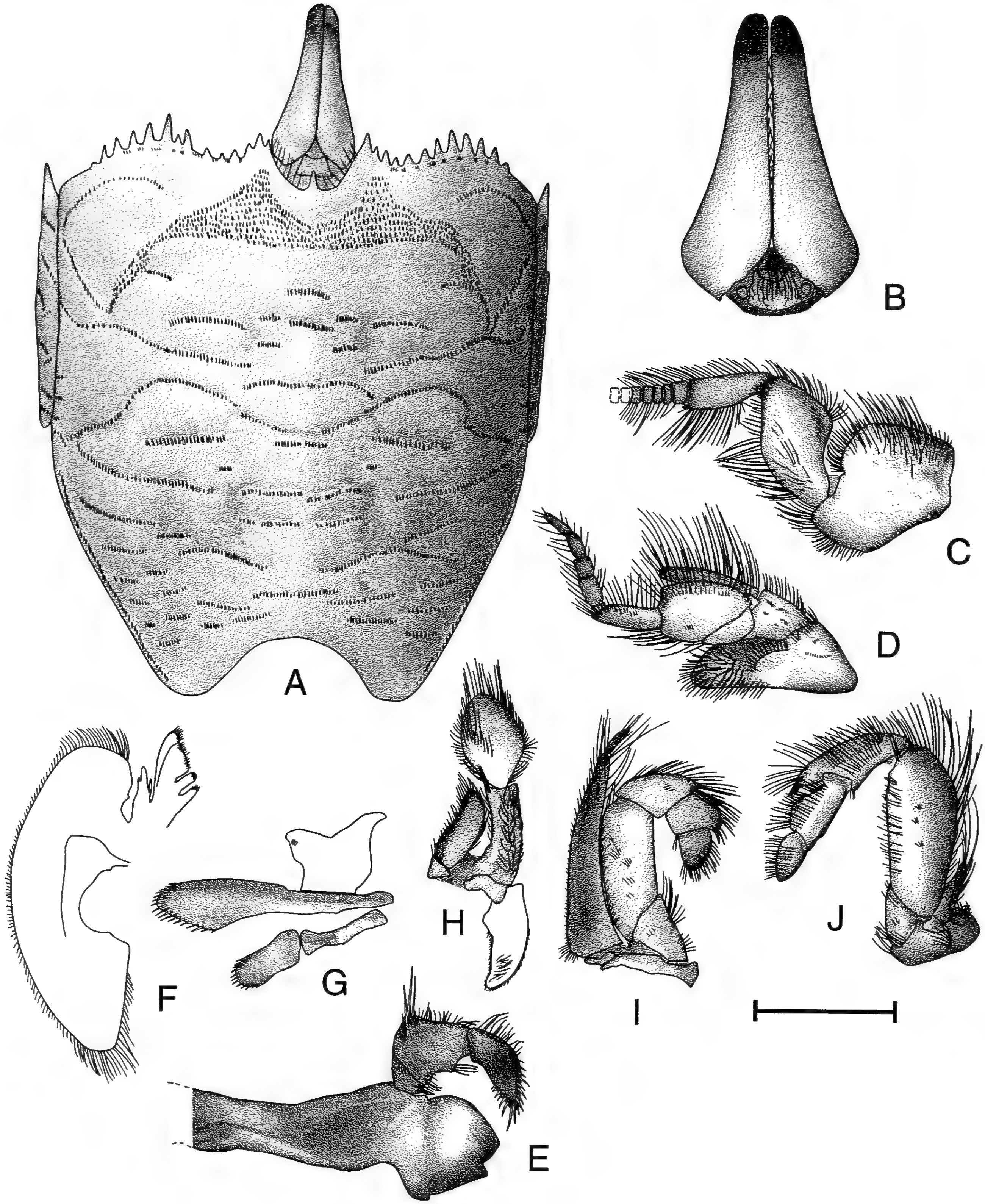

Fig. 3. *Albunea speciosa* Dana, 1852. A, male, 9.0 mm CL, USNM 260868, neotype; B–J, male, 10.4 mm CL, USNM 287087. A, carapace and eyes, dorsal view; B, eyes, dorsal view; C, left antennule, lateral view; D, left antenna, lateral view; E, left mandible; mesial view; F, right maxilla, lateral view; G, left maxillule, lateral view; H, left maxilliped I, lateral view; I, right maxilliped II, lateral view; J, left maxilliped III, lateral view. Scale = 1.6 mm (B, E, G), 2.2 mm (I), and 3.3 mm (A, C, D, F, H, J).

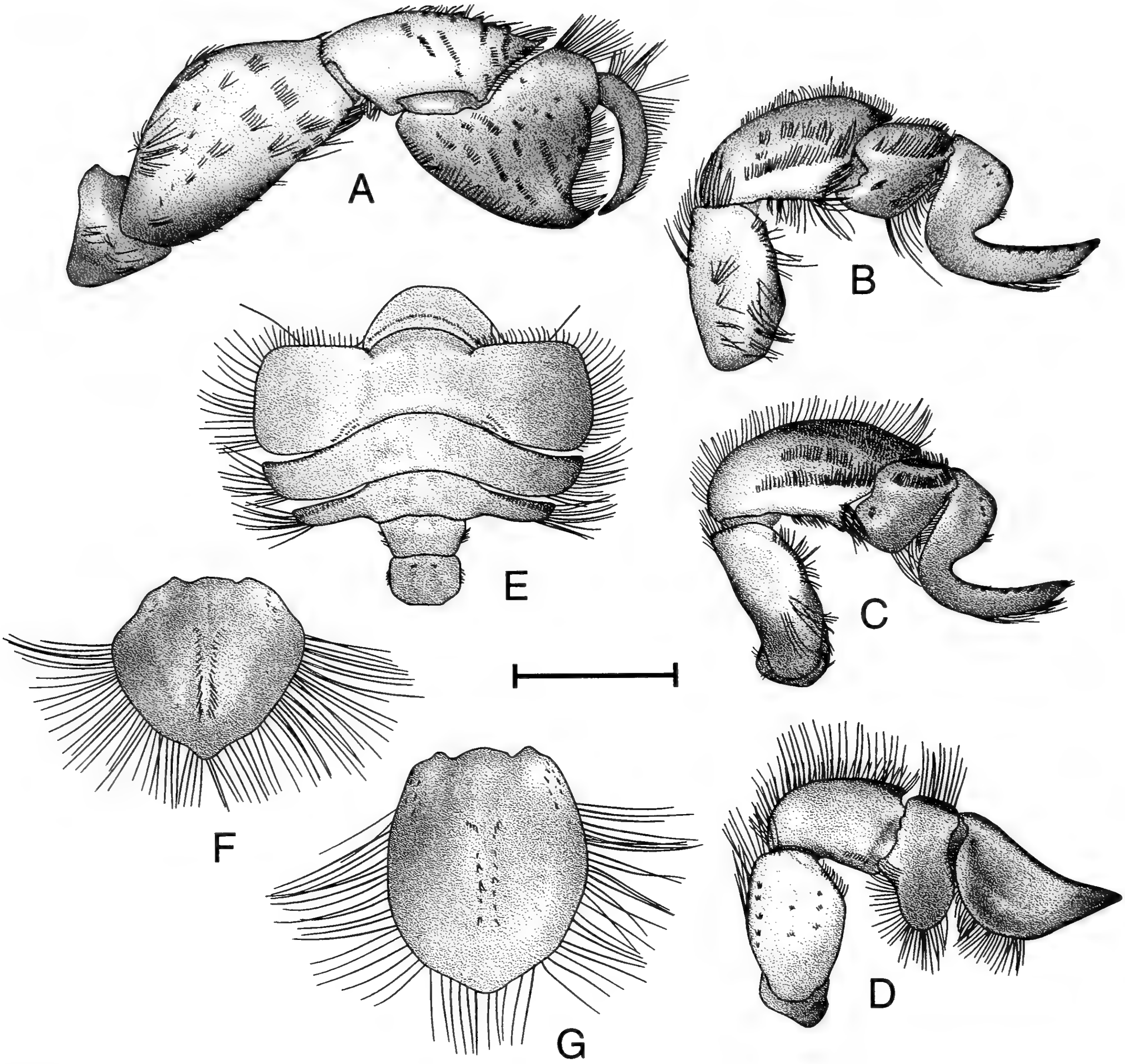

Fig. 4. *Albunea speciosa* Dana, 1852. A–E, male, 10.4 mm CL, USNM 287087; F, male, 9.0 mm CL, USNM 260868, neotype; G, female, 14 mm CL, USNM 287087. A, right pereopod I, lateral view; B, right pereopod II, lateral view; C, right pereopod III, lateral view; D, right pereopod IV, lateral view; E, abdominal somites I–VI, dorsal view; F, telson of male, dorsal view; G, telson of female, dorsal view. Scale = 3.0 mm (F, G), 4.0 mm (A–D), and 4.2 mm (E).

male, 6.6 mm CL, 1 broken unsexable/unmeasurable specimen (QM W22284); Halonu Blow Hole dive site, south shore, Oahu, 12.2–13.7 m, coll. R. Holcom, 4 Apr 1997: 2 males, 6.4–7.1 mm CL, 3 females, 5.7–9.5 mm CL, 6 juveniles, 3.3–4.1 mm CL (QM W22285); Oahu, coll. R. Holcom, Apr 1997: 2 ovigerous females, 7.5 mm CL (QM W22286); "Hawaii," coll. C. M. Cook Jr., 1897: 1 female, 10 mm CL (YPM 21133).

Australia: Bay on north side of Point Cloates, lee side of reef, Western Australia, 113°38′E, 22°41′S, depth 3.7 m, coll. WAM Ningaloo Expedition, 23 Aug 1968: 1 male, 8.7 mm CL, 1 carapace, 9.1 mm CL (WAM 489-97); southwest of Point Cloates, Western Australia, 113°39′30″E, 22°43′30″S, coll. WAM Ningaloo Expedition, 7 Sep 1968: 1 ovigerous female, 9.7 mm CL (WAM 490-97).

Seychelles: Mahé, coll. Mission Zoologique MRAC-ULB, July–Sep 1966: 1 ovigerous female, 9.9 mm CL (MRAC 53.894).

Maldives: Hulule, Male Atoll, coll. J. S. Gardiner: 1 male, 8.4 mm CL (UMZC).

Type locality.—Sandwich Islands (= Hawaiian Islands) (Dana, 1852) herein restricted by neotype selection to Oahu, Hawaii, USA, Pacific Ocean.

Type material.—It is unclear exactly how many specimens of this species Dana (1852) had before him when writing the description of this species, but the description suggests that there was only one. No type material of this species is extant in either USNM, the Museum of Comparative Zoology, Harvard University, or the British Museum (Natural History) (Evans 1967; Boyko, pers. obs.). Because these institutions are the only known repositories for Dana's extant type material (Evans 1967), the type material of *A. speciosa* must be considered lost. In light of the new information about the range of *A. speciosa,* and the discovery of a new species of albuneid in the Hawaiian Islands which has been repeatedly misidentified as *A. speciosa,* it is appropriate to follow the suggestion of Serène (1973) and select a neotype for the species. A male, 9.0 mm CL (USNM 260868) is herein designated as the neotype for *Albunea speciosa.*

Diagnosis.—Carapace slightly longer than wide, covered with strongly setose grooves. Anterior margin with 13–17 teeth on either side of ocular sinus. Setal field with narrow lateral elements and concave anterior margin; posterior lateral elements extending to posterior lateral elements of CG1. CG1 with separate posterior lateral elements but with anterior and posterior elements united by posterior elements of setal field; CG4 with 2–3 short anteriorly displaced medial elements; CG5 entire, nearly reaching margins of CG6; CG6 and CG7 separate; CG8 with 1–2 median elements separated from lateral elements; CG11 present. Rostrum reaching just beyond proximal margin of ocular plate. Ocular plate subquadrate. Ocular peduncles dorsoventrally flattened and elongate, rounded at tip, approximate along mesial margin; lateral margin concave; mesial margin straight. Cornea at tip of ocular peduncle. Antennule with 48–53 flagellar exopod and 2 endopodal segments. Antenna with 5–6 flagellar segments; acute spine on dorsolateral surface of peduncle segment I. Dactyli of pereopods II, III with heels low and smoothly rounded. Coxa of pereopod III of males with small male pore. Telson of male spatulate, laterally expanded, dorsoventrally flattened; produced slightly at tip. Telson of female flattened, rounded at tip.

Redescription.—Carapace (Fig. 3a) slightly wider than long. Anterior margin concave on either side of ocular sinus, becoming convex laterally with 10–12 large and 3–4 small spines along length. Rostrum a small acute tooth, reaching just beyond proximal margin of ocular plate. Ocular sinus smoothly concave, unarmed. Frontal region smooth; setal field broad posteriorly, narrowing anteriorly, with narrow anterior lateral elements and concave anterior margin; posterior lateral elements reaching to posterior lateral elements of CG1. Medial portion of CG1 parallel to anterior margin of carapace, sinuous, slightly crenulate, divided into medial fragment and curved posteriorly-displaced lateral elements, but with medial and lateral elements connected by posterior lateral elements of setal field. Mesogastric region smooth; CG2 short, with 1–2 elements; CG3 broken into 2 longer lateral elements and 1–3 short medial elements; CG4 with 2–3 short medial elements displaced anteriorly, with gap at midline between short elements. Hepatic region smooth with long setose groove at median of lateral margin. Epibranchial region approximately triangular, smooth; posterolateral margin with 3 short rows of setae. Metagastric region smooth; CG5 ranging from entire to 4 elements, nearly reaching margins of CG6. CG6 strongly crenulate, strongly anteriorly concave medially and sloping out to anteriorly convex lateral thirds. CG7 nearly straight relative to anterior margin of carapace and separate from CG6. Cardiac region smooth; CG8 with 1–

2 median elements separated from lateral elements. CG9 present as 2 lateral grooves with short gap at midline. CG10 present as 2 curved lateral fragments, with gap between fragments about half length of single fragment. CG11 present. Branchial region with numerous short, transverse rows of setae. Posterior margin deeply and evenly convex, with submarginal groove reaching about half-way either side of posterior concavity. Branchiostegite with short anterior submarginal spine; anterior region with scattered short transverse lines ventral to linea anomurica; with many short rows of setae and sparsely covered with long plumose setae ventrally; posterior region membranous, with numerous irregular fragments, and sparsely covered with long plumose setae.

Ocular plate (Fig. 3b) subquadrate, with broad median indentation; proximal ocular segments (Fig. 3b) reduced to small rounded calcified area on either side of ocular plate. Ocular peduncles (Fig. 3b) elongate, with medially concave lateral margins, tapering to rounded distal corneae; mesial margins approximated along entire length; mesial and ventral margins of peduncle with sparse row of long plumose setae; tuft of plumose setae at proximal lateral ventral angle.

Antennule (Fig. 3c) segment III narrow proximally, expanding distally to twice proximal width; with plumose setae on dorsal and ventral margins; dorsal exopodal flagellum with 48–53 segments and long plumose setae on dorsal and ventral margins; ventral endopodal flagellum short, with 2 segments and plumose setae on dorsal and ventral margins. Segment II medially inflated in dorsal view, with plumose setae on dorsal and ventral margins, and setae scattered on ventrolateral third of surface. Segment I wider than long, unarmed; dorsal third of lateral surface faintly rugose with long plumose setae; long plumose setae on dorsal and ventral margins.

Antenna (Fig. 3d) segment V about 3 times longer than wide, with long plumose setae on dorsal and ventral margins; flagellum 5–6 segmented, with long plumose setae on dorsal, ventral and distal margins. Segment IV expanded distally, with long plumose setae on dorsal, ventral and distal margins, and row of setae on dorsolateral margin. Segment III with long plumose setae on ventral margin. Segment II short, widening distally, with plumose setae on margins; antennal acicle long, thin, reaching to distal margin of segment IV, with long plumose setae on dorsal margin. Segment I rounded proximally, flattened ventrolaterally with long plumose setae on margins; lateral surface with acute spine dorsally, with low semicircular dorsolateral lobe ventrodistal to spine; segment with ventromesial antennal gland pore.

Mandible (Fig. 3e) incisor process with 1 tooth; cutting edge with 1 tooth. Molar process with 1–2 teeth. Palp 3-segmented, with plumose setae on margins and long, thick, simple setae arising from bend in second segment.

Maxilla (Fig. 3f) exopod evenly rounded, with plumose setae along distal margin. Scaphognathite bluntly angled on posterior lobe, with plumose setae. Endopod and endites without distinctive characters.

Maxillule (Fig. 3g) distal endite proximally narrow, widening to inflated distal end, with thick simple setae on distal margin. Proximal endite with thick simple setae on distal margin. Endopodal external lobe truncate distally and curled under; internal lobe reduced, with 3 thick setae at distolateral margin.

Maxilliped I (Fig. 3h) epipod with plumose setae on distal margin and distolateral surface. Endite tapered distally, subequal to first segment of exopod. Exopod with 2 segments; proximal segment narrow, margins parallel and with plumose setae; distal segment spatulate, about as long as wide, broadest medially, margins with long plumose setae. Endopod flattened and elongate, reaching to distal end of proximal exopodal segment; with plumose setae on margins.

Maxilliped II (Fig. 3i) dactylus evenly rounded, length equal to width, with thick simple setae distally. Propodus 1.5 times wider than long, with plumose setae on dorsal margin and long simple setae on distal margin. Carpus not strongly produced dorsodistally, about 2 times longer than wide, with long simple setae on dorsal margin. Merus about 3 times longer than wide, margins parallel, with simple setae on ventrolateral margin and plumose setae on dorsolateral margin. Basi-ischium incompletely fused, with plumose setae on margins. Exopod ¼ times longer than merus, with flagellum 1-segmented.

Maxilliped III (Fig. 3j) dactylus evenly rounded; with long plumose setae on dorsal margin and lateral surface. Propodus with longitudinal median row of plumose setae on lateral surface; dorsal margin with plumose setae. Carpus slightly produced onto propodus; lateral surface with row of plumose setae ventromedially; plumose setae on dorsal margin. Merus unarmed, with plumose setae on all margins. Basi-ischium incompletely fused, without crista dentata. Exopod 2-segmented, proximal segment small; distal segment styliform, tapering, approximately ⅓ length of merus, with plumose setae scattered on surface; without flagellum.

Pereopod I (Fig. 4a) subchelate. Dactylus curved and tapering; lateral and mesial surfaces smooth; dorsal margin with long plumose and short simple setae; ventral margin with short simple setae. Propodus lateral surface with numerous short, transverse rows of setose rugae; dorsal margin unarmed; ventral margin produced distally into acute spine; cutting edge lacking teeth, lined with long plumose setae; dorsal margin with long plumose setae, ventral margin with short simple setae. Carpus dorsodistal angle produced into strong corneous-tipped spine, dorsal margin with few large and small spines posteriorly along distal third; dorsal and distal margins with long plumose setae; lateral surface with small distal rugose area, with few transverse setose ridges on distal half of surface; mesial surface smooth with few scattered rows of long plumose setae, dorsal and ventral margins with long plumose setae. Merus unarmed; lateral surface with scattered transverse rows of long plumose setae, dorsal, ventral and distal margins with long plumose setae; mesial side with few short rows of setae. Basi-ischium incompletely fused, unarmed. Coxa unarmed.

Pereopods II–IV dactyli laterally compressed and dorsoventrally expanded.

Pereopod II (Fig. 4b) dactylus smooth; with base to heel straight, heel smoothly rounded, heel to tip with rounded broad indent, tip acute, tip to base broadly convex; lateral surface smooth, with several small tufts of short setae in approximately straight line across medioproximal surface, several widely-spaced submarginal tufts of short setae dorsodistally; mesial surface smooth, ventral margin with long plumose setae, dorsal margin with short simple setae, with patch of long plumose setae at base. Propodus dorsal surface smooth, ventral margin inflated and rounded; oblique row of long plumose setae on distal margin of lateral surface; distal and ventral margins with long plumose setae; dorsolateral surface a narrow, oblique, flattened shelf, with short setae on dorsal margin and long plumose setae on ventral margin; mesial surface with elevated, curved, setose ridge from ventral junction with dactylus almost to ventral proximal junction with carpus. Carpus slightly produced dorsodistally; lateral surface nearly smooth, with irregular broken row of rugae and submarginal elevated ridge ventrally, rugae and ridge with long plumose setae; dorsodistal projection with mat of short setae on lateral surface; margins with long plumose setae; mesial surface smooth with long plumose setae in scattered patches on surface, and on margins. Merus lateral surface with large decalcified window and few scattered setae on surface and margins; mesial surface nearly smooth with few setae. Basi-ischium incompletely fused, unarmed. Coxa with small spine on anterior margin.

Pereopod III (Fig. 4c) dactylus with base to heel straight, heel broadly rounded and low, heel to tip with broad evenly rounded indent, tip acute, tip to base smoothly convex to straight; lateral surface smooth, with several small tufts of short setae in roughly straight line across medioproximal surface, dorsodistal margin with tufts of short setae; ventromesial margin with long plumose setae, dorsal margin with short simple and plumose setae; mesial surface smooth, with plumose setae proximally at junction with propodus. Propodus not inflated dorsoventrally; lateral surface smooth, with long plumose setae distally, with simple setae on dorsal margins, and long plumose setae on ventral margin; dorsolateral surface narrow, oblique, flattened; mesial surface with scattered long setae on and near distal margin. Carpus produced dorsodistally, exceeding proximal margin of propodus by about ¼ length of propodus, pointed but not acute; dorsolateral margin unarmed; lateral surface slightly rugose dorsodistally, with mat of short setae and 2 longer rows of setae ventrally; mesial surface smooth, with long plumose setae on margins and scattered on surface. Merus smooth with large decalcified window; dorsal and ventral margins unarmed, with long plumose setae; laterodistal margin with long plumose setae; mesial surface smooth. Basi-ischium incompletely fused and unarmed. Coxa unarmed. Female with large gonopore on anterior mesial surface of coxa, surrounded with short plumose setae; male with small pore on coxa.

Pereopod IV (Fig. 4d) dactylus with base to tip proximally convex becoming concave, heel and indent absent, tip acute, tip to base straight distally becoming convex proximally; lateral surface smooth, ventral margin with long plumose setae, dorsal margin with short simple setae; mesial surface with dorsal decalcified window, demarcated ventrally by longitudinal elevated ridge bearing row of short setae; with setose punctae ventral to decalcified window. Propodus expanded dorsally and ventrally; ventral expansion exceeds ventral margin of dactylus, margin with long plumose setae; dorsal expansion with row of long plumose setae medially; lateral and mesial surfaces smooth. Carpus not produced dorsodistally; lateral and mesial surfaces smooth; dorsal margin with short simple and long plumose setae; ventral margin with short simple setae; mesial surface with decalcified window. Merus lateral surface with scattered short transverse rows of setae, dorsal and ventrodistal margins with long plumose setae; mesial surface with large decalcified window proximoventrally. Basi-ischium incompletely fused and unarmed. Coxa unarmed.

Pereopod 5 reduced, slender, lacking distinctive features. Coxa of male with large mesioproximal gonopore.

Abdomen (Fig. 4e) somite I approximately as long as wide, widest posteriorly; dorsal surface with anterior margin straight; posterior margin straight, with elevated submarginal row of short setae; with small transverse decalcified windows laterad to segment midline. Somite II dorsal surface with submarginal transverse ridge anteriorly; with small transverse decalcified windows laterad to segment midline just anterior to submarginal ridge; with tuft of setae at posterolateral angle, extending onto pleura posteromesially; posterior margin with indistinct punctate submarginal groove laterally; pleura expanded and directed slightly anteriorly; lateral margins rounded, anterior and lateral margins with long plumose setae, posterior margin with short setae. Somite III similar to somite II, but narrower, shorter, and lacking anterior submarginal ridge; small tuft of short thick setae on posterolateral angle; pleura thinner and shorter than on somite II, directed anterolaterally, with setae as in somite II; anterolateral angle acute; dorsal surface obliquely flattened anterolaterally. Somite IV similar to somite III, but thinner and shorter; dorsal surface with thick setae posterolaterally; pleura thinner and shorter than on somite III, directed posterolaterally; dorsal surface obliquely flattened anterolaterally; margin with long plumose setae. Somite V narrower than somite IV; lateral margins with short plumose setae; pleura absent. Somite VI subequal to somite V in width but longer; dorsal surface with short transverse rows of setae laterad to midline anteriorly; lateral margins with long plumose setae; pleura absent.

Females with uniramous, paired pleopods on somites II–V; males lacking pleopods.

Uropods lacking distinctive features.

Telson of male (Fig. 4f) spatulate, laterally expanded, with length subequal to width, produced into short rounded tip distally; weakly calcified except for large triangular anterior plate; median longitudinal groove long, extending to distal end of calcified plate, lined with long thin simple setae; calcified plate slightly elevated medially but without ridge. Telson of female (Fig. 4g) ovate, longer than wide, broadly triangular, dorsal surface smooth, with median longitudinal groove anteriorly; with row of setose punctae lateral to midline from median of longitudinal groove to distal end of groove; margins with long plumose setae.

Coloration.—Off-white with whitish setae in life and in preservative.

Distribution.—Indo-West Pacific: Hawaii; Western Australia; Seychelles; Maldives; 3.7–13.7 m.

Remarks.—This species can easily be separated from all of the other Indo-West Pacific species of *Albunea,* except *A. madagascariensis,* by the concave shape of the lateral margins of the eyes. Although a direct comparison of *A. speciosa* with *A. madagascariensis* material is desirable, the types (and only known specimens) of *A. madagascariensis* apparently were not deposited in the Muséum National d'Histoire Naturelle (MNHN), contrary to Thomassin (1973) (Nguyen, pers. comm.). Nevertheless, based on Thomassin's (1973) description and illustrations, the two species can tentatively be separated by several characters. *A. speciosa* has a short rostrum that does not reach the distal margin of the ocular plate, a CG4 comprised of two medial elements, a more truncate heel of pereopod III, and a rounded distal tip on the telson of the male, while *A. madagascariensis* has a long rostrum that well exceeds the distal margin of the ocular plate, a CG4 of 1 medial element, a rounded heel of pereopod III, and a pointed distal tip on the telson of the male. Given a larger sample size, particularly from the westernmost Indo-Pacific, all of these characters may prove to represent only intraspecific variation of *A. speciosa,* in which case *A. madagascariensis* would become a synonym of *A. speciosa.* Two of Thomassin's specimens exhibited a peculiar orange and brown banding pattern (Thomassin 1973: 268, pl. 1). No other species of *Albunea* have been reported with anything but almost uniform coloration, suggesting the possibility that this may have been an artifact of the environment. More study is needed to determine whether this is similar to the type of environmentally-induced color changes observed in mole crabs of the genus *Hippa* Fabricius, 1787 (e.g., Bauchau & Passelecq-Gérin 1987).

Little is known about the biology of this species other than the few records of ovigerous females herein reported. Several *A. speciosa* specimens (QM W22285) were collected together with the holotype of *Albunea danai* new species, but it is unknown if the two species regularly coexist.

Specimens of *A. speciosa* have been reported only three times in the literature (Dana 1852, Borradaile 1904, Serène 1973). Examination of Borradaile's (1904) specimen from the Maldives confirms its identity as this species, making Borradaile's (1904) record the first from outside Hawaii, although his paper was overlooked by subsequent researchers.

Because *A. speciosa* is now known to be a wide-ranging Indo-Pacific species, rather than a Hawaiian endemic, it would be useful to understand the origin and subsequent distribution of this species in order to better understand albuneid biogeography. The Hawaiian specimens of *A. speciosa* are far removed from other populations of this species, a phenomenon that has been shown for other wide-ranging Hawaiian shallow-water fauna with western Indo-Pacific affinities (Newman 1986), and they probably reached the relatively young Hawaiian Islands by long distance dispersal. However, the closest locality where this species has been reported is not from the Philippines or nearby islands in the northern Indo-Pacific, but rather from Western Australia to the south. Unless the species is found on the east coast of Australia or in the island groups to the east, such as the New Hebrides or Society Islands, it is difficult to hypothesize the eastward dispersal route by which *A. speciosa* reached the Hawaiian Islands. A northern or southern dispersal route across the Pacific appears equally likely, given the evidence currently available.

Albunea danai, new species
Figs. 5, 6

Type material.—Holotype: Hawaii, Halonu Blow Hole dive site, south shore, Oahu, 12.2–13.7 m, coll. R. Holcom, 4 Apr 1997: 1 male, 16.7 mm CL (QM W23105). Allotype: Kailua, Oahu, Mar 1938: 1 female, 16.8 mm CL (BPBM S11782). Paratypes: Waikiki, Oahu, 22.7 m, coll. Smith and Allen, 23 May 1948: 1 male, 11.6 mm CL (BPBM S5343); off Waikiki, Oahu, 6.1 m, coll. Allen and Smith, 30 May 1948: 1 female, 10.8 mm CL (AMNH 17716); Kahana Bay, Oahu, 7.6–9.1 m, coll. "Pele" Expedition, 25 Jul 1959: 1 male, 8.6 mm CL (BPBM S6775); off Sand Island, Oahu, 4.8-7.6 m, coll. "Pele" Expedition, 17 July 1959: 1 male, 10.4 mm CL (AMNH 17717); Diamond Head, Oahu, 7.6–13.6 m, coll. "Pele" Expedition, 9 Sep 1959: 1 female, 13.0 mm CL (BPBM S6777); [Mamala Bay], off Honolulu, Oahu, 27.4–40.2 m, coll. T. Richert, Feb–Mar 1962: 1 male, 16.4 mm CL, 1 female, 15.5 mm CL (WAM 481-97); [Mamala Bay], off Ewa Beach, near Pearl Harbor, Oahu, 27.4 m, coll. B. R. Wilson on R/V "Pele," 5 Jul 1964: 1 ovigerous female, 10.8 mm CL (WAM 143-70).

Additional material examined (non type).—Hawaii: Kanoehe Bay, Oahu, 1924: 1 male (poor condition), 4.0 mm CL (BPBM S7806).

Type locality.—Halonu Blow Hole dive site, south shore, Oahu, Hawaii, USA, Pacific Ocean.

Diagnosis.—Carapace slightly longer than wide, covered with lightly setose grooves. Anterior margin with 8–9 teeth. Setal field with narrow lateral elements and slightly concave anterior margin; posterior lateral elements not extending to posterior lateral elements of CG1. CG1 with separate posterior lateral elements; CG4 with 2–4 short medial elements; CG5 divided into 2 lateral elements, not nearly reaching margins of CG6; CG6 and CG7 separate, but almost approximate; CG8 with 1–2 posteriorly displaced median elements separated from lateral elements; CG11 absent. Rostrum present, not reaching proximal margin of ocular plate. Ocular plate subquadrate. Ocular peduncles dorsoventrally flattened and elongate, pointed at tip, approximate along mesial margin; lateral margin convex; mesial margin straight proximally, convex distally. Cornea at lateral margin of tip. Antennule with 87–92 flagellar exopodal and 3–4 endopodal segments. Antenna with 7 flagellar segments; acute spine on dorsolateral surface of peduncle segment I. Dactyli of pereopods II, III with heels low and smoothly rounded. Coxa of pereopod III of males with small male pore. Telson of male triangular, dorsoventrally flattened laterally and distally, inflated medially. Telson of female flattened, rounded at tip.

Description.—Carapace (Fig. 5a) slightly wider than long. Anterior margin slightly concave on either side of ocular sinus, becoming convex laterally, with 8–9 large spines along length. Rostrum a small acute

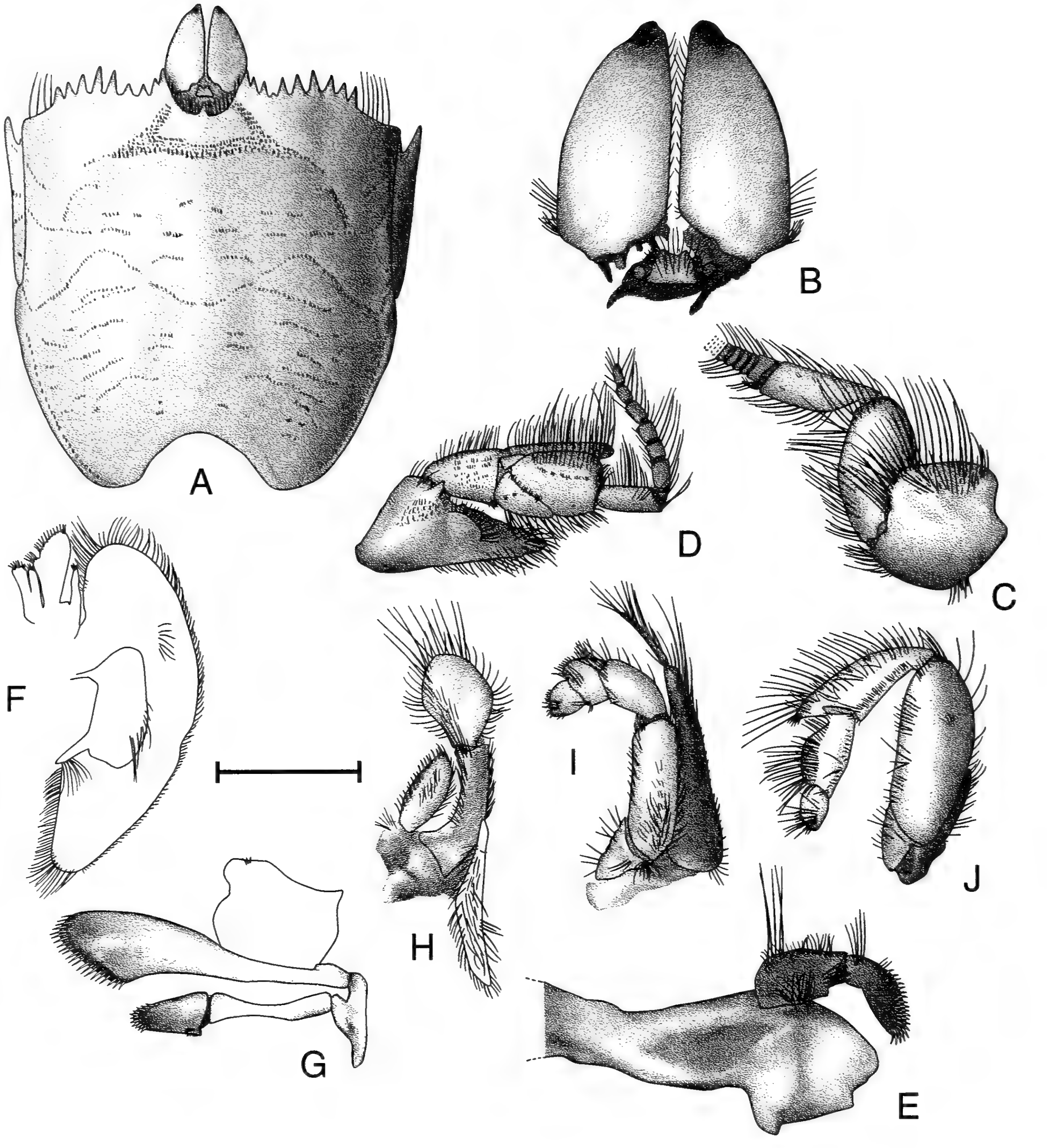

Fig. 5. *Albunea danai,* new species. A, male, 16.7 mm CL, QM W23105, holotype; B–F, H–J, ovig. female, 10.8 mm CL, WAM 143-70; G, male 11.6 mm CL, BPBM 5343. A, carapace and eyes, dorsal view; B, eyes, dorsal view; C, left antennule, lateral view; D, right antenna, lateral view; E, left mandible, lateral view; F, left maxilla, lateral view; G, left maxillule, lateral view; H, left maxilliped I, lateral view; I, left maxilliped II, lateral view; J, left maxilliped III, lateral view. Scale = 1.2 mm (C, D, F, H, J), 1.6 mm (B, E, G), 2.2 mm (I), and 6.7 mm (A).

tooth, extending only half the distance between distal margin of ocular sinus and ocular plate. Ocular sinus smoothly concave and unarmed. Frontal region smooth; setal field broad posteriorly, narrowing anteriorly, with narrow anterior lateral elements and slightly concave anterior margin; posterior lateral elements thin and not reaching to posterior lateral elements of CG1. CG1 medial portion parallel to anterior margin of carapace, faintly sinuous, strongly crenulate, divided into medial fragment and curved, posteriorly displaced lateral elements. Mesogastric region smooth; CG2

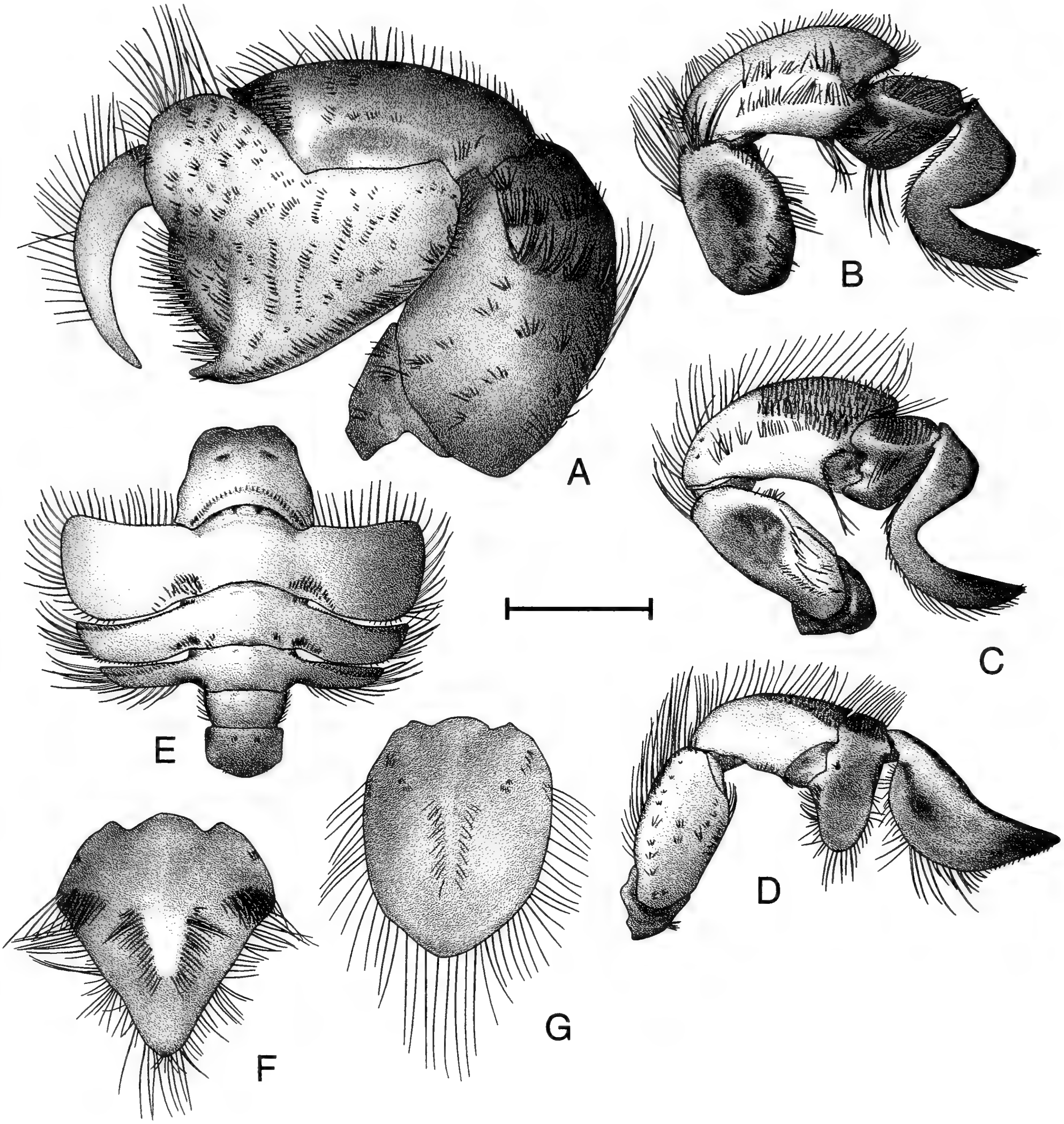

Fig. 6. *Albunea danai,* new species. A, F, male, 16.7 mm CL, QM W23105, holotype; B–E, male 11.6 mm CL, BPBM 5343; G, female, 16.8 mm CL, BPBM S11782, allotype. A, left pereopod I, lateral view; B, right pereopod II, lateral view; C, right pereopod III, lateral view; D, right pereopod IV, lateral view; E, abdominal somites I–VI, dorsal view; F, telson of male, dorsal view; G, telson of female, dorsal view. Scale = 3.0 mm (F, G) and 4.4 mm (A–E).

absent; CG3 broken into 6 short elements approximately equally spaced between posterior lateral elements of CG1; CG4 with 2–4 short medial elements spaced approximately equally between longer lateral elements of CG4. Hepatic region smooth with oblique setose groove at median of lateral margin. Epibranchial region roughly triangular, smooth; posterolateral margin with 2 short rows of setae. Metagastric region smooth; CG5 divided into 2 short lateral elements. CG6 strongly crenulate, strongly anteriorly concave medially and sloping out to anteriorly convex lateral thirds, median and lateral thirds separated by short setae-free gap lateral to small depressions. CG7 oblique, almost reaching lateral margins of median segment of CG6. Cardiac region smooth; CG8 present as 2 very short lateromedial elements displaced posteriorly from longer lateral elements. CG9 present as 2 short lateral grooves with gap at midline. CG10 present as 2 curved lateral fragments, with gap between fragments approximately equal to length of single fragment. CG11 absent. Branchial region with numerous short, transverse rows of setae. Posterior margin deeply and evenly convex, with submarginal groove reaching about half-way either side of posterior concavity. Branchiostegite with short anterior submarginal spine; anterior region with scattered short transverse lines ventral to linea anomurica; with many short rows of setae and sparsely covered with long plumose setae ventrally; posterior region membranous with numerous, irregular fragments and sparsely covered with long plumose setae.

Ocular plate (Fig. 5b) subquadrate with narrow indentation; proximal ocular segments (Fig. 5b) reduced to small rounded calcified area on either side of ocular plate. Ocular peduncle (Fig. 5b) elongate, with medially convex lateral margins, tapering to rounded distal cornea located in lateral notch; mesial margin approximate almost all of length; mesial and proximolateral margins of segment with sparse row of long plumose setae; tuft of plumose setae at proximolateral ventral angle.

Antennule (Fig. 5c) segment III narrow proximally, expanding distally to twice proximal width; with plumose setae on dorsal and ventral margins and sparsely scattered on lateral surface; dorsal exopodal flagellum with 87–92 segments and long plumose setae on dorsal and ventral margins; ventral endopodal flagellum short, with 3–4 segments and plumose setae on dorsal and ventral margins. Segment II medially inflated in dorsal view, with plumose setae on dorsal and ventral margins and scattered setae on ventrolateral third of surface. Segment I wider than long, unarmed; dorsal third of lateral surface rugose with long plumose setae; long plumose setae on dorsal and ventral margins.

Antenna (Fig. 5d) segment V about 2 times longer than wide, with long plumose setae on dorsal margin and scattered setae on distal half of lateral surface; flagellum 7-segmented, with long plumose setae on dorsal, ventral and distal margins. Segment IV expanded distally with long plumose setae on dorsal, ventral and distal margins, and 2 rows of setae on dorsolateral surface. Segment III with long plumose setae on dorsal and ventral margin. Segment II short, widening distally, with plumose setae on margins and scattered on lateral surface; antennal acicle long, thin and exceeding distal margin of segment IV by ¼ the length of segment IV, with long plumose setae on dorsal margin. Segment I rounded proximally, flattened ventrolaterally, with long plumose setae on margins; lateral surface with acute spine dorsally, with low semicircular dorsolateral lobe ventrodistal to spine; segment with ventromesial antennal gland pore.

Mandible (Fig. 5e) incisor process with 1 tooth; cutting edge with 1 tooth. Molar process with 2–3 teeth. Palp 3-segmented, with plumose setae on margins and long, thick, simple setae arising from bend in second segment.

Maxilla (Fig. 5f) exopod evenly rounded, with plumose setae along distal margin. Scaphognathite bluntly angled on posterior lobe, with plumose setae. Endopod and endites without distinctive characters.

Maxillule (Fig. 5g) distal endite proximally narrow, widening to inflated distal end, with thick simple setae on distal margin. Proximal endite with thick simple setae on distal margin. Endopodal external lobe truncate distally, and curled under; internal lobe reduced, with 3 thick setae at distolateral margin.

Maxilliped I (Fig. 5h) epipod with plumose setae on margins, distolateral surface and mesial surface (epipod shown curled in Fig. 5h). Endite tapered distally and subequal to first segment of exopod. Exopod with 2 segments; proximal segment narrow, margins parallel, margins with plumose setae; distal segment spatulate, about as long as wide, broadest medially, margins and mesioventral surface with long plumose setae. Endopod flattened and elongate, reaching to distal end of proximal exopodal segment; plumose setae on margins and median of lateral surface.

Maxilliped II (Fig. 5i) dactylus evenly rounded, length equal to width, with thick simple setae distally and on distolateral surface. Propodus 2 times wider than long, slightly produced at dorsodistal angle, with plumose setae on dorsal margin and long simple setae on dorsodistal margin. Carpus not produced dorsodistally, about 2 times longer than wide; long simple setae on dorsal and distal margins. Merus about 3 times longer than wide, margins parallel; with simple setae on ventrolateral margin and plumose setae on dorsolateral margin. Basi-ischium incompletely fused, plumose setae on margins. Exopod ⅓ times longer than merus, with flagellum 1-segmented.

Maxilliped III (Fig. 5j) dactylus with rounded tip; with long plumose setae on dorsal margin and lateral surface. Propodus with longitudinal median row of plumose setae on lateral surface; dorsal margin with plumose setae. Carpus slightly produced onto propodus; lateral surface with row of plumose setae ventromedially; plumose setae on dorsal margin. Merus unarmed, with plumose setae on dorsal and ventral margins and scattered on lateral surface. Basi-ischium incompletely fused, with weak crista dentata of about 2 teeth. Exopod 2-segmented: proximal segment small; distal segment styliform, tapering, approximately ⅓ length of merus; with plumose setae on surface; without flagellum.

Pereopod I (Fig. 6a) subchelate. Dactylus curved and tapering; lateral and mesial surfaces smooth; dorsal margin with long plumose and short simple setae; ventral margin with short simple setae. Propodus lateral surface with numerous short, transverse rows of setose rugae; dorsal margin unarmed; ventral margin produced distally into acute spine; cutting edge lacking teeth, lined with long plumose setae; dorsal margin with long plumose setae, ventral margin with short simple setae. Carpus with dorsodistal angle produced into strong corneous-tipped spine; dorsal margin otherwise unarmed; dorsal and distal margins with long plumose setae; lateral surface with small distal rugose area, with few transverse setose ridges on distal half of surface; mesial surface smooth with few median rows of setae, margins with long plumose setae. Merus unarmed; lateral surface with scattered transverse rows of long plumose setae, margins with long plumose setae; mesial side with few short rows of setae. Basi-ischium incompletely fused, unarmed. Coxa unarmed.

Pereopods II–IV with dactyli laterally compressed and dorsoventrally expanded.

Pereopod II (Fig. 6b) dactylus smooth; base to heel straight, heel smoothly rounded, heel to tip with wide acute indent, tip acute, tip to base broadly convex distally and slightly concave proximally; lateral surface smooth, with several small tufts of short setae in roughly straight line across medioproximal surface, several widely spaced submarginal tufts of short setae dorsodistally; mesial surface smooth, ventral margin with long plumose setae, dorsal margin with short simple setae, with patch of long plumose setae at base. Propodus dorsal surface smooth, ventral margin inflated and rounded; oblique row of long plumose setae on distal margin of lateral surface; distal and ventral margin with long plumose setae; dorsolateral surface a narrow, oblique, flattened shelf, with short setae on dorsal margin and long plumose setae on ventral margin; mesial surface with elevated, curved setose ridge from ventral junction with dactylus almost to ventral proximal junction with carpus. Carpus produced and gently rounded dorsodistally, dorsal margin unarmed; lateral surface smooth, with irregular broken row of rugae and submarginal elevated ridge ventrally, rugae and ridge with long plumose setae; margins with long plumose setae; mesial surface smooth with long plumose setae in scattered patches on dorsal half of surface and on margins. Merus with large median decalcified window covering nearly all of lateral surface, with few scattered setae on surface and margins; mesial surface nearly smooth with few setae, with decalcified area on proximal ¼ near junction with basi-ischium. Basi-ischium incompletely fused and unarmed. Coxa with small spine on anterior margin.

Pereopod III (Fig. 6c) dactylus with base to heel straight, heel broadly rounded and slightly produced, heel to tip with broadly concave indent, tip acute, tip to base smoothly convex distally to straight proximally; lateral surface smooth, with several small tufts of short setae in approximately straight line across medioproximal surface, dorsodistal margin with tufts of short setae; ventral margin with long plumose setae, dorsal margin with short simple and plumose setae; mesial surface smooth with plumose setae proximally at junction with propodus. Propodus not inflated dorsoventrally; lateral surface smooth, with long plumose setae distally, with simple setae on dorsal margins; dorsolateral surface narrow, oblique, flattened; mesial surface with scattered long setae on and near distal margin. Carpus produced dorsodistally, exceeding proximal margin of propodus by about ⅓ length of propodus, rounded; dorsolateral margin unarmed; lateral surface slightly rugose dorsodistally, with mat of short setae and row of setae ventrally; mesial surface smooth, with long plumose setae on margins and scattered on surface. Merus smooth, with large decalcified window covering nearly half of lateral surface medially; dorsal and ventral margins unarmed, with long plumose setae; laterodistal margin with long plumose setae; mesial surface smooth. Basi-ischium incompletely fused and unarmed. Coxa with tubercle on anterior margin. Female with large gonopore on anterior mesial margin of coxa, surrounded with short plumose setae; male with small pore on coxa.

Pereopod IV (Fig. 6d) dactylus with base to tip proximally convex becoming distally concave, heel and indent absent, tip acute, tip to base straight distally, becoming convex proximally; lateral surface smooth, ventral margin with long plumose setae, dorsal margin with short simple setae; mesial surface with dorsal decalcified window, demarcated ventrally by longitudinal elevated ridge with row of short setae; with setose punctations ventral to decalcified window. Propodus expanded dorsally and ventrally; ventral expansion exceeds ventral margin of dactylus, margin with long plumose setae; dorsal expansion with row of long plumose setae medially; lateral and mesial surfaces smooth. Carpus not produced dorsodistally; ventral ¾ of lateral surface and mesial surface smooth, dorsal ¼ of lateral surface with mat of short setae; mesial surface with decalcified window; dorsal margin with short simple and long plumose setae; ventral margin with short simple setae. Merus lateral surface with scattered short transverse rows of setae, dorsal and ventrodistal margins with long plumose setae; mesial surface with large decalcified window proximoventrally. Basi-ischium incompletely fused and unarmed. Coxa unarmed.

Pereopod 5 reduced, slender, lacking distinctive features. Coxa of male with large mesioproximal gonopore.

Abdomen (Fig. 6e) somite I approximately as long as wide, widest posteriorly; dorsal surface with anterior margin straight; posterior margin straight with elevated submarginal row of short setae; with small transverse decalcified windows laterad to segment midline. Somite II dorsal surface with submarginal transverse ridge anteriorly; with small transverse decalcified windows laterad to segment midline just anterior to submarginal ridge; with tuft of setae at posterolateral angle, extending onto pleura posteromesially; pleura expanded and directed slightly anteriorly; lateral margins rounded, anterior and lateral margins with long plumose setae, posterior margin with short setae. Somite III similar to somite II, but narrower, shorter, and lacking anterior submarginal ridge; small tuft of short thick setae on posterolateral angle; pleura thinner and shorter than on somite II, directed posterolaterally, with setae as in somite II; anterolateral angle acute; dorsal surface obliquely flattened anterolaterally. Somite IV similar to somite III, but thinner and shorter; dorsal surface with few thick setae posterolaterally; pleura thinner and shorter than on somite III, directed posterolaterally; dorsal surface obliquely flattened anterolaterally; margins with long plumose setae. Somite V subequal to somite IV; lateral margins with plumose setae; pleura absent. Somite VI subequal to somite V in length but wider; dorsal surface with short transverse rows of setae laterad to midline anteriorly and posteriorly; lateral margins with long plumose setae; pleura absent.

Females with uniramous, paired pleopods on somites II–V; males without pleopods.

Uropods lacking distinctive features.

Telson of male (Fig. 6f) triangular, slightly longer than wide, with smoothly rounded tip; proximal half heavily calcified, distal half weakly calcified except for large median region; median longitudinal groove extending to distal end of calcified area, line with long thin simple setae; junction of proximal and distal regions demarcated by strong line of long setae laterally; calcified plate slightly elevated medially but without ridge. Telson of female (Fig. 6g) ovate, longer than wide, rounded distally; dorsal surface smooth, with median longitudinal groove anteriorly; with row of setose punctae lateral to midline from posterior end of longitudinal groove to ¾ length of telson; margins with long plumose setae.

Coloration.—In life, brownish with reddish-brown setae. Preserved, uniform off-white to tan.

Distribution.—Known only known from Oahu, Hawaii; 4.8–40.2 m.

Etymology.—Named after James D. Dana (1813–1895), famed carcinologist and describer of *A. speciosa,* and many other species of Indo-Pacific Crustacea. Gender: masculine.

Remarks.—This species is most similar to *A. carabus* (Linnaeus, 1758), from the Mediterranean and western Africa, in the shape of the dactyli of pereopods II–IV and telson morphology. *Albunae carabus* can be easily separated from *A. danai,* new species, by its CG8 of four medial elements, more strongly crenulated CGs, more pronounced heel on the dactyli of pereopods II and III, and a less inflated maxilliped III merus. *A. danai* new species can be distinguished from other Indo-West Pacific species by the triangular shape of the telson of the male, the rounded dactyl of pereopod III, and setal patterns on the carapace of both sexes. All other species of *Albunea* from the Indo-West Pacific region with smoothly rounded heels on pereopod III (e.g., *A. speciosa*) also have much more strongly setose carapace grooves than *A. danai,* new species, and distinctive male telson morphologies.

As previously indicated, the holotype was collected with specimens of *A. speciosa* (QM W22285).

This species, unlike *A. speciosa,* appears to be a true Hawaiian endemic based on all available data. However, this conclusion should be accepted cautiously, given the "endemic" label applied to *A. speciosa* prior to this study and that endemicity appears to be the exception, rather than the rule, in the Hawaiian biota (Newman 1986). As a whole, the Hawaiian albuneids seem to fit in the category of attenuated Indo-West Pacific fauna (Newman 1986), given the markedly greater diversity of albuneids (17 species in six genera) throughout the rest of the Indo-West Pacific.

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Two new species of *Hansenium* (Crustacea: Isopoda: Asellota) from Madang, Papua New Guinea

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Abstract.—Two new species of *Hansenium, H. tropex* and *H. thomasi,* are described from Paddock Reef, Madang, Papua New Guinea. *H. tropex* is characterized by the possession of a broad oar-shaped lobe of the carpus of pereopod 1 in the male. *H. thomasi* is characterized by a narrow tapering mesially-directed lobe of the carpus of pereopod 1 of the male. The genus is redefined, with its chief character being the presence of a large carpal lobe on the first male pereopod. The eight stenetriid genera are compared on the basis of six characters.

The shallow water marine crustaceans (with the exception of the Amphipoda) of the Papua New Guinea region are poorly known. The Isopoda have received scant attention (in all, only about 15 species have been recorded from the region.) Stebbing (1900), recorded three cirolanids, one cymothoid and one sphaeromatid from New Britain, New Guinea, Nobili (1905) described a corallanid and a bopyrid, while Nierstrasz (1931) lists three cymothoids, two cirolanids, three corallanids, and one sphaeromatid in his catalogue of isopod records. Bruce (1982, 1993, 1994) has described cirolanids from the Madang area, while Keable (1997) added further cirolanid records; Jones et al. (1983) described three species of corallanids; Williams & Bunkley-Williams (1992) described two new species of cymothoids. No asellote isopods have been reported. The finding of two very distinctive stenetriids was, therefore, thought to be well worth recording.

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Suborder Asellota
Family Stenetriidae Hansen, 1905
Genus *Hansenium* Serov & Wilson, 1995

Hansenium Serov & Wilson, 1995: 72.

Diagnosis.—Lateral tooth of cephalon moderately well developed, antennal tooth subequal to lateral, or rounded. Rostrum short, rectangular, anterior margin truncate. Eyes reniform, of 13–19 ommatidia. Pereopod 1 in male with carpus produced posterodistally into lobe; propodus longer than width of palm, latter often with few teeth close to articulation of dactylus. Pleopod 2 in male with rounded protopodal lobe distally, appendix masculina of endopod distally somewhat broadened, truncate, often ringed by cuticular hairs.

Type species.—*Stenetrium hanseni* Nobili, 1906.

Remarks.—Serov & Wilson (1995), divided the genus *Stenetrium* into five separate genera, and reviewed the remaining three genera in the family Stenetriidae. They also listed the constituent species for each of the genera. Examination of the two present species, as well as undescribed material from the Indian Ocean has led us to revise the diagnosis of *Hansenium,* as given above. The presence of a variously developed posterodistal lobe on the carpus of pereopod 1 in the male would seem to be the most characteristic synapomorphy of the genus, along with the presence of one or more teeth on the short propodal palm. The extreme development of this lobe into the expanded and flattened oar-like structure seen in *H. tropex* and *H. wilsoni* (Müller, 1991a) is approached in two undescribed species from the Indian Ocean. A review of the 13 species of *Hansenium* listed by Serov & Wilson (1995) shows that only *Stenetrium bowmani* Kensley, 1984, and *S. gilbertense* Nordenstam, 1946 do not possess a carpal lobe on pereopod 1 in the male.

Table 1 summarizes the six characters thought most significant in defining the eight genera of the Stenetriidae.

Species included in Hansenium.

Hansenium caicosense (Kensley & Heard, 1991). Turks & Caicos Islands.

Hansenium dodo (Müller, 1991b). Réunion Island.

Hansenium entale (Nordenstam, 1946). Gilbert Islands.

Hansenium hanseni (Nobili, 1906). Tuamotu Islands.

Hansenium monodi (Nordenstam, 1946). Gulf of Suez; Seychelles.

Hansenium spathulicarpus (Kensley, 1984). Belize.

Hansenium stebbingi (Richardson, 1902) (= *Stenetrium antillense* Hansen, 1904, and = *Stenetrium occidentale* Hansen, 1904). Bermuda; Belize; St. Thomas, West Indies.

Hansenium thomas n. sp. Madang, Papua New Guinea.

Hansenium tropex n. sp. Madang, Papua New Guinea.

Hansenium wilsoni (Müller, 1991a). Moorea.

Hansenium tropex, new species
Figs. 1–2

Material examined.—Holotype, USNM 253348, ♂ tl 4.8 mm, Paratypes, USNM 253349, 2 ovigerous ♀ tl 3.5 mm (damaged), 5.0 mm, Paddock Reef, Madang, Papua New Guinea, coral rubble, 3–4 m, coll. J. D. Thomas, 14 Jan 1989.

Description.—Body slender, about 4 times as long as wide, cephalon about twice as wide as long. Rostrum short, rectangular, apically truncate, subequal in length to antennal teeth. Antennal teeth elongate, acute. Lateral teeth pronounced, subequal to antennal teeth. Frontal margin of cephalon below rostrum slightly convex. Eyes reniform, consisting of about 14 ommatidia.

Antennule, flagellum of about 20 articles; 1 aesthetasc on first article, 2 on second article. Mandible with 4-cusped incisor; 3-cusped lacinia mobilis; left mandible with spine row of 4 comb setae; right mandible spine row with 7 comb setae and 3 simple setae; molar with 8 plumose setae below marginal serrations. Maxilla 1 inner lobe with 2 large fringed setae and 2 smaller simple setae; outer lobe with 8 fringed setae. Maxilla 2 outer lobe with 4 stout fringed setae and 1 simple seta; middle lobe with 5 stout fringed setae; inner lobe with 8 simple setae and 4 stout plumose setae on mesial margin. Maxilliped palp with 3 proximal articles wider than 2 distal articles, latter longer than wide; endite broad with 6 broad flattened fan setae distally; mesial margin with 5 coupling hooks.

Pereonites 1–4 decreasing in length posteriorly, with anterolateral margins acute; pereonites 5–7 increasing in length posteriorly; pereonites 5–6 with rounded posterolateral margins; pereonite 7 with angular posterolateral margins. Male pereopod 1 elongate, slender; dactylus equal in length

Table 1.—Comparison of the genera in the isopod family Stenetriidae.

	Antennal and lateral tooth of cephalon	Rostrum	Eyes	Pereopod 1 ♂ propodus	Pereopod 1 ♂ carpus	Pleopod 2 ♂ appendix masculina
Hansenium Serov & Wilson, 1995	lateral tooth well developed; antennal tooth acute or rounded	short, rectangular, anterior margin truncate	reniform, of 13–19 ommatidia	longer than width of palm	strongly produced postero-distally	distally widened, truncate
Liocoryphe Serov & Wilson, 1995	antennal and lateral teeth absent; anterolateral area angular or rounded	short, anterior margin convex	small rounded group of 3–4 ommatidia	distally broadened, as wide as long, palm sloping oblique-posteriorly	rarely produced	distally widened, truncate, subdistal row of short barbs
Mizothenar Serov & Wilson, 1993	lateral tooth short; antennal tooth absent	poorly defined or absent	rounded group of 9–10 ommatidia	distally broadened, as wide as long, palm with row of oblique dentate setae	not produced	distally widened, truncate
Protallocoxa Schultz, 1978	lateral tooth strong; antennal tooth absent	large, robust, triangular-linguiform	rounded group of about 8 ommatidia	distally broadened, as long as wide, palm with row of oblique dentate setae	not produced	distally widened, margin concave, subdistal row of short barbs
Stenetrium Haswell, 1881	lateral and antennal tooth well developed, subequal	short, rounded to subtriangular	reniform, of about 18 ommatidia	longer than width of palm	rarely produced	distally widened, subdistal row of barbs
Stenobermuda Schultz, 1979	lateral tooth well developed; antennal tooth shorter than lateral	narrow, triangular	rounded group of 3–4 ommatidia	~twice longer than palm, with row of pectinate setae	not produced	with distal fringed lamella and sperm tube
Tenupedunculus Schultz, 1982	lateral tooth well developed; antennal tooth small	short, anterior margin rounded or truncate	reniform or absent	as long as palm width	not produced	distally widened, truncate, subdistal row of barbs
Tristenium Serov & Wilson, 1995	lateral tooth short or absent; antennal tooth rounded or absent	triangular with broad base and narrowed distally	rounded group of 3–5 ommatidia	slightly longer than palm	not produced	distally tapered to acute process, subterminal elongate setae

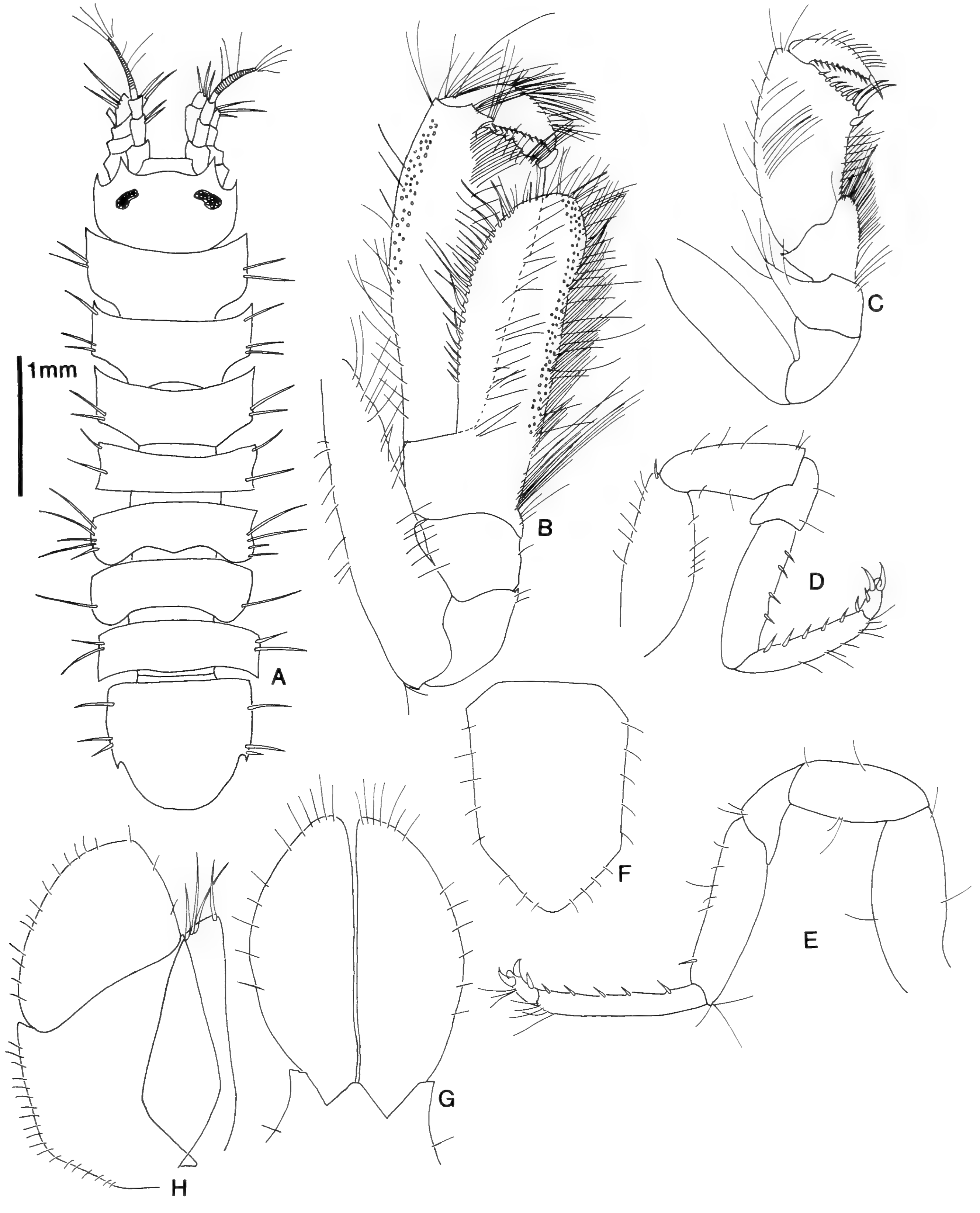

Fig. 1. *Hansenium tropex,* new species. A, ♂, dorsal view; B, Pereopod 1 ♂; C, Pereopod 1 ♀; D, Pereopod 2; E, Pereopod 7; F, Operculum ♀; G, Pleopod 1 ♂; H, Pleopod 3.

to propodal palm; short unguis extending beyond proximal spine of propodal palm; propodal palm serrate; carpus with large stout distally rounded densely setose lobe projecting anteroventrally, about 0.8 times length of propodus (Fig. 1B). Female pereopod 1 significantly smaller than in male, with sparser setae; dactylus equal in length

Fig. 2. *Hansenium tropex,* new species. A, Right mandible; B, Left mandible; C, Mandibular palp; D, Maxilla 1; E, Maxilliped; F, Maxilla 2; G, Antennule.

to propodal palm, with 10 short simple setae on posterodistal margin; propodal palm with 6 short simple setae, terminating in 2 long setae; carpal lobe much less prominent than in male.

Pleon having 2 vestigial pleonites plus pleotelson; posterolateral spines pronounced; postanal margin nearly semicircular. Male pleopod 1 biramous with rami elongate; mesial margins of rami parallel; lateral margins rounded and sparsely setose. Female pleopod 2 1.4 times longer than wide, pentagonal, with outer margins sparsely setose. Pleopod 3 operculiform, with outer ramus broad, sparsely setose; inner ramus narrow and nearly triangular, with 4 terminal setae.

Remarks.—Hansenium tropex bears the closest resemblance to *H. wilsoni* (Müller, 1991a), but several features distinguish the two. In *H. tropex,* the antennal spines are clearly longer than the lateral spines, while in *H. wilsoni,* the antennal spines are reduced, rounded, and shorter than the lateral spines. The anterior margin of the cephalon in *H. tropex* is convex, straight in *H. wilsoni.* In *H. tropex* the maxilliped has six flattened fan setae on the endite where *H. wilsoni* has three. In pereopod 1 of the male in *H. tropex,* the carpal process extends about ¾ the length of the propodus, the propodal palm terminates in a simple blunt seta, the merus is not produced and the ischium is sparsely setose; in *H. wilsoni,* the carpal lobe extends beyond the propodus and the dactylus distally, the propodal palm has no articulated seta, the merus is slightly produced, and there is a dense cluster of setae on the ischium. Pleopod 1 in *H. tropex* females is nearly pentagonal, with setae at regular intervals on the lateral margins; in *H. wilsoni,* the female pleopod 1 operculum has only four setae and is more triangular in shape. Pleopod 1 in the male of *H. tropex* is nearly semicircular, tapering proximally and distally, while in *H. wilsoni* the male pleopod 1 only narrows distally.

Etymology.—The specific name is derived from the Greek 'tropex', an oar, refers to the paddle-like carpal lobe of the male pereopod 1, and is used as a noun in apposition.

Hansenium thomasi, new species
Figs. 3–5

Material examined.—Holotype, USNM 253350, ♂ tl 4.3 mm, Paratypes, USNM 253351, 3 ♂, 8 ovigerous ♀ tl 3.4–4.5 mm, 4 juveniles, Paddock Reef, Madang, Papua New Guinea, 1.5–4 m, coll. J. D. Thomas, 14 Jan 1989.

Diagnosis.—Body about 3.5 times longer than wide, width of cephalon about 1.5 times length. Rostrum short, rectangular, anterior margin truncate; frontal margin of cephalon convex posterior to rostrum. Antennal spines equal in length to rostrum; lateral spines subequal in length to antennal spines. Eyes reniform with about 19 ommatidia.

Antennule of about 8 articles; 2 aesthetascs on terminal article; 1 aesthetasc on subterminal; 1 aesthetasc on following article. Mandible with 4-cusped incisor and 3-cusped lacinia mobilis; left mandible with spine row of 4 comb setae, left molar with 8 fringed setae; right mandible with spine row of 7 comb setae, 2 plumose setae, and 2 simple setae; right molar with 5 plumose setae. Maxilla 1 inner ramus with 3 stout plumose setae, 1 shorter simple seta; outer ramus with 5 stout comb setae and 5 stout simple setae. Maxilla 2 outer lobe with 2 long fringed terminal setae, 2 shorter simple setae, mesial margin with 6 simple setae; middle lobe with 3 long fringed terminal setae, 1 simple terminal seta, 6 simple setae on mesial margin; inner lobe with 6 fringed setae and 6 simple setae. Maxillipedal endite broad; distal margin with 6 round flattened fan setae and 5 narrow fringed setae, with 1 short stout simple terminal seta; mesial margin with 4 coupling hooks, 4 fringed setae.

Pereonites 1–3 increasing in length posteriorly; pereonite 4 longer than pereonite 5; pereonite 6 longer than pereonite 7; cox-

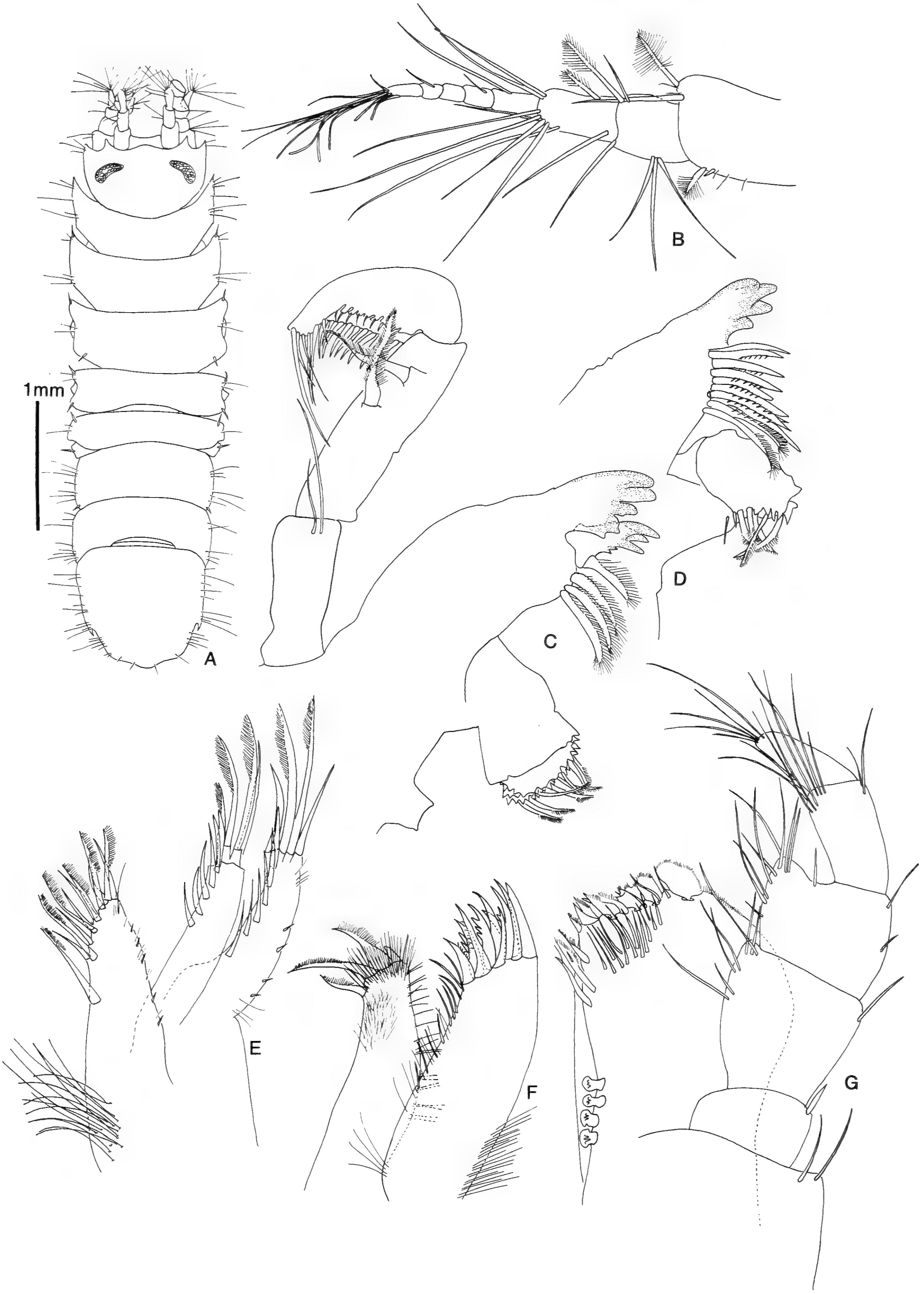

Fig. 3. *Hansenium thomasi,* new species. A, ♂, dorsal view; B, Antennule; C, Left mandible; D, Right mandible; E, maxilla 2; F, Maxilla 1; G, Maxilliped.

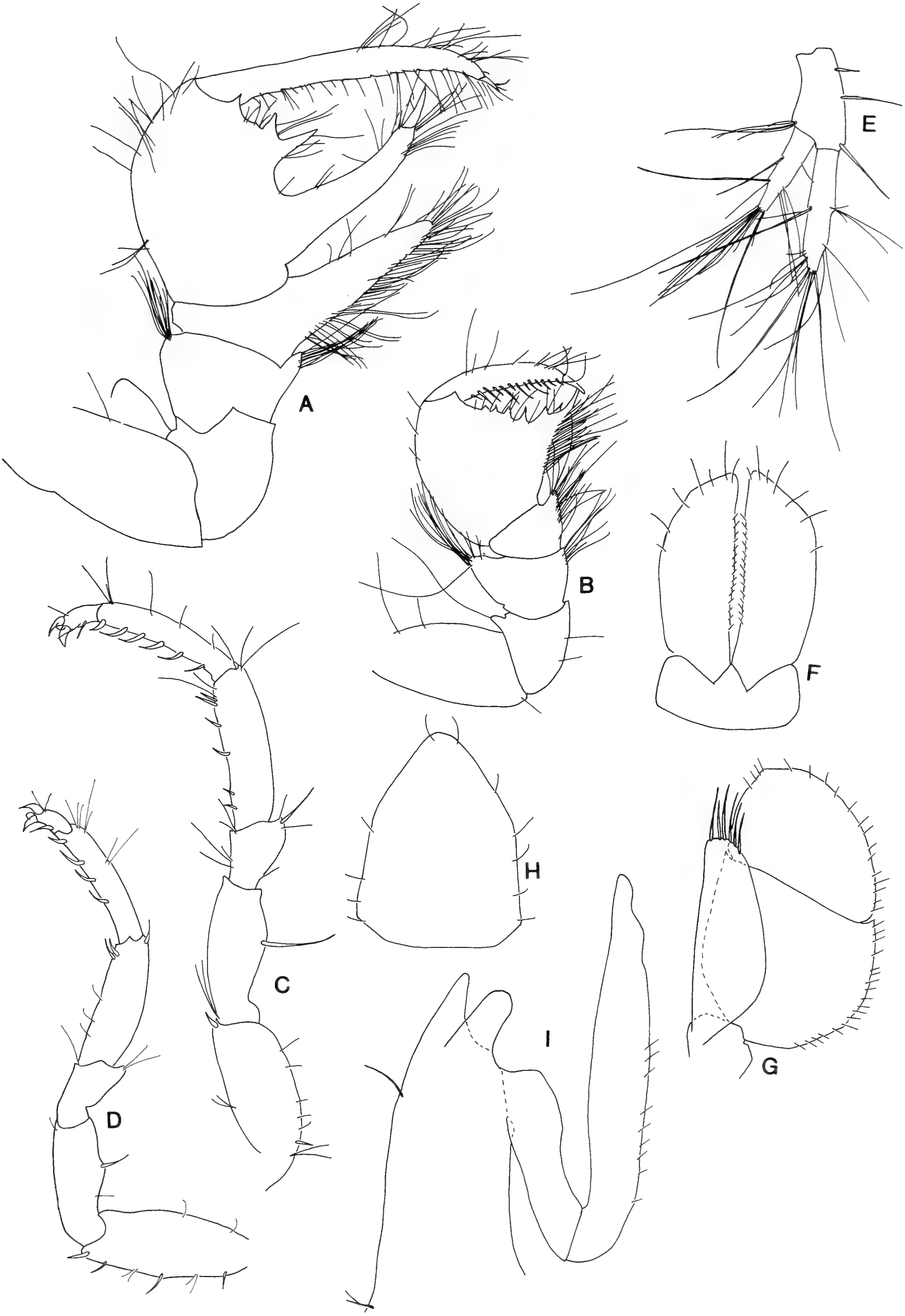

Fig. 4. *Hansenium thomasi,* new species. A, Pereopod 1 ♂; B, Pereopod 1 ♀; C, Pereopod 2; D, Pereopod 7; E, Uropod; F, Pleopod 1 ♂; G, Pleopod 3; H, Operculum ♀; I, Pleopod 2 ♂.

Fig. 5. *Hansenium thomasi,* new species. A, Cephalon in dorsal view; B, Left and right pereopod 1 ♂ in situ.

ae visible on pereonites 1 and 3–5; pereonites 1–2 with acute anterolateral angles; pereonites 3–4 with concave lateral margins; pereonite 5 with flat lateral margins, rounded posterolateral angle; pereonites 6–7 laterally broad and rounded.

Male pereopod 1 dactylus elongate, narrow with acute unguis, extending far beyond propodal palm; propodal palm broad, with 3 sharp teeth, posterodistal angle greatly produced into narrow lobe terminating in simple stout seta; carpus with strongly produced posterodistal setose lobe; merus with small posterodistal projection and tufts of setae on postero- and anterodistal margins. Female pereopod 1 much smaller than in male; dactylus equal in length to broad propodal palm, with row of short setae along posterodistal margin; propodal palm broader than in male, with 7 teeth; carpal process much smaller than in male; merus with setal tufts and low anterodistal lobe. Pereopods 2–7 similar, carpus with 2 posterodistal setae; propodus with 4–6 stout setae on posterior margin.

Pleon with 2 vestigial pleonites plus pleotelson, latter with single produced posterolateral spine on each lateral margin; postanal region gently convex. Male pleopod 1 mesial margins finely setose, parallel; lateral margin convex with 6–7 setae distally. Male pleopod 2 endopod simple, outer margin with about 9 setae; protopod distally subacute, exopod rounded. Female pleopod 2 operculum subtriangular, 1.3 times longer than wide, sparsely setose. Pleopod 3 rami together sub-circular, with lateral margin of exopod setose; endopod nearly triangular with 6 distal spines.

Remarks.—Hansenium thomasi bears considerable resemblance to *H. entale* (Nordenstam, 1946) from the Gilbert Islands in the Pacific. Comparison of the male pereopod 1, however, easily distinguishes the two species. The dactylus of *H. thomasi* is less curved. There are three teeth on the propodal palm of *H. thomasi,* more apically acute than the four found on *H. entale.* The propodal teeth of *H. thomasi* are well separated from each other, whereas in

H. entale their fused bases join the propodal palm. *Hansenium thomasi* has a large posterodistal propodal lobe, separate from the teeth, which terminates distally in a simple stout seta. *Hansenium entale* has a similar large toothlike process, but it is more directly a part of the propodal palm, close to the other four teeth. Both *H. thomasi* and *H. entale* have produced carpi in the male pereopod 1, but the process is more setose and distally rounded in *H. thomasi.* The meral process in *H. thomasi* is much shorter than in *H. entale,* where it extends almost half the length of the carpus.

The anterior margin of the cephalon in *H. thomasi* is gently convex, straight in *H. entale. Hansenium entale* has a characteristic pigment pattern, with a line across the anterior cephalon and a broad band between the eyes; *H. thomasi* apparently has no pigmentation. In *H. entale,* the coxae are visible on pereonites 3 and 4 only, while in *S. thomasi* they are visible on pereonites 3–5.

Etymology.—The species is named for James Darwin Thomas, amphipod specialist, who collected the specimens.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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Caecidotea simulator, a new subterranean isopod from the Ozark Springfield Plain (Crustacea: Isopoda: Asellidae)

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Abstract.—With the description of *Caecidotea simulator,* a phreatobitic isopod reported herein from Arkansas and Kansas, a total of six species of subterranean asellids is now known from the Springfield Plain section of the Ozark Plateau. The presence of *C. macropropoda* in Arkansas, a subterranean species previously known with certainty only from Oklahoma, is confirmed by two collections examined from northeastern Arkansas.

The Springfield Plain is a region of gently rolling karst landscape formed on flat-bedded limestones in the southwestern part of the Ozark Plateau. This area of the central United States includes parts of southwestern Missouri, northwestern Arkansas, northeastern Oklahoma, and a tiny piece of southeastern Kansas. Previously reported from the Springfield Plain were the subterranean asellids *Caecidotea ancyla* (Fleming, 1972), *C. antricola* Creaser (1931), *C. macropropoda* Chase & Blair (1937), *C. stiladactyla* Mackin & Hubricht (1940), and *C. steevesi* (Fleming 1972). The type specimens of *C. steevesi* were examined and three species were found to be present: (1) *C. steevesi* from Carrico Cave, Dade County, Missouri (type-locality), and Gitten Down Mountain Cave, Adair County, Oklahoma; (2) *C. antricola,* also in the Carrico Cave collection; and (3) the new species described below from Baxter Springs, Cherokee County, Kansas.

Caecidotea simulator, new species
Figs. 1, 2a, c–f, 3a, b

Asellus steevesi Fleming 1972: 491–494 [Baxter Springs, Kansas record]; 1973: 295, 300 [in part].

Material examined.—Kansas: Cherokee County, Baxter Springs, seeps off 7th Avenue, 12 Jun 1964, J. R. Holsinger, 10♂♂, 13♀♀.—Arkansas: Washington County, O. A. Lasterling's well, 0.25 mile west Highway 71, Fayetteville, 22 Jul 1965, E. H. Schmitz, 15♂♂, 11♀♀.

An 11.0mm ♂ from Baxter Springs, Kansas is designated as the holotype (USNM 216971), with paratypes from Baxter Springs (USNM 222477) and Lasterling's well (USNM 216972). All of the material has been deposited in the collection of the National Museum of Natural History, Smithsonian Institution.

Description.—Eyeless, unpigmented, longest male to 19mm, female to 13mm. Body slender, linear, about 6.5× as long as wide. Margins of head, pereonites, and pleotelson moderately setose. Head about 1.5× as wide as long, anterior margin concave, postmandibular lobes moderately produced. Pleotelson about 2× as long as wide, sides subparallel, caudomedial lobe slightly 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 flagellum to 18 segments, esthete formula 3-0-1-0-1. Antenna 2, last segment of peduncle about 1.2× length of preceding segment, flagellum of 19mm ♂ with 168 segments.

Male pereopod 1, propus 1.5× as long as

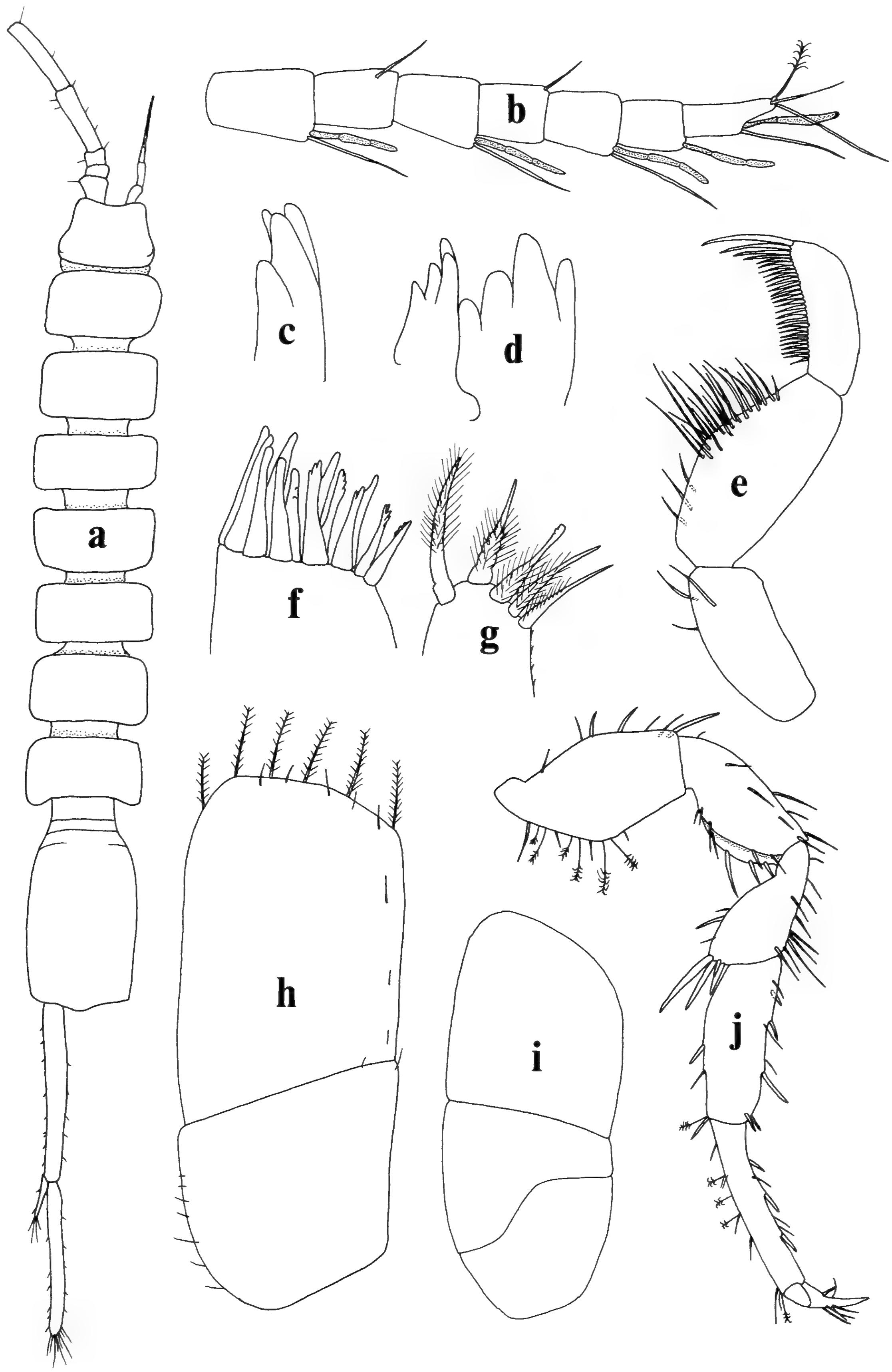

Fig. 1. *Caecidotea simulator,* male from Baxter Springs, Cherokee Co., Kansas: (a) habitus, (b) distal segments of antenna 1 flagellum, (c) right mandible, incisor, (d) left mandible, incisor and lacinia mobilis, (e) mandibular palp, (f) maxilla 1, outer lobe, (g) same, inner lobe, (h) pleopod 3, (i) pleopod 5, (j) pereopod 4.

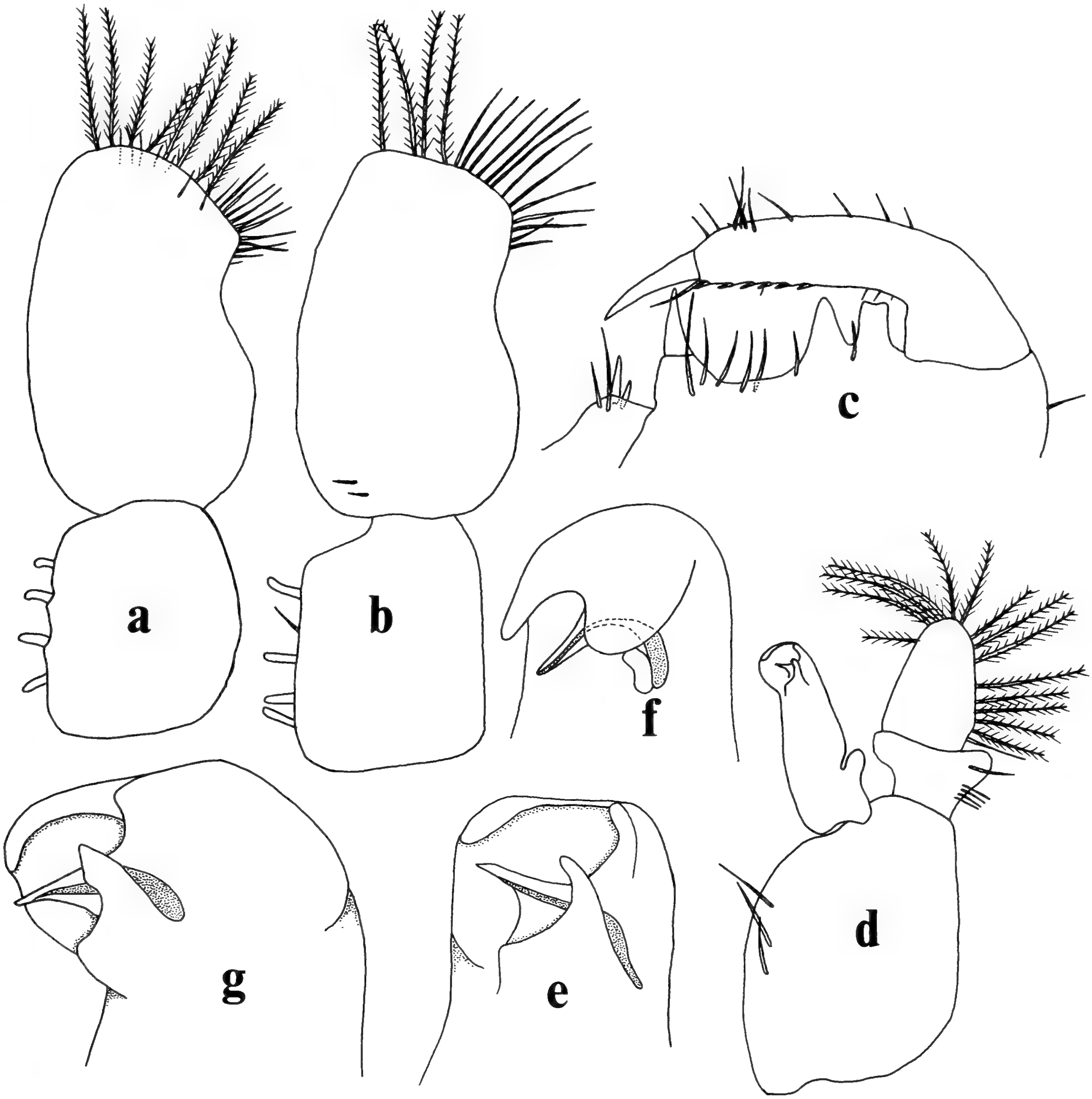

Fig. 2. *Caecidotea simulator,* (a, c–f) male from Baxter Springs, Cherokee Co., Kansas, and *Caecidotea steevesi,* (b, g) male from Carrico Cave, Dade Co., Missouri: (a) pleopod 1, (b) same, (c) gnathopod propus, palmar margin, (d) pleopod 2, (e) same, endopod tip, (f) same, caudal processes folded over anterior processes under coverslip, (g) pleopod 2, endopod tip.

wide, palm with raised proximal spine, median triangular process and slightly bicuspid distal process close together, sexual dimorphism absent. Pereopods 2–7 with moderate setation as figured, sexual dimorphism for clasping slight with male pereopod 4 carpus 2.6× as long as wide female 2.9×.

Male pleopod 1, protopod about 0.6× length of exopod, with 4 retinacula. Exopod about 1.6× as long as wide; lateral margin concave, distal margin with 6–8 long plumose setae. Pleopod 2, protopod with 3 mesial setae. Exopod, proximal segment with about 5 lateral setae, distal segment with about 15 long plumose setae along margin. Endopod with distinct basal apophysis, endopod tip twisted in appearance, processes directed away from axis of endopod, cannula tapering to a stylet, mesial process tapering and becoming digitiform, decurved

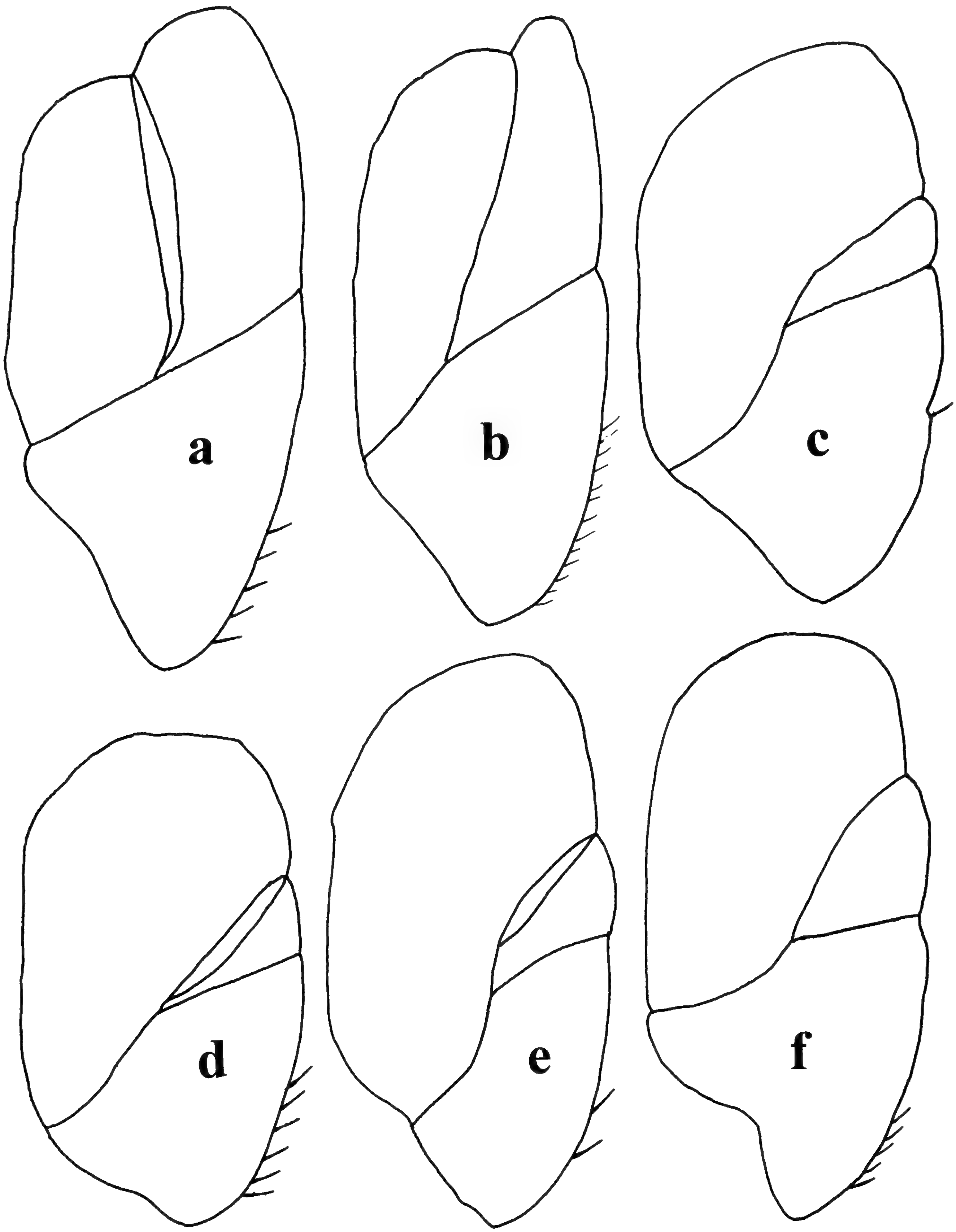

Fig. 3. Fourth pleopod exopods of related subterranean *Caecidotea* from the Springfield Plain: (a) *C. simulator,* Baxter Springs, Cherokee Co., Kansas, (b) *C. simulator,* Lasterling's well, Washington Co., Arkansas, (c) *Caecidotea stiladactyla,* small seeps 4.0 m. S. Boxley, Newton Co., Arkansas, (d) *C. steevesi,* Gittin Down Mountain Cave, Adair Co., Oklahoma, (e) *C. steevesi,* Carrico Cave, Dade Co., Missouri, (f) *C. steevesi,* War Eagle Cave, Madison Co., Arkansas.

mesiad, caudal process heavily sclerotized, thickened laterally and mesially. Pleopod 3 exopod, proximal segment about 9.7× length of distal segment, with about 6 plumose setae on distal margin. Pleopod 4 with up to 18 proximolateral setae, two false sutures present. Pleopod 5 with 2 sutures. Uropods of male about 2× length of pleotelson, equal to length of pleotelson in female.

Etymology.—The noun "simulator", from the Latin meaning imitator or pretender, indicates the close resemblance of *C. simulator* to *C. steevesi.* The vernacular name suggested for this species is the Springfield Plain groundwater isopod.

Habitat and range.—Caecidotea simulator is known from the type-locality in southeastern Kansas and one locality in the adjacent corner of northwestern Arkansas. From its vermiform, eyeless, unpigmented appearance *C. simulator* is clearly an inhabitant of subterranean waters. *Caecidotea simulator* has not been found in caves and presumably lives in the saturated soil interstices that supply groundwater to the two sites from which it has been taken, a well and a seep spring.

Relationships.—Caecidotea simulator and *C. steevesi* are very similar morphologically. The gnathopods of both species are nearly identical. The apex of the first pleopod exopod has elongate plumose setae in both species, a characteristic also shared with all species of the Hobbsi Group (Lewis, 1982). In *C. simulator* these setae occur all the way across the distal margin of the pleopod and are about 7–8 in number. In *C. steevesi* the setae are located only on the mesial half of the distal margin and number 4–5 (Fig. 2b).

Due to torsion of the second pleopod endopod the taxonomically important tip processes are difficult to interpret and compare in *C. simulator* and *C. steevesi,* a characteristic shared with *C. macropropoda* and *C. stiladactyla.* The critical features are not easily seen without applying a coverslip, and the positions of the tip processes are quite distorted under the pressure of the glass (as the endopod twists). The endopod tips illustrated in Fig. 2 are the result of numerous attempts to gain the same perspective for both *C. simulator* and *C. steevesi.* The endopods appear to be fundamentally similar, although side by side comparison (Fig. 2e–g) illustrates minor differences of questionable importance. For example, the mesial process in *C. simulator* tapers to a narrow, cylindrical digitiform process, while in *C. steevesi* it is wider and obliquely truncate.

The best way to separate *C. simulator* from *C. steevesi* is by the structure of the fourth pleopod exopod (Fig. 3a–b, d–f), which has two false sutures in *C. simulator* (and *C. macropropoda,* Lewis, 1982, Fig. 3h), but only a single sigmoid suture in *C. steevesi* (and *C. stiladactyla,* Fig. 3c).

Caecidotea macropropoda Chase & Blair, 1937

Material examined.—Arkansas: Carroll County, White River at Beaver Down, G. C. Kephart, Jul 1978, 4♂♂, 5♀♀.—Washington County, spring 2.2 miles north Dutch Mills, L. Hubricht, 21 May 1942, 6♂♂, 5♀♀; seep, 1.5 miles north Winslow, L. Hubricht, 22 May 1940, 31♂♂, 7♀♀.

Remarks.—Lewis (1982) synonymized *C. ozarkana* with *C. macropropoda* and redescribed the species. Dearolf (1953) reported this species from two sites in Arkansas, but the validity of the records was unknown (Lewis, 1982). The records provided here substantiate those of Dearolf for the occurrence of *C. macropropoda* in Arkansas. The species is endemic to the Springfield Plain, where it is found in cave streams, springs, and seeps.

Acknowledgments

The late Dr. Thomas E. Bowman provided the loan of type-specimens of *Caecidotea steevesi* from the collections of the Smithsonian Institution, read the manu-

script, and offered suggestions for its improvement.

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Collocherides brychius, a new species (Copepoda: Siphonostomatoida: Asterocheridae) from a deep-water hydrothermal site in the northeastern Pacific

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Abstract.—*Collocherides brychius* is described from a depth of 2253 m at a hydrothermal site on the Juan de Fuca Ridge in the northeastern Pacific. The species is close to *C. astroboae* Stock 1971, but may be distinguished from that species by its relatively small size (length of female 0.57 mm) and by the inner terminal seta on the caudal ramus of the female being approximately as long as the caudal ramus, instead of more than 3 times its length. Although its three congeners are associated with ophiuroid echinoderms in shallow water, the new species was recovered free in microfaunal samples in the deep sea.

The copepod genus *Collocherides* Stock 1971 (Siphonostomatoida: Asterocheridae), contains three species. *Collocherides astroboae* Stock 1971, lives in the stomach of the basket star *Astroboa nuda* (Lyman) at Eilat in the Gulf of Aqaba and at the Dahlak Archipelago (depth about 50 cm) in the Red Sea (Stock 1971). It has also been recovered from the stomach of *Astroboa albatrossi* Döderlein in Indonesia (precise locality unknown but probably Java Sea) (Stock 1971). Large numbers of *C. astroboae* were found on *A. nuda* in 18 m at Nosy Bé, northwestern Madagascar (Humes 1973). *Collocherides singularis* Humes 1986, lives with *Astroboa nuda* (depth 5 m) at Poelau Gomumu, Moluccas, 01°50′00″S, 127°30′54″E (Humes 1986). *Collocherides bleptus* Humes 1993, occurs intertidally on the ophiuroid *Macrophiothrix* sp. at Nosy Bé, northwestern Madagascar (Humes 1993).

Sixty-seven species of copepods have been recorded in deep water from hydrothermal vents and cold seeps in the world's oceans (Humes & Segonzac 1998). These species consist for the most part of siphonostomatoids, with fewer calanoids, misophrioids, cyclopoids, poecilostomatoids, and harpacticoids. In this paper a new species of the siphonostomatoid genus *Collocherides* is described from a deep-water hydrothermal site in the northwestern Pacific. With the addition of this new species, a new erebonasterid poecilostomatoid reported by Martinez Arbizu (1999), and a new aegisthid harpacticoid described by Conroy-Dalton & Huys (1999), the number of copepods known from deep-sea hydrothermal vents and cold seeps rises to 70.

Materials and Methods

The copepods were collected at a low temperature vent, where the highest reading was 52° Celcius. The vent (Marker M) was situated on new lava flows, and is believed to be relatively young. (Vents at older mature lavas are believed to support more heterogeneous faunas, with more species, than young vents (Milligan & Tunnicliffe 1994).) The diving submersible *Alvin* used its arm or "claw" to gather tube worms (Vestimentifera) and associated fauna and deposit them in a biobox mounted on a basket. The sample was preserved for later sorting, during which copepods were recovered (Tsurumi, pers. comm.).

The copepods, which had been preserved in ethanol, were cleared and dissections made in lactic acid, using the wooden slide method described by Humes & Gooding (1964). All figures were drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn.

Siphonostomatoida Thorell, 1859
Asterocheridae Giesbrecht, 1899
Collocherides Stock, 1971

Collocherides brychius, new species

Figs. 1–3

Type material.—9 ♀♀, 3 ♂♂, in 2253 m, Juan de Fuca Ridge, Segment Cleft, North Field, Vent Marker M, northeastern Pacific, 44°58.97′N, 130°12.35′W, 28 Aug 1990. Holotype ♀ (USNM 243645), allotype ♂ (USNM 243646), and 6 paratypes (5 ♀♀, 1 ♂) (USNM 243647) deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Remaining specimens (dissected) in the collection of the author.

Female.—Body slender (Fig. 1a), not flexed between prosome and urosome (Fig. 1b). Average length (not including setae on caudal rami) 0.57 mm (0.55–0.58 mm) and average width 0.18 mm (0.17–0.19 mm), based on 9 specimens. Dorsoventral thickness (at level of slight protuberance between maxillipeds and first pair of legs) 127 μm. Epimera of metasomal somites rounded (Fig. 1b). Ratio of length to width of prosome 2.03:1. Ratio of length of prosome to that of urosome 1.31:1.

Urosome with 5 somites. Somite bearing leg 5 (Fig. 1c) 47 × 83 μm. Genital double-somite in dorsal view 81 μm long and 81 μm wide at widest part. In lateral view (Fig. 1d), this double-somite with dorsal and ventral sides slightly rounded. Genital areas located laterally in anterior half of double-somite (Fig. 1c, d). Each genital area with small seta and minute spine (Fig. 1d). Three postgenital somites from anterior to posterior 36 × 53, 31 × 40, and 23 × 36 μm. Genital double-somite and 3 postgenital somites with pairs of small posterolateral spinelike processes or spinules (Fig. 1d, e), those on anal somite prominent.

Caudal ramus (Fig. 1e) moderately elongate, unornamented, length including terminal pointed process 44 μm, length without process 35 μm, width 16 μm. Ratio of length (without process) to width 2.19:1, ratio including process 2.75:1. With 6 smooth setae, 1 long and 5 short, longest seta 52 μm long, much longer than other setae and slightly swollen proximally. Long seta slightly longer than ramus, ratio 1.18:1.

Body surface with few sensilla on urosome, otherwise unornamented.

Egg sac (Fig. 1d), seen on only 1 female, large, oval, 179 × 99 μm.

Rostral area (Fig. 1f) triangular, not protruding. Antennule (Fig. 2a) 20-segmented, 187 μm long, with aesthetasc 60 μm long on segment 18. Formula for armature: 1, 2, 2, 2, 2, 2, 2, 2, 6, 2, 2, 2, 2, 2, 2, 2, 2, 2+1 aesthetasc, 2, and 9. All setae smooth. Antenna (Fig. 2b) 99 μm long, including terminal spine 22 μm. First segment (coxa) short and unarmed. Second segment (basis) with 1 minute seta (exopod). Third segment long and unarmed. Short fourth segment bearing 2 short setae and 1 long terminal spine, its truncated tip with few extremely minute setules.

Oral cone (Fig. 1f) short, oval in ventral view, prominent in lateral view (Fig. 1b).

Mandible (Fig. 2c) with slender 2-jointed palp 60 μm long. Gnathobase (Fig. 2d) 50 μm long., with several blunt terminal teeth. Maxillule (Fig. 2e) with 1 seta on slender outer lobe and 4 setae on stout inner lobe. Maxilla (Fig. 2f) 2-segmented, first segment unarmed, second segment bearing recurved claw with truncated minutely spinulose tip. Maxilliped (Fig. 2g) 5-segmented. First segment with inner distal seta. Second segment elongate (52 μm long) with 1 seta on inner margin. Third and fourth segments short with 1 seta. Fifth segment elongate

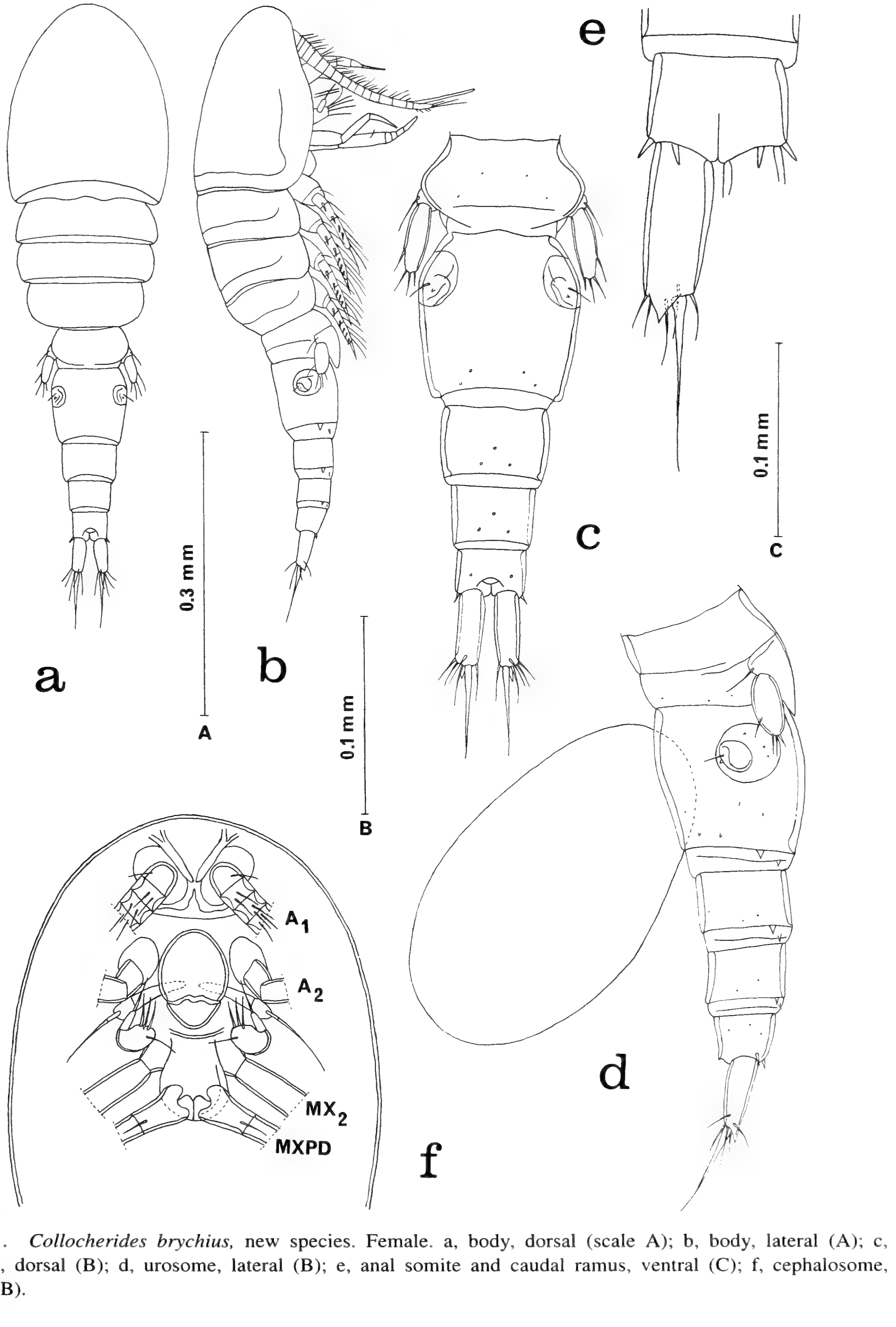

Fig. 1. *Collocherides brychius,* new species. Female. a, body, dorsal (scale A); b, body, lateral (A); c, urosome, dorsal (B); d, urosome, lateral (B); e, anal somite and caudal ramus, ventral (C); f, cephalosome, ventral (B).

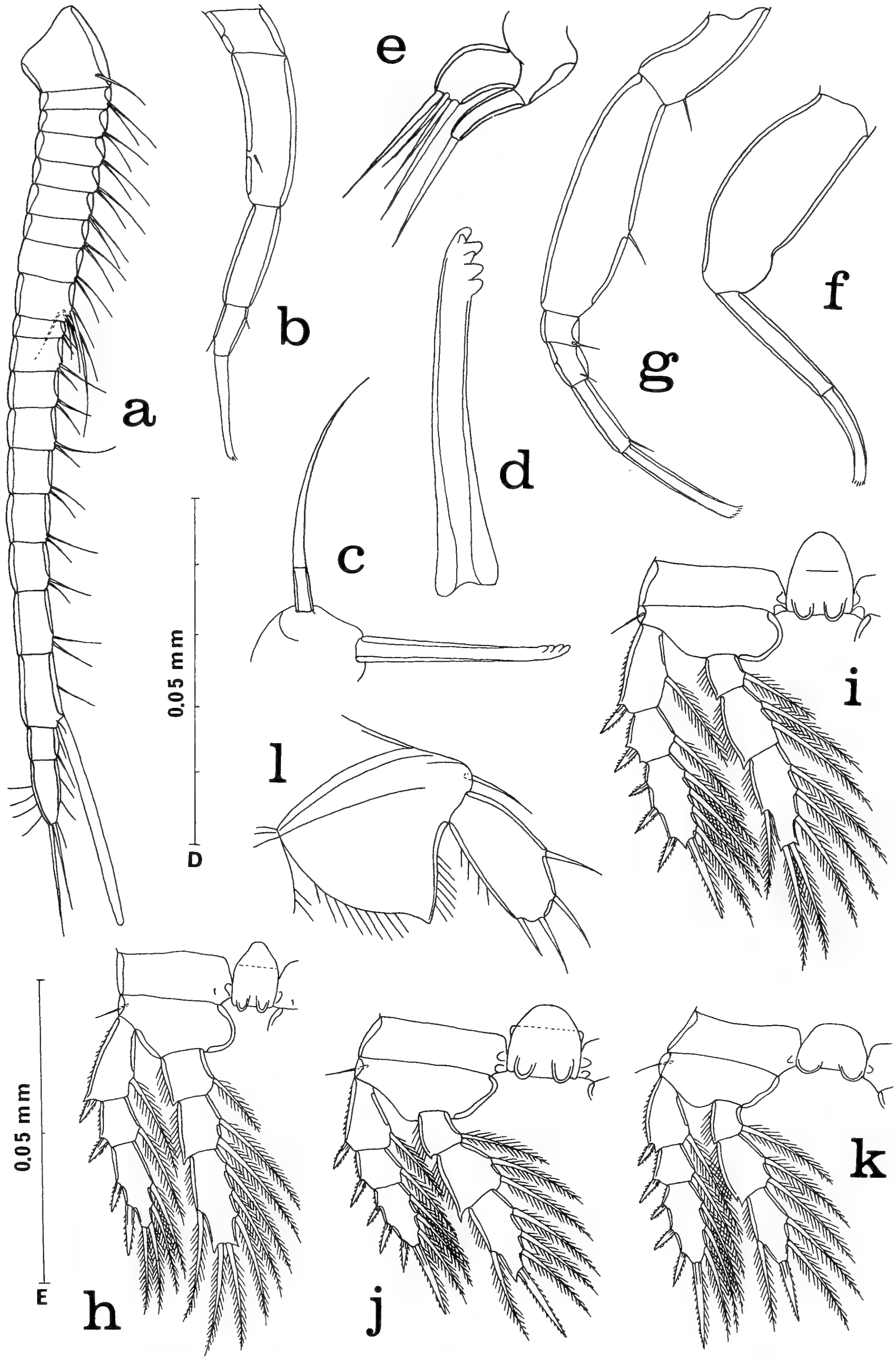

Fig. 2. *Collocherides brychius,* new species. Female. a, antennule, ventral (scale C); b, antenna, dorsal (C); c, mandible, ventral (C); d, gnathobase of mandible, flat view (D); e, maxillule, anterior (C); f, maxilla, posterior (C); g, maxilliped, posterior (C); h, leg 1 and intercoxal plate (E); i, leg 2 and intercoxal plate, posterior (E); j, leg 3 and intercoxal plate, anterior (E); k, leg 4 and intercoxal plate, anterior (E); l, leg 5, ventral (C).

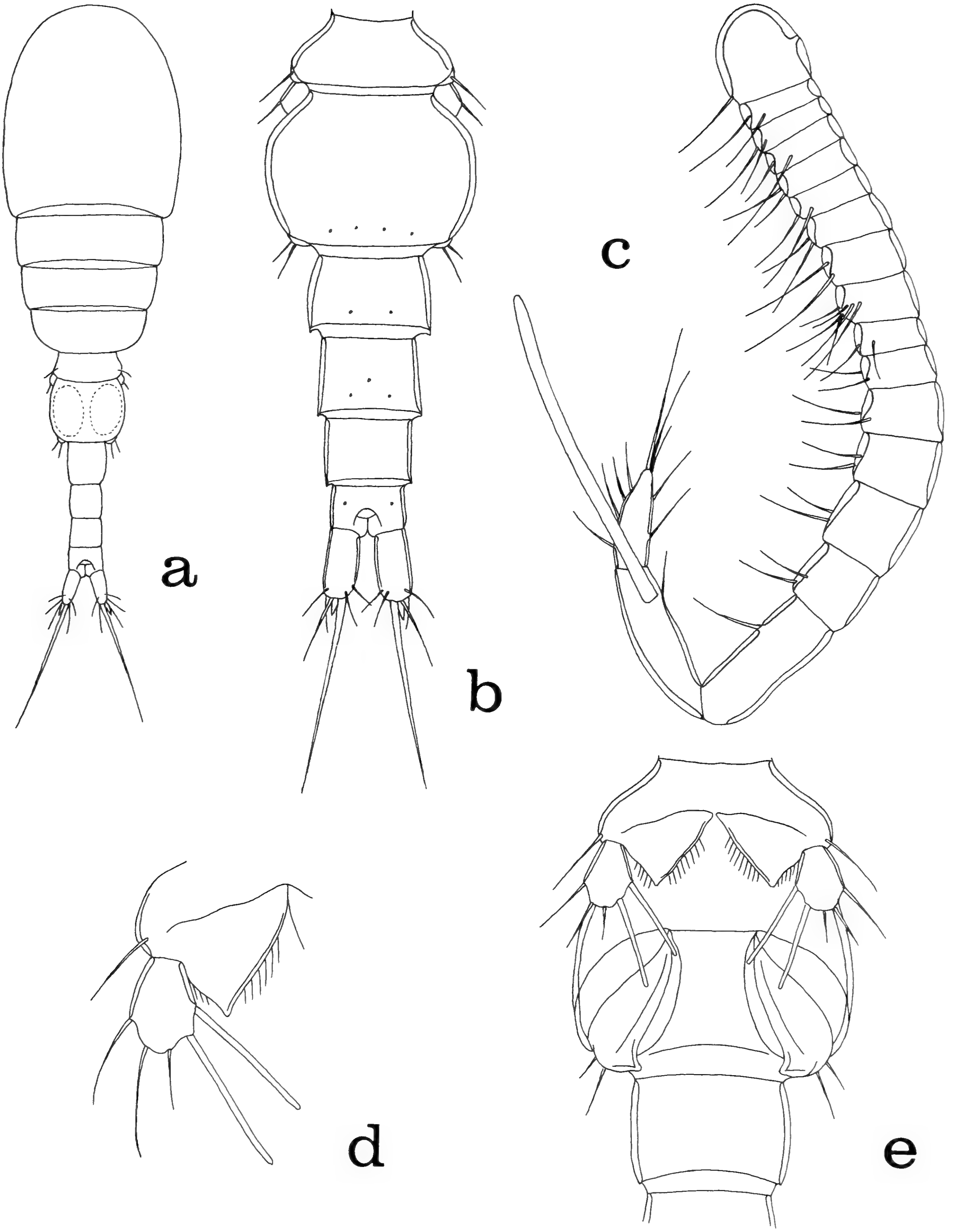

Fig. 3. *Collocherides brychius,* new species. Male. a, body, dorsal (scale A); b, urosome, dorsal (B); c, antennule, ventral (C); d, leg 5, ventral (C); e, somites 1–3 of urosome, showing legs 5 and 6, ventral (E).

with 1 distal seta. Claw (26 μm long) with truncated tip bearing minute spinules.

Ventral area between maxillipeds and first pair of legs (Fig. 1f) slightly protuberant (Fig. 1b).

Legs 1–4 (Fig. 2h–k) biramous with 3-segmented rami. Formula for spines (Roman numerals) and setae (Arabic numerals) as follows:

P_1	coxa 0-0	basis 1-0	exp I-1;	I-1;	II, 2, 2
			enp 0-1;	0-2;	1, 2, 3
P_2	coxa 0-0	basis 1-0	exp I-1;	I-1;	III, I, 4
			enp 0-1;	0-2;	1, 2, 3
P_3	coxa 0-0	basis 1-0	exp I-1;	I-1;	III, I, 3
			enp 0-1;	0-2;	1, I, 3
P_4	coxa 0-0	basis 1-0	exp I-1;	I-1;	III, I, 3
			enp 0-1	0-2,	1, I, 2

Inner coxal seta absent in all 4 legs. Outer margins of exopod segments of all 4 legs with very small spinules.

Leg 5 (Fig. 2l) 2-segmented. First segment with outer seta and produced medially as broad triangular flap, pointed at tip, and having inner and outer setules. Second segment 31 × 14 μm, ratio 2.2:1, bearing 4 setae and ornamented along inner margin with few setules.

Leg 6 represented by seta and small spiniform process on genital area (Fig. 1d)

Color of living specimens unknown.

Male.—Body (Fig. 3a) elongate, slender, and, as in female, not flexed. Length (not including setae on caudal rami) 0.50 mm (0.50–0.51 mm) and greatest width 0.15 mm (0.15–0.16 mm), based on 3 specimens. Greatest dorsoventral thickness at level of small ventral protuberance 96 μm. Ratio of length to width of prosome 1.98:1. Ratio of length of prosome to that of urosome 1.36:1.

Urosome (Fig. 3b) with 6 somites. Somite bearing leg 5 32 × 70 μm. Genital somite 60 × 83 μm, with rounded lateral margins. Four postgenital somites from anterior to posterior 34 × 49, 32 × 39, 26 × 32, and 21 × 31 μm.

Caudal ramus similar to that of female, 37 × 15 μm including terminal process. Inner terminal seta 143 μm long, relatively much longer than in female, 3.86 times longer than ramus.

Rostral area like that of female. Antennule (Fig. 3c) 18-segmented, geniculate. Aesthetasc on segment 17 59 μm long. Armature: 1, 2, 2, 2, 2, 2, 2, 2, 6, 2, 2, 2, 2, 2, 2, 1, 1 + aesthetasc, and 9. Antenna as in female.

Oral cone, mandible, maxillule, maxilla, maxilliped, and legs 1–4 like those of female.

Leg 5 (Fig. 3d) with second segment 20 × 12 μm, ratio 1.67:1, bearing 3 slender outer setae and 2 broad, hyaline, inner setae, 33 μm, with blunt tips.

Leg 6 (Fig. 3e) usual posteroventral flap on genital somite bearing 2 setae.

Color of living specimens unknown.

Etymology.—The specific name *brychius,* from Greek *brychios,* meaning from the depths of the sea, refers to the depth at which specimens of the new species was found.

Remarks.—The female of *Collocherides brychius* may be differentiated from its three congeners as follows:

From *C. astroboae* Stock 1971, in which the long terminal seta on the caudal ramus is approximately 3.6 times longer than the ramus, and the body length is 0.62 mm (measurements based on an average of five specimens from *Astroboa nuda* from the Dahlak Archipelago (Zoölogisch Museum Amsterdam, cat. no. 101.090).

From *C. singularis* Humes, 1986, in which the caudal ramus lacks a terminal process, the long terminal seta on the caudal ramus is approximately 1.8 times longer than the ramus, the second segment of the endopod of legs 1–3 has one inner seta, and the average body length is 0.64 mm.

From *C. bleptus* Humes, 1993, in which the ratio of the innermost terminal seta on the caudal ramus to the length of the ramus itself is approximately 2.51:1, the genital double-somite is 120 × 80 μm, distinctly longer than wide, the average body length is 0.77 mm, and the ventral surfaces of the genital and postgenital somites have numerous small scalelike spines.

In *C. brychius* sexual dimorphism occurs in the length of the inner terminal seta on the caudal ramus, which in the female is 42 μm, but in the male is 143 μm and less swollen proximally than in the female.

The four species of *Collocherides* may be further distinguished by the following key.

Key to females of the genus *Collocherides*

1. Genital double-somite distinctly longer than wide, ratio 1.4:1; body length 0.77 mm (0.75–0.78 mm) .... *C. bleptus*
   Genital double–somite quadrate or nearly so, ratio approximately 1:1; body length not exceeding 0.67 mm 2
2. Long inner terminal seta on caudal ramus 3.6 times longer than ramus .... *C. astroboae*
   Longest seta on caudal ramus 1.18 times (or less) longer than ramus 3
3. Body length 0.57 mm (0.55–0.58 mm); legs 1–3 with second segment of endopod having 2 inner setae ..... *C. brychius*
   Body length 0.64 mm (0.63–0.65 mm); legs 1–3 with second segment of endopod with 1 inner seta .... *C. singularis*

The ecological and host relationships within the genus *Collocherides* are poorly known. *Collocherides astroboae, C. singularis,* and *C. bleptus* are associated with shallow-water ophiuroids, while *C. brychius* lives in deep–water hydrothermal sites and was recovered free in meiofaunal samples. However, much more information is needed to understand these relationships. The possibility that there may have been ophiuroids at the deep-sea vent site cannot be excluded. Ophiuroids, known from abyssal depths (e.g., Lauermann and Kaufman 1998), have been reported from deep-sea hydrothermal sites (Hessler and Smithey 1983; Grassle 1986; Tunnicliffe 1991, 1998; Segonzac 1992; Sibuet & Olu 1998). A new genus and species of ophiuroid, *Ophioctenella acies,* was described from the Mid-Atlantic Ridge by Tyler et al. (1995). However, no ophiuroids are yet known from Juan de Fuca vents, where the *C. brychius* was found (Tunnicliffe, pers. comm.).

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Cymbasoma californiense, a new monstrilloid (Crustacea: Copepoda: Monstrilloida) from Baja California, Mexico

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Abstract.—*Cymbasoma californiense* is described from three adult females collected during three cruises carried out in an area adjacent to Bahia Magdalena, a large coastal system on the southwest coast of the Baja California Peninsula, and in the southern Gulf of California. The new species is very closely related to at least three other *Cymbasoma* (*C. longispinosum* (Bourne) and its allies), but can be distinguished by a combination of features including: the presence of cuticular striations on the forehead, cephalothorax, and genital somite; relatively long antennules; the structure of the fifth legs, and the relative length of the ovigerous spines. *Cymbasoma californiense* is the first species of this genus recorded in the Californian region and the Eastern Tropical Pacific.

Monstrilloids are protelean parasitic copepods which are free-living only as first nauplii and adults (Raibaut & Trilles 1993). The first nauplius is the infective stage, but later stages complete their development as endoparasites of benthic organisms such as polychaetes and prosobranch molluscs. Adults are free-swimming, exclusively reproductive, and have no feeding appendages (Isaac 1975; Davis 1984).

The number of described species has been estimated as about 90 (Grygier 1994a), and they are grouped into three recognized genera (*Monstrilla, Monstrillopsis,* and *Cymbasoma*). The generic nomenclature of the group is still unclear, and efforts have been made to solve this problem, particularly with regard to the genus *Cymbasoma* (Grygier 1994a, 1997). This genus contains now about 57 described species, with about half of them being described under the invalid genus name *Thaumaleus* (Razouls 1996).

There are several (six) records of monstrilloid copepods in the Northeastern Pacific region (Park 1967, Grygier 1995, Razouls 1996). However, only three species of monstrilloid copepods have been recorded in lower latitudes, such as the California region or the Eastern Tropical Pacific. All three regional records are of the genus *Monstrilla. Monstrilla capitellicola* Hartman, 1961 was recorded at La Jolla Canyon as a parasite of a polychaete of the genus *Capitella* (Hartman 1961), and was described upon V stage copepodids. *Monstrilla spinosa* Park, 1967, originally described from the Strait of Georgia, was recorded by Suárez-Morales & Vásquez-Yeomans (1996) off Bahía de Todos Santos, Baja California, and *M. gibbosa* Suárez-Morales & Palomares-García, 1995 was collected on the southeastern coast of the Baja California Peninsula (Suárez-Morales & Palomares-García 1995).

As part of a survey of the main coastal systems along the southern portion of the Baja California Peninsula, plankton samples were collected at Bahia de Magdalena, a large bay located on the western coast. Our taxonomic analysis of the copepods in the samples revealed the presence of several monstrilloids which turned out to belong to an undescribed species. The description of the new species is presented herein following the standards set by Grygier & Ohtsuka (1995) for descriptions of monstrilloid copepods.

Materials and Methods

Plankton samples were collected during the BAMA8611, BAMA9710, and CERRALVO9609 cruises. The first two were carried out in Bahia Magdalena (BAMA), a large coastal system on the southern portion of the western coast of the Baja California Peninsula, Mexico. The other cruise took place in the southern portion of the Gulf of California, along the southeastern coast of the Baja California. One female of the same previously undescribed species of monstrilloid copepod as captured during each of the three cruises: one at station K2 (BAMA9710), on 27 October 1997, another at station R2 (BAMA9611), on 5 February 1996, and the third was collected at station SIIG49 (CERRALVO9609), 20 September 1996 (Fig. 1). Samples were collected during surface hauls with a standard plankton net (0.333 mm mesh-size). Zooplankton was fixed with a buffered formalin solution. Monstrilloid copepods were sorted and transferred to 70% ethanol. Observations were made under a Zeiss microscope and drawings were made with the aid of a camera lucida. Standard terminology for copepod morphology (Huys & Boxshall 1991) and for monstrilloid antennular armature (Grygier & Ohtsuka 1995) was followed.

Order Monstrilloida
Family Monstrillidae Dana, 1849
Cymbasoma Thompson, 1888
Cymbasoma californiense, new species, Suárez-Morales

Material examined.—Holotype, 2.1 mm, adult female, undissected, ethanol-preserved. Sta. K2 (coordinates in decimal notation: 24.69°N, 112.07°W) BAMA9710 cruise, Bahía Magdalena, South Baja California, Mexico, 27 Oct 1997. Vial deposited in the Collection of Crustacea, National Museum of Natural History, Smithsonian Institution, Washington D.C., under number USNM-261422. Paratype adult female, partially dissected, permanent slide, mounted in CMC. Sta. SIIG49 (24.27°N, 109.85°W) CERRALVO9609 cruise, Isla Cerralvo, Southern Gulf of California, Mexico, 20 Sep 1996. Deposited in the NMNH, USNM-261422. Paratype adult female, total length: 2.03 mm, ethanol-preserved. Station R2 (24.41°N, 111.65°W), BAMA8611 cruise, Bahía Magdalena, Baja California Sur, Mexico, 5 Feb 1986. Vial deposited in the Zooplankton Collection of El Colegio de la Frontera Sur Unidad Chetumal, México, under number ECO-CH-Z-00369.

Type locality.—Bahía Magdalena, southern portion of the eastern coast of the Baja California Peninsula, Mexico. Water column.

Etymology.—The species is named after the Californian region in which this species was collected.

Description of female.—Average body length of 3 individuals, 2.1 mm measured from forehead to posterior margin of anal somite. Cephalothorax (incorporating first pedigerous somite) accounting for almost 65% of total body length (Fig. 2A, B). Ventral margin of anteriormost portion of cephalothorax slightly curved. Oral papilla as in Fig. 2A, lying midventrally 0.21 of way back along cephalothorax. Forehead with strong cuticular striations mainly between antennule bases, and, more dorsally, a circular, spiral pattern with two anterior and two posterior whorls, present in all the individuals. Nauplius eye present, weakly developed, ocelli slightly pigmented with rounded shape (Fig. 3E). Pair of low bumps on ventral side of cephalothorax between antennule bases and oral papilla, surrounded by circles with wrinkles arranged in spiral-shaped pattern. Cuticular ornamentation also on lateral posterior margin of cephalothorax: clear vertical striations (Fig. 2B). Antennules four-segmented, armed with 0, I; 1,V; 2, I; 10, VII setae (Arabic numbers) and spines (Roman

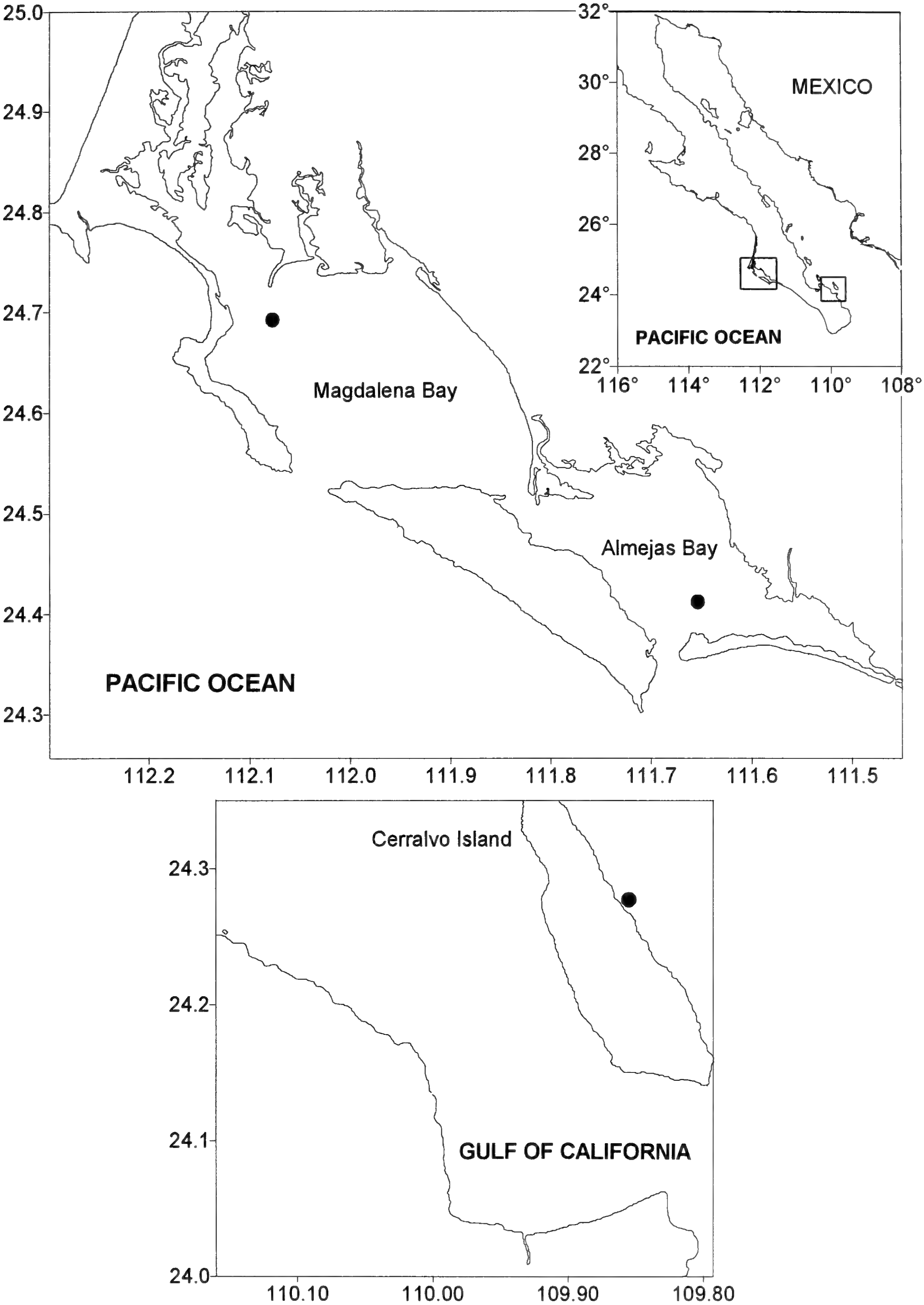

Fig. 1. Study area showing the sites in which specimens of the new species were collected.

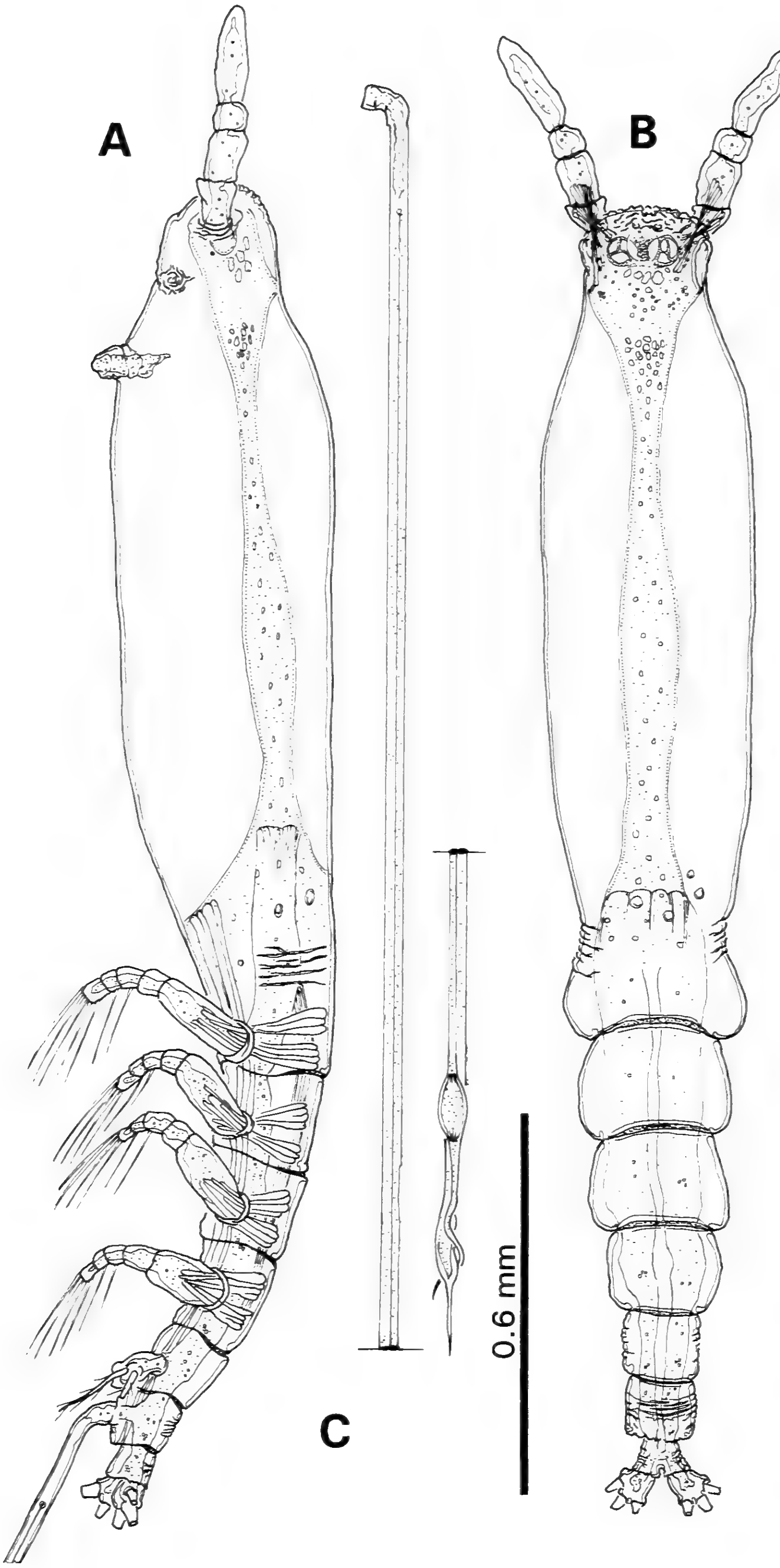

Fig. 2. *Cymbasoma californiense* n. sp., holotype female. A. habitus, lateral. B. habitus lateral. C. ovigerous spine.

numbers) (Fig. 3B, C). Terminal two spines asymmetrical, forming chela-like structure. Last segment with one small aesthetasc on distal margin, large aesthetasc (4aes) on proximal outer margin. Most spines and setae of general pattern described by Grygier & Ohtsuka (1995) present (Fig. 3C). Only setae b5 and b6 missing on last segment of right and left antennules, setae b1–4 unbranched. Ratio of lengths of antennule segments: 11.3 : 23.1 : 14.3 : 51.3 = 100. Antennule slightly lon-

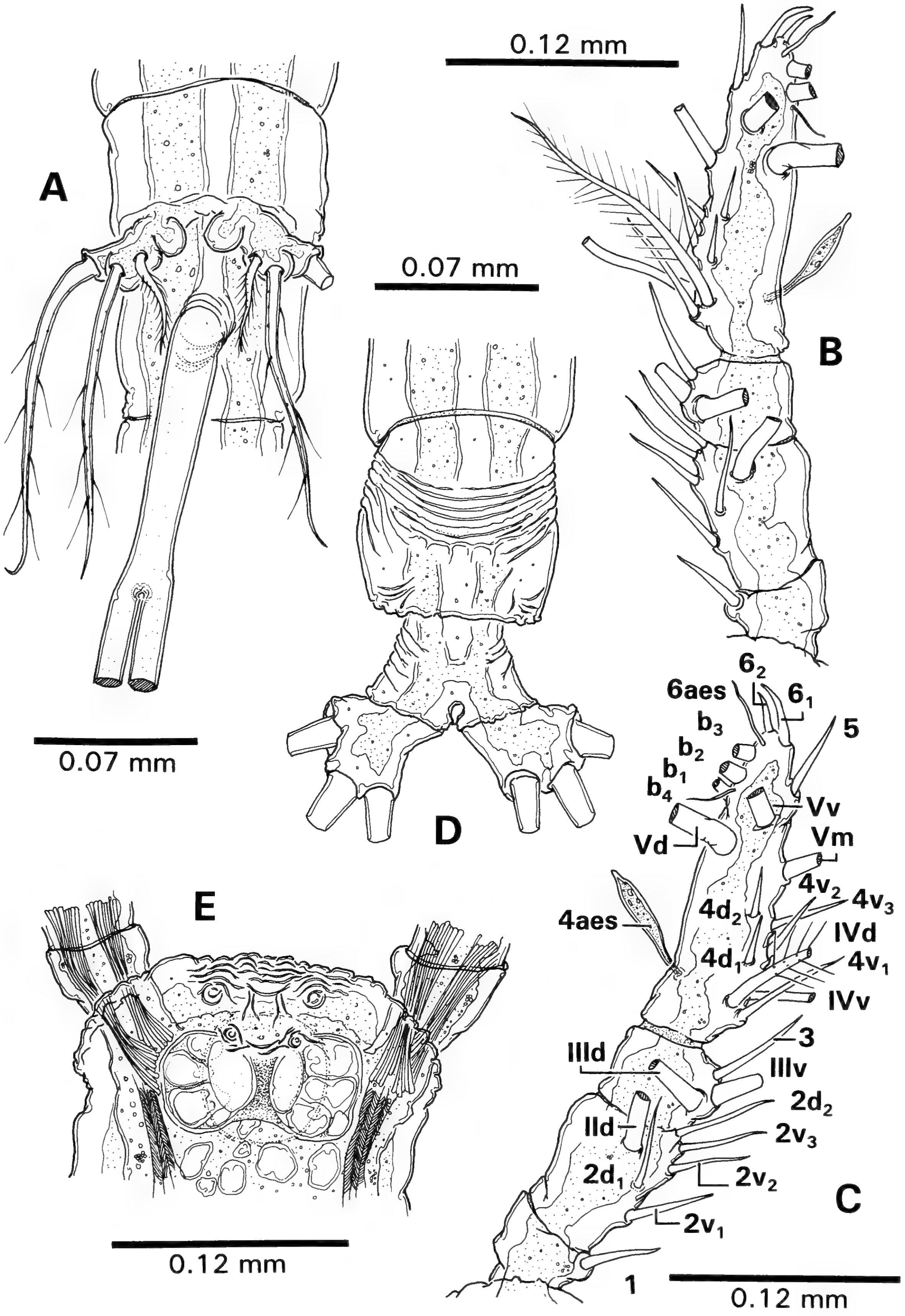

Fig. 3. *Cymbasoma californiense* n. sp., holotype female. A. genital complex and fifth legs, ventral. B right antennule, dorsal. C. left antennule, dorsal, with armature following the nomenclature of Grygier & Ohtsuka (1995). D. urosome and furcal rami, dorsal. E. forehead, dorsal.

ger than 17.5% of total body length, and 25.5% of cephalothorax length.

Incorporated first pedigerous somite and three free succeeding pedigerous somites (latter accounting for 22% of total length in dorsal view) each bearing a pair of biramous swimming legs (Fig. 4A–D). Endopodites and exopodites of legs 1–4 triarticulated. Legs 1–4 decreasing in size posteriorly. Armature of swimming legs as:

	basis	endopodite	exopodite
leg 1	1-0	0-1; 0-1; 1, 2, 2	I-1; 0-1; I, 1, 3
legs 2–4	1-0	0-1; 0-1; 1, 2, 2	I-1; 0-1; I, 2, 3

Basis separated from coxa posteriorly by diagonal articulation, with lateral hair-like seta on legs 1–4; seta on leg 3 at least 1.5 times longer and noticeably thicker than the others, and plumose, while others are simple. Inner seta on first exopodite segment of legs 1–4 plumose, long, reaching to distal margin of endopodite. Inner margin of first endopodal segments and outer margin of second and third exopodal segments of legs 1–4 with short hairs. Outer exopodal apical seta of legs 1–4 with row of setules along inner side, but bearing row of small, closely spaced denticles along outer side. Most setae biserially plumose.

Fifth legs joined medially; each with rounded endopodal lobe. Exopodal lobe 2 times longer than wide, with two long, equal plumose setae, and one short inner, plumose seta, about 28% as long as the other two (Fig. 3A).

Urosome consisting of fifth pedigerous somite, genital double somite, one free abdominal (anal) somite, and furcal rami, altogether representing 14.3% of total body length. Genital double-somite slightly longer than one-third total length of urosome (35%). Ratio of lengths of fifth pedigerous somite, genital double somite, and free abdominal somite: 37.5 : 35.5 : 26.6 = 100. Genital somite with strong transverse cuticular wrinkles on lateral margins and dorsal surface (Fig. 3D). Medial portion of genital double somite moderately swollen, bearing long, basally conjoined, ovigerous spines. Spines separate from level of posterior margin of furcal rami. Spines slender at their base, swollen distally, in dorsal view, left one of holotype shorter than right one (Fig. 4E). Spines about 1.4 times total body length (Fig. 2C). Caudal rami short, 1.2 times longer than wide, moderately divergent, bearing three strong, terminal setae, as usual in genus. Middle seta slightly thicker than others (Fig. 3D).

Male.—unknown.

Remarks.—The new species from Baja California is assigned to the genus *Cymbasoma* by virtue of the presence of two urosomal somites in the female, with only one free somite between the genital double somite and the caudal rami (Isaac 1975).

According to the most comprehensive key to the species of this genus (Isaac 1975), the Californian specimens would be identified as females of *C. longispinosum* (Bourne, 1890). However, other species such as *C. chelemense* Suárez-Morales & Escamilla, 1997, recently described from the Gulf of Mexico, and *C. morii* Sekiguchi, 1982, redescribed by Grygier (1994b) from Japan are closely related to and can also be confused with *C. longispinosum.* The female specimens of *C. californiense* share several features with *C. longispinosum, C. morri,* and *C. chelemense,* such as the relatively long cephalothorax, the general structure of the fifth legs, with a rounded endopodal lobe, the position of the oral papilla, the antennule/cephalothorax length ratio, the dorsal striations on the genital double segment, the swollen tips and the asymmetry of the ovigerous spines, and relatively long ovigerous spines conjoined at the base. However, the new species differ from these other species in several key structures generally regarded as important in monstrilloid taxonomy, such as the morphological details of the fifth legs, the structure of the genital complex, and the body proportions.

In the females of *C. californiense* the cephalothorax represents 65% of the total

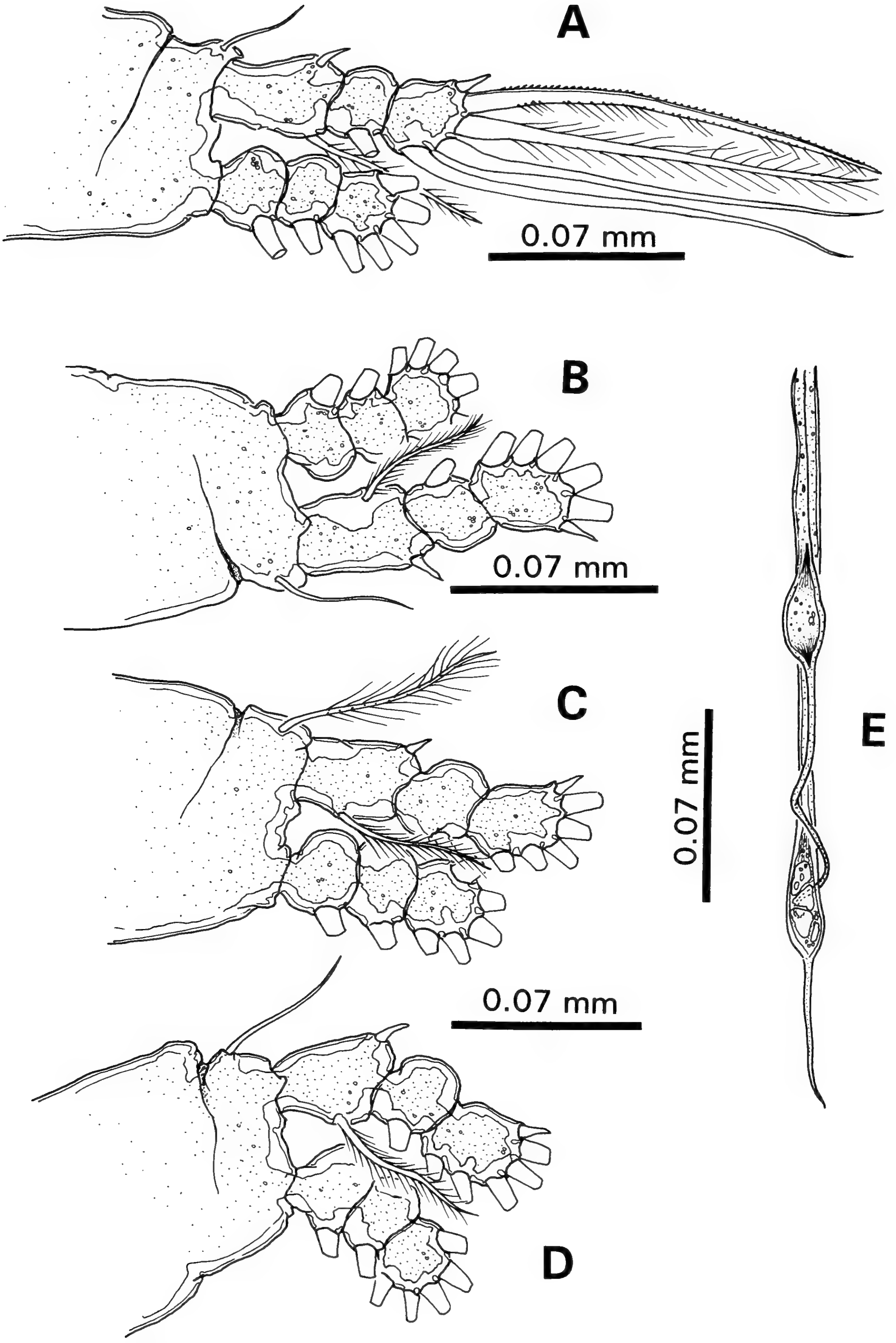

Fig. 4. *Cymbasoma californiense* n. sp., holotype female. A. right leg 1, posterior. B. left leg 2, posterior. C. right leg 3, posterior. D. right leg 4, posterior. E. ovigerous spines, detail of distal portion.

body length; the figure for *C. chelemense* is 68%, while in *C. longispinosum* it is less than 65%, and in *C. morii* the reported range (Grygier 1994b) is 66–73%. In the new species the oral papilla is relatively much smaller and shows a different aspect with respect to those of *C. chelemense* and *C. morii,* but is similar to that of *C. longispinosum.* The strong cuticular protuberances on the forehead of the new species are shared only by *C. chelemense,* but are different; in the latter, the striations show a more complex pattern. The forehead is only slightly rugose in *C. morii* (see Grygier 1994b). *Cymbasoma californiense* shows anteroventral knobs (nipples), which were described for *C. morii,* and *C. chelemense* and are probably also present in *C. longispinosum.* However, in the new species these knobs are reduced, not protruding as far as those described for the other species.

The fifth leg's endopodal lobe in *Cymbasoma longispinosum* has a clearly triangular-elongated shape (Giesbrecht 1892; Sars 1921; Isaac 1975), while the same structure is completely rounded in the new species, as it is in both *C. morii* (Grygier 1994b) and *C. chelemense* (Suárez-Morales & Escamilla 1997). However, this structure is relatively smaller in *C. morii* than in the other two species.

The fifth legs inner seta in *C. californiense* is relatively short in comparison with those of the other species. It is about 28% as long as the other two setae (3.5 times shorter), while this figure is 62.5% in *C. chelemense* (1.6 times shorter), 40% (2.5 times shorter) in *C. morii,* and 66% (1.5 times shorter) in *C. longispinosum.*

The armature of the antennules is similar in the four species. The new species shows the same antennular armament pattern as described in *C. morii* and *C. chelemense,* with only slight differences in the size and position of some of the smallest setae. The largest aesthetasc on the distal segment is relatively shorter in *C. californiense* than it is in *C. chelemense* and in *C. morii.* Proportions of antennular segments are similar in these species, with the terminal segment representing more than 50% of the total antennular length. However, the antennules in the new species are relatively longer than in the other species compared herein, representing 25.5% of the cephalothorax length versus 21–22% in the other three species considered herein.

In *C. californiense* and *C. chelemense,* the genital double somite's posterior margin is about 40% wider than the anterior margin of the succeeding free (anal) somite. From Giesbrecht's (1892) illustrations, in *C. longispinosum* the proportional value is less than half (16%) that measured for the new species; in *C. morii* the value is around 30%, and the posterior margin of the genital double somite is slender and somewhat convex. This margin is slender in the other species and clearly irregular in the new species.

The proportional length of the ovigerous spines differs among the four species. In *C. longispinosum* and *C. chelemense* the spines are only 14% longer than the body (Giesbrecht 1892; Sars 1921; Suárez-Morales & Escamilla 1997). In *C. morii* they are much longer, about twice as long as the body, whereas in the new species they are 42% longer than the body. All four species have a long common base for the two ovigerous spines.

Cymbasoma californiense shows cuticular wrinkles along the lateral margins of the fifth pedigerous and anal somites, and on the posterior lateral margins of the cephalothorax. These features are absent in the other species and could be considered as a key character to recognize this species. The total body length recorded for *C. californiense* (2.2 mm) is slightly under the range reported for *C. longispinosum* and *C. chelemense* (2.3 to 3.16 mm) (Isaac 1975, Suárez-Morales & Escamilla 1997), but is slightly over the average length of *C. morii* (2.18 mm) (Grygier 1994b).

There are several species of *Cymbasoma* with a long, slender cephalothorax: *C. morii* (Sekiguchi, 1982), *C. longispinosum*

Table 1.—Comparison of features present in females of two groups of species of *Cymbasoma* with a relatively long cephalothorax.

Species	*C. gigas*	*C. morii*	*C. chelemense*	*C. longispinosum*	*C. californiense*	*C. bowmani*	*C. reticulatum*
Lobes on fifth leg	2	2	2	2	2	1	1
Inner lob	ovate	rounded	rounded	subtriangular	rounded	—	—
Nipples	?	present	present	present	reduced	absent	absent
Ovig. spines	?	joined at base	joined at base	joined at base	joined at base	separated at base	separated at base
O.S. longer than body	?	2 times	14% longer	14% longer	43% longer	shorter	shorter
Striation on gen. som.	?	present	present	not described	present	absent	absent
Striation on anal som.	?	absent	absent	not described	present	absent	absent
Striation on forehead	?	present (light)	present (strong)	not described	present (strong)	present (light)	absent

(Bourne, 1890), *C. chelemense* (Suárez-Morales & Escamilla), 1997, *Cymbasoma gigas* (A. Scott, 1909), *C. reticulatum* (Giesbrecht, 1892), and *C. bowmani* (Suárez-Morales & Gasca), 1998. As suggested by Suárez-Morales & Gasca (1998), these *Cymbasoma* species can be divided into two groups (see Table 1). In the first group, with a bilobed fifth leg, nipple-like ventral cephalic protuberances, striated genital somite, and basally fused genital spines which are longer (1.5–2 times) than the body, *C. morii, C. longispinosum, C. chelemensis,* probably *C. gigas,* and now *C. californiense,* could be included. The second group shares a single-lobed fifth leg, the absence of nipple-like ventral protuberances, and basally separated genital spines that are shorter than the body (*C. reticulatum, C. bowmani*).

The lack of comparative biogeographical information on monstrilloids is related to several factors: the scarcity of the group in plankton collections, the unsolved taxonomy of the group, the uncertainty in recognizing the male and female of the same species from plankton samples, and the irregular putative distributional patterns throughout the group (Isaac 1975). However, it is relevant to mention the known geographical ranges of the four species compared herein. The Mediterranean, Great Britain, Mindanao, Portugal, Black Sea, Gulf of Suez, Vietnam, and the Arabian Gulf for *C. longispinosum* (Isaac 1975); the wide distribution reported for this species could be the result of overlooking closely related species. This has been suggested by Grygier & Ohtsuka (1995) for *Monstrilla helgolandica* Claus (1863). *Cymbasoma morii* has been recorded from Japan, supposedly Vietnam, and probably India (Grygier 1994b); *C. chelemense* from the southern Gulf of Mexico (Suárez-Morales & Escamilla 1997), and *C. californiense* from Baja California. Presumably, the geographical isolation of the new species with respect to the others would favour the conception of a different taxon.

This new species of *Cymbasoma* represents the second record of the genus in the Northeastern Pacific region; the only previous record was of *C. rigidum* Thompson, 1888, near the Kodiak Island, Alaska (Threlkeld 1977). It is also the first record of the genus in the California region.

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Early development of the deep-sea ampharetid (Polychaeta: Ampharetidae) *Decemunciger apalea* Zottoli

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Abstract.—Early development of the opportunistic, deep-sea ampharetid polychaete *Decemunciger apalea* Zottoli is described from specimens removed from wood panels placed on the deep-sea floor by Turner (1973). Larvae with less than 8 setigers were not found. Larval spatulate notosetae and neuropodial uncini on segments 3–6 formed during early development are eventually lost by the 14-setiger stage making segment 7 the first uncinigerous thoracic segment in juveniles and adults. Early development of this species is generally similar to that described for other shallow and deep-sea ampharetids.

The deep-sea ampharetid polychaete *Decemunciger apalea* Zottoli inhabits galleries in wood originally excavated by bivalve molluscs belonging to the genera *Xylophaga* and *Xyloredo* (Family Pholadidae, subfamily Xylophagainae) (Turner 1973, 1977; Zottoli 1982). The wood was placed by R. D. Turner, using the submersible DSRV *Alvin,* at four experimental bottom stations in the North Atlantic to "test the hypothesis that wood is an important source of nutrients and contributes to diversity in the deep-sea" (Turner 1973, 1977). This study is based on a detailed examination of 393 complete juvenile and adult specimens from wood panel N31 (DOS2) (Fig. 1). Early development and further role of this species in deep-sea ecosystems is discussed.

Materials and Methods

Three experimental islands, each with 12, one foot spruce cubes, were placed by Turner (1977), for a period of five years at the following locations: Deep Ocean Station 1 (DOS-1), 39°46′N, 70°41′W, 110 miles south of Woods Hole, Mass., in 1830 m; Deep Ocean Station 2 (DOS-2), 38°18.4′N, 69°35.6′W, 190 miles southeast of Woods Hole, Mass., in 3506 m; Tongue of the Ocean, Bahama Islands (TOTO Tower 3), 24°53.2′N, 77°40.2′W, in 2066 m.

Each experimental island is surrounded by wood panels (24″ × 5″ × 1″) which are removed and replaced each time the islands are visited. Each panel is enclosed in a mesh bag when it is retrieved, to prevent loss of specimens. The mesh bags and their contents are then transferred to retrieval boxes carried on the DSRV *Alvin* basket. The contents of the bags may be preserved at the time the boxes are closed for return to the surface by puncturing plastic bags containing glutaraldehyde, previously placed in the retrieval boxes. In certain cases, the panels were preserved immediately upon reaching the surface. Wood panel N31 (DOS 2) was submerged by *Alvin* on dive 601, 5 Sep 1975, and removed on dive 777, 3 Aug 1977 harboring 393 whole ampharetids. Refer to Turner (1973, 1977) for a more detailed description of the methods used to place and retrieve the panels from experimental islands.

Systematics

Ampharetid polychaetes are for the most part widest anteriorly, tapering gradually towards the posterior end. The prostomium, a pre-segmental structure, is situated imme-

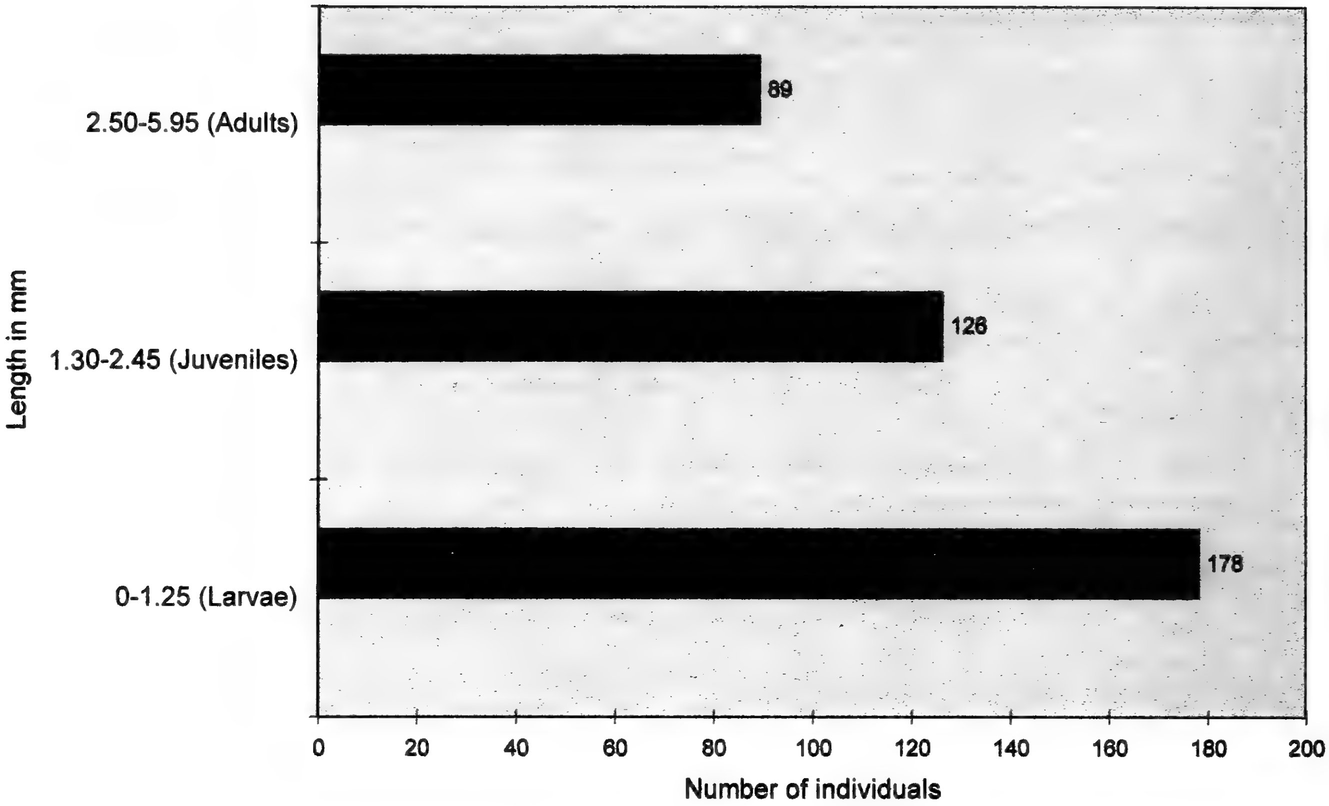

Fig. 1. Frequency histogram for length from a collection of 393 *Decemunciger apalea* from wood panel N31 (DOS2).

diately in front of the peristomium. Segments 1 and 2 that are fused together follow behind the peristomium. Refer to Zottoli (1974) for additional information on the formation of these structures. The segmental numbering system used in this paper is that of Malmgren (1865–1866) and Fauvel (1927) who recognized two segments in front of the paleal segment (segment 3). The thorax begins on segment 4. Segment 3 in some species has one dorsolateral bundle of paleal setae, or notopod with a bundle of winged capillary setae, on each side. Segment 3 is achaetous in adult *Decemunciger apalea*; however, small notopods with larval, hooded, flared (spatulate) notosetae or winged capillary setae are present in early stages. Adult worms have 13 thoracic setigers, the last 10 of which are uncinigerous, and 14 abdominal uncinigerous segments (Zottoli 1982). In addition, 4 pairs of smooth branchiae are present on the dorsal surface of segments 3–5. Refer to Zottoli (1982) for a more complete description of adult characteristics.

Larval and juvenile stages of *D. apalea* in this study are named according to the total number of segments bearing spatulate and/or capillary notosetae (setigers). Post-setigerous segments are those that follow these setigers and bear uncinigerous pinnules (neuropodia with uncini). For adults the word setiger refers to any segment with setae of either the capillary or uncinate type. The number of thoracic segments with both capillary notosetae and neuropodial uncini is a diagnostic feature of juveniles and adults but not larvae since larvae gain and lose setae during development, and the thorax is not fully formed.

Early Development

The eight female *D. apalea* with mature eggs in their body cavities ranged from 2.5 to 5.6 mm in length and from 0.5 to 0.7 mm in maximum width, whereas the 13 males with mature sperm ranged from 2.6 to 5.95 mm in length and from 0.42 to 0.7 mm in maximum width. Therefore, specimens with the full complement of adult setigers and ranging from 1.3 to 2.45 mm in length are considered juveniles. Worms less than 1.3 mm in length and lacking the full complement of adult setigers are considered larvae. On this basis, 89 adults, 126 juveniles and 178 larvae were identified from the 393 whole specimens removed from Panel N31 (DOS 2) (Fig. 1). Sexually mature specimens of this species previously studied (Zottoli 1982) ranged from 3.6 to 6.3 mm in length and from 0.54 to 0.9 mm in maximum width.

8-Setiger Stage.—The 8-setiger stage (Fig. 2) is named for its eight segments bearing notosetae. Larvae with less than 8 setigers were not found. In the 8-setiger stage (Fig. 2), larval ciliary bands were not evident; a short, medial, ventrally ciliated tentacle protrudes from the mouth. A muscular ventral bulb is visible internally, just below the pharynx and above the lower lip. Pharynx, esophagus, stomach and intestine are visible through the transparent body wall. The digestive tract is filled with particulate matter as well as occasional *Xylophaga* larvae, suggesting that they feed in the manner described for *Hobsonia florida* by Zottoli (1974): "larvae begin feeding on microscopic plant and animal material at about the two-setiger stage by forcing material from the mud surface into the digestive tract through the action of the ventrally located buccal mass and by cilia on the upper lip."

Prostomial and pygidial pigment spots are lacking. Fused segments 1 and 2 are situated immediately behind the prostomium. Segments 3–6 (setigers 1–4) bear 2 small dorsolateral notopods each with 1 spatulate (hooded, flared) seta (about 11 μm long, 6 μm maximum width) (Fig. 3A) and 1–2 smooth, winged, bilimbate capillary setae (about 25 μm long, 2 μm wide basally) (Fig. 3A). The number of smooth, winged, bilimbate capillary setae per notopod increases as the larva grows from the 8- to the 14-setiger stage (Table 1).

One uncinus (about 6 μm long) is embedded in the epidermis, below the notopod, on each side of segments 3–6 (setigers 1–4). Each of the first 4 pairs of uncini have about 12 teeth above a basal prow (Fig.

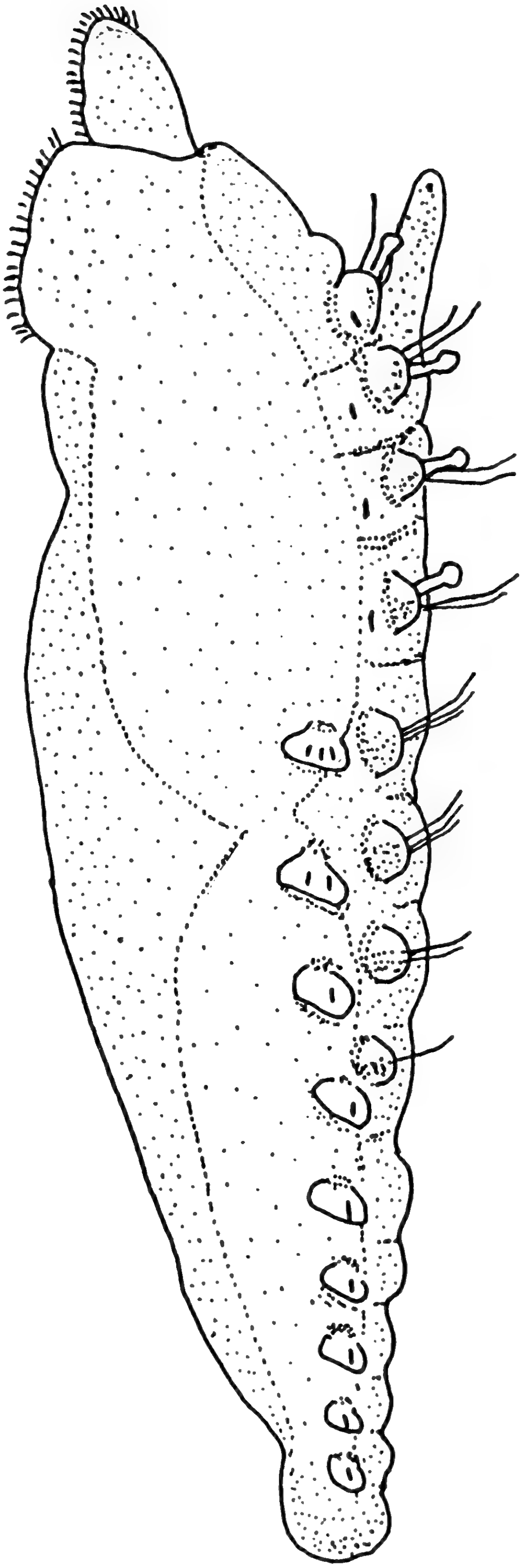

Fig. 2. *Decemunciger apalea* 8-setiger larva. Lateral view of entire worm, 0.6 mm long.

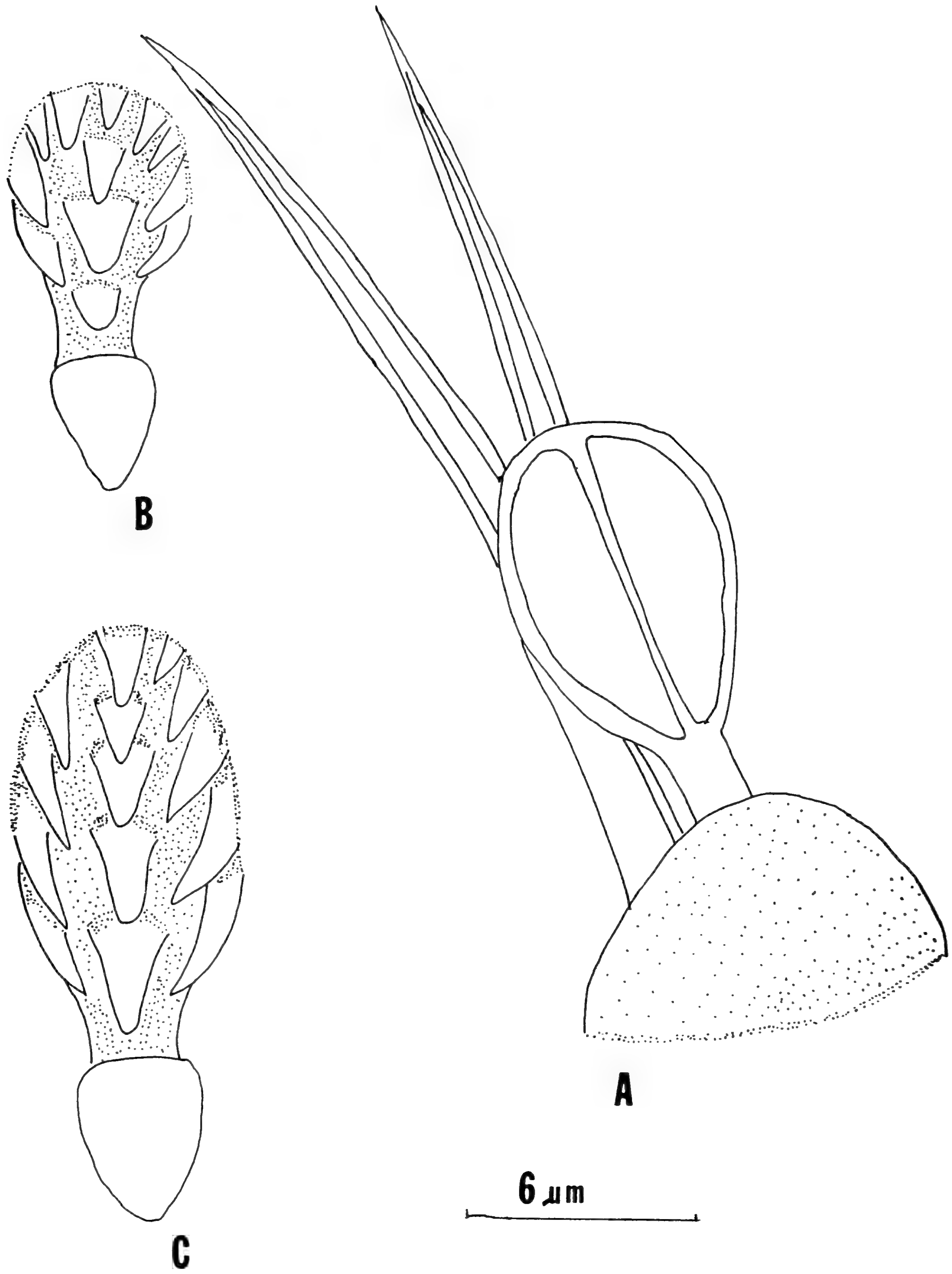

Fig. 3. *Decemunciger apalea* 8-setiger larva. A. Single spatulate seta and 2 smooth, winged, bilimbate capillary setae from the left notopod of the second setiger; B. Uncinus, frontal view, from the same setiger as above; C. Uncinus, frontal view, from the left uncinigerous pinnule of the 5th setiger.

Table 1.—Number of smooth, winged, bilimbate capillary setae per notopodium on "setigerous" segments of the 8- to 14-setiger stages of *Decemunciger apalea.* Note the loss of 1 setiger between the 14b- and 13a-setiger stages.

		Setiger stage								
Segment	Setiger	8	11	12	14a	14b	13a	13b	13c	13d
3	1	1	1	2	1	1	0	0	0	0
4	2	2	3	3	2	3	3	3	6	4
5	3	2	3	5	3	3	3	4	6	4
6	4	2	4	5	3	3	5	6	8	6
7	5	3	3	5	4	6	6	7	8	8
8	6	2	2	3	3	6	6	6	8	8
9	7	2	2	3	3	5	6	6	9	8
10	8	1	2	2	3	4	6	6	9	9
11	9		1	2	4	4	5	6	8	9
12	10		1	2	3	4	5	5	8	9
13	11		1	2	3	4	4	5	8	8
14	12			2	3	4	4	5	8	6
15	13				3	3	4	5	7	6
16	14				2	2	3	3	7	6

8 = 0.6 × 0.19 mm (1 pair br.), 11 = 1.0 × 0.19 mm (1 pair br.), 12 = 0.9 × 0.18 mm (2 pair br.), 14a = 1.4 × 0.28 mm (3 pair br.), 14b = 1.56 × 0.30 mm (3 pair br.), 13a = 1.75 × 0.30 mm (4 pair br.), 13b = 2.10 × 0.75 mm (4 pair br.), 13c = 3.50 × 0.50 mm (4 pair br.), 13d = 5.00 × 0.80 mm (4 pair br.), 14b = 1.56 × 0.30 mm (3 pair br.), br = branchiae.

3B); they disappear in later stages making segment 7 (setiger 5) the first uncinigerous thoracic segment in juveniles and adults. Segments 7–10 (setigers 5–8) bear 2 dorsolateral notopods each with one or two smooth, winged, bilimbate capillary notosetae (about 25 μm long and 2 μm wide basally) (Fig. 2; Table 1). Uncini (about 8 μm long) from segments 7–15 (setigers 5–8 and postsetigers 1–5), are borne on ventrolateral extensions of the body (uncinigerous pinnules), one pair per segment (Fig. 2). Uncini have about 14 teeth above a basal prow (Fig. 3C). The numbers of uncini per uncinigerous pinnule on all setigers, except those of segments 3–6 (setigers 1–4) gradually increase from the 8- to the 14-setiger stage (Table 2).

There are 5 post-setigerous segments (segments 11–15) bearing uncinigerous pinnules but lacking notopodia and notosetae. The pygidium lies immediately behind segment 15. One pair of branchiae is present on the dorsoposterior edge of segment 3. There is a narrow mid-dorsal gap between the branchium of each side.

Larvae at this stage were found in membranous tubes covered by fine particulate matter. The membranous lining is most likely mucus secreted by the thick, glandular pads on the ventral surface of most thoracic setigerous segments.

11-Setiger Stage.—The 11-setiger stage (Fig. 4), named for its eleven segments bearing notosetae, is similar to the 8-setiger stage except for an increase in number of segments and setae (Table 1), an increase in length of the median tentacle, addition of 2 lateral tentacles, loss of larval spatulate setae on setiger 4, and loss of larval uncini on setigers 1 and 2 (Table 2).

12-Setiger Stage.—By the 12-setiger stage, named for its twelve segments bearing notosetae, the larval uncini on setigers 3 and 4 (Table 2), and the larval spatulate setae on setigers 1–3 disappear. There is an increase in the number of smooth, winged, bilimbate capillary notosetae per notopodium (Table 1) and in the total number of "setigerous" and "post-setigerous" segments (Table 2). There is an increase in the length of the median tentacle, and a second

Table 2.—Number of uncini per uncinigerous pinnule on "setigerous" and "post-setigerous" segments of the 8- to 14-setiger stages of *Decemunciger apalea.* Note the loss of 1 setiger between the 14b- and 13a-setiger stages. Stage lengths are listed in Table 1.

		Setiger stage								
Segment	Setiger	8	11	12	14a	14b	13a	13b	13c	13d
3	1	1	0	0	0	0	0	0	0	0
4	2	1	0	1	0	0	0	0	0	0
5	3	1	1	1	0	0	0	0	0	0
6	4	1	2	1	0	0	0	0	0	0
7	5	3	5	7	14	11	15	25	29	30
8	6	2	3	6	11	11	14	24	29	28
9	7	1	2	4	9	9	11	18	27	26
10	8	1	1	3	8	8	13	18	25	21
11	9	1	1	3	8	6	10	16	23	20
12	10	1	1	2	6	5	8	15	23	19
13	11	1	1	1	5	5	8	14	21	18
14	12	1	1	1	4	3	7	14	18	13
15	13	1	1	1	3	3	6	14	17	10
16	14		1	1	2	2	5	14	17	
	"Post setiger" (Abdomen)									
17	15			1	2	2	3	5	16	10
18	16				1	2	3	5	10	10
19	17				1	2	3	5	10	9
20	18				1	2	3	5	8	9
21	19				1	1	3	5	7	9
22	20				1	1	2	5	7	6
23	21				1	1	2	5	7	7
24	22					1	1	5	7	5
25	23						1	5	5	4
26	24						1	4	5	4
27	25								4	4
28	26								2	3
29	27								3	

pair of branchiae appears on the dorsolateral, posterior surface between segments 4 and 5. Later, a third pair of branchiae arises from the dorso-lateral surface of segment 5.

14-Setiger Stage.—By the 14-setiger stage, all larval uncini on segments 3–6 have disappeared (Table 2, 14a, b). There is a general increase in the number of notosetae (Table 1) and uncini (Table 2). A fourth pair of branchiae arises from the anterior, dorsolateral surface of segment 6. Notosetae are eventually lost on segment 3, thus creating the 13-setiger stage described below (Table 1).

13-Setiger Stage.—The early 13-setiger stage (Fig. 5) (Tables 1–2, 13a) has the full complement of adult thoracic setigerous segments of which 10 are uncinigerous. Uncinigerous thoracic segments begin on segment 7. Changes that occur between this stage and adult worms (Tables 1–2, 13c, d) include an increase in number of capillary notosetae per notopod, an increase in number of uncini per uncinigerous pinnule, an increase in number of teeth per uncinus to about 20, and an increase in number of uncinigerous abdominal segments to 12–14.

Uncini are first formed in the dorsal portion of each uncinigerous pinnule. They range in length from 6–8 μm in an 8-setiger stage to 6–13 μm in a 12-setiger stage and from 12–18 μm in a 13-setiger stage. As new, longer uncini are created, older,

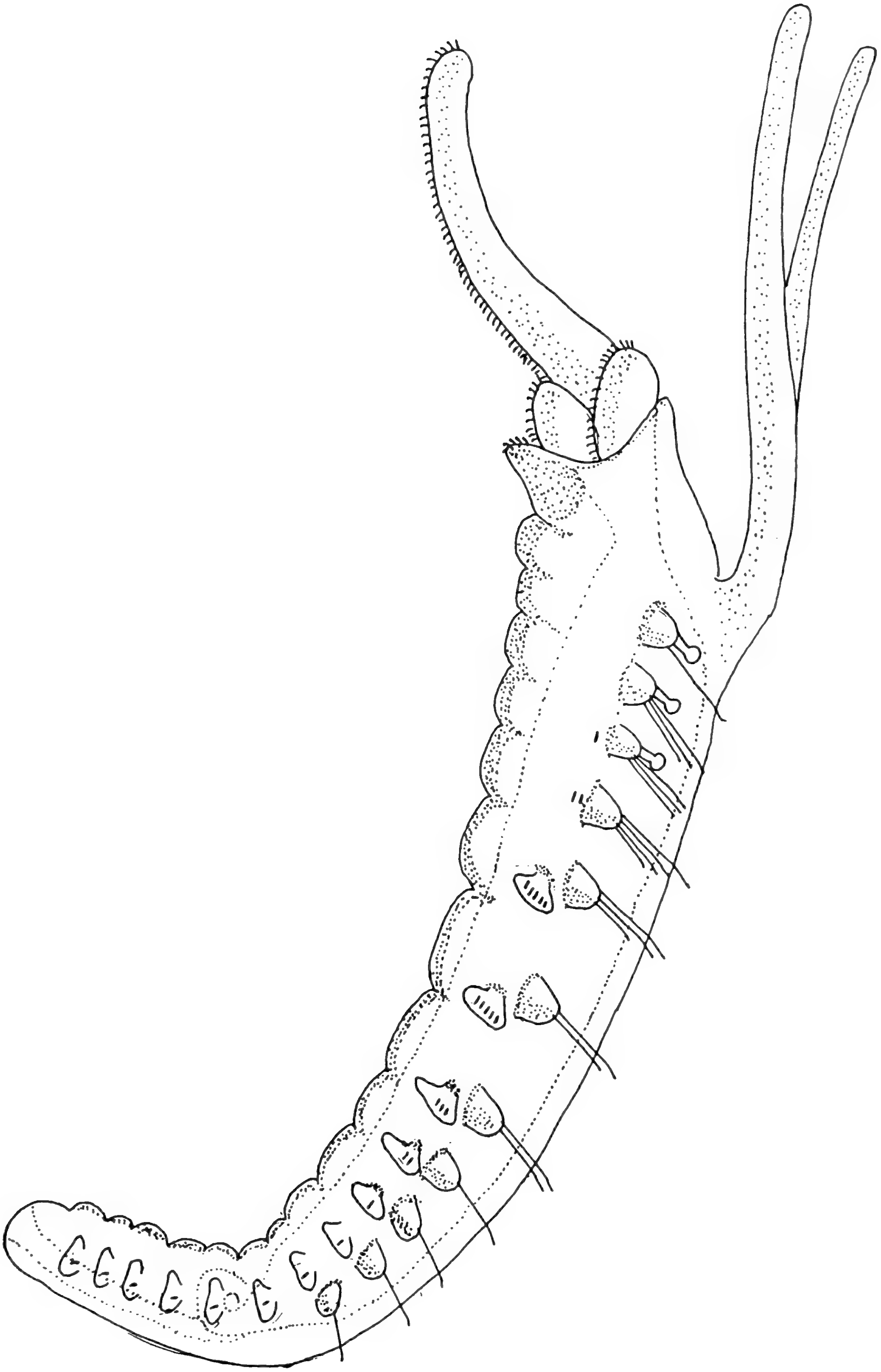

Fig. 4. *Decemunciger apalea* 11-setiger larva. Lateral view of entire worm, 1.0 mm long.

and shorter ones are pushed ventrally and eventually re-absorbed. This process is similar to that in *A. galapagensis* (Zottoli 1983) and *E. nebulosa* (Bhaud & Grémaré 1988). Few of the originally formed uncini remain in late juvenile and adult stages, suggesting an overall rapid growth rate for *D. apalea.*

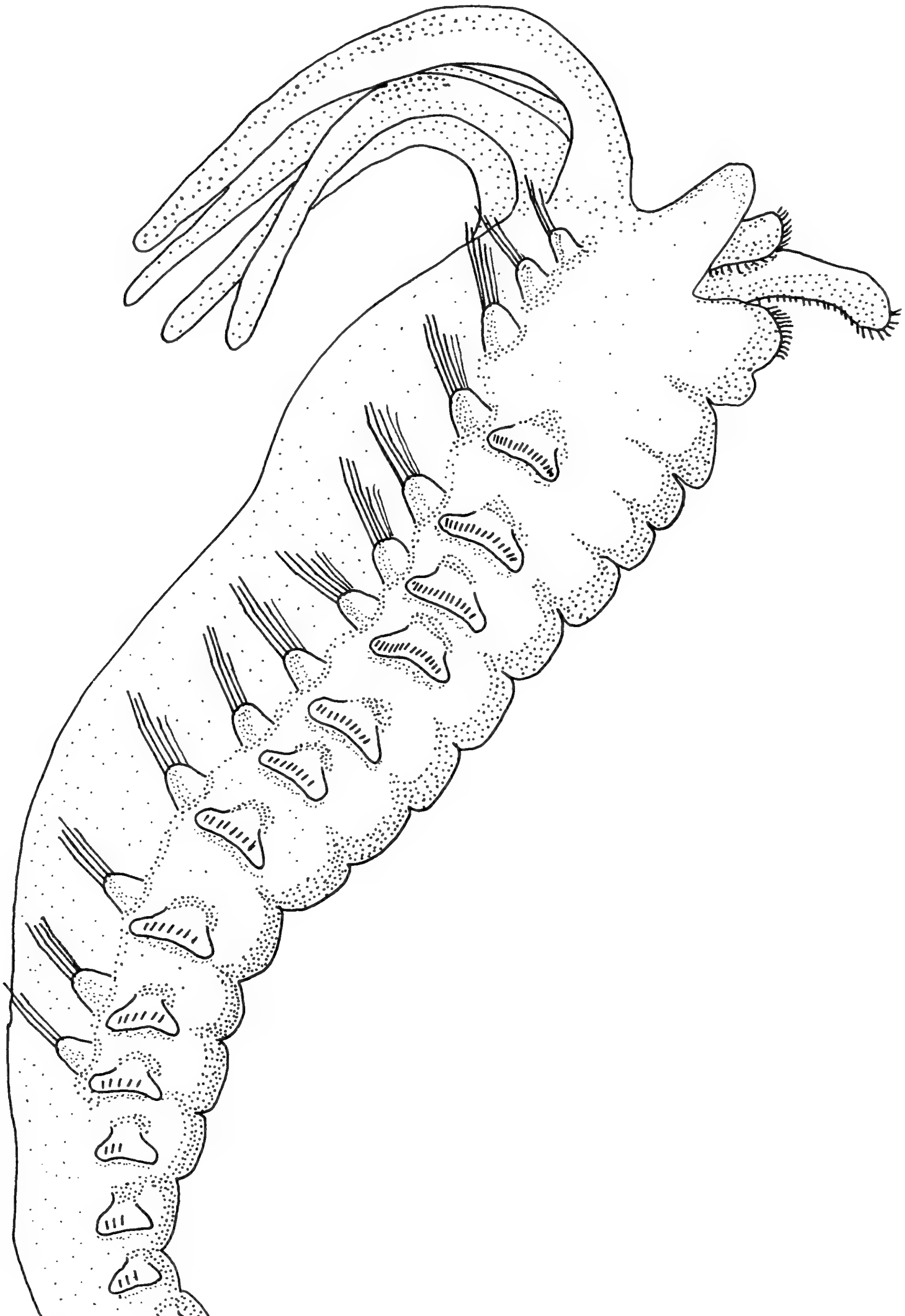

Fig. 5. *Decemunciger apalea* 13-setiger juvenile. Lateral view of entire worm, 1.75 mm long.

Discussion

Larval ciliated bands, although not found in *D. apalea,* disappear at about the 6-setiger stage in *H. florida* (Hartman) (Zottoli 1974), the 7-setiger stage in *Alkmaria romijni* Horst (Cazaux 1982), and were not found by Zottoli (1983) in later stages of *Amphisamytha galapagensis.*

Spatulate setae similar to those described in *D. apalea* are found in notopods of the first 3 setigers of larval *A. galapagensis* Zottoli (Zottoli 1983), *H. florida* (Hartman) (Zottoli 1974), and *Schistocomus sovjeticus* Annekova (Okuda 1947) and in the notopods of the first 4 setigers of larval *Ampharete acutifrons* (Grube) (Clavier 1984) and *Melinna palmata* (Grehan et al. 1991). What appear to be hooded, flared notosetae can be observed on Nyholm's (1950) photograph of a 3-setiger *Melinna cristata* Sars. Curiously, none were reported by Cazaux (1982) for *A. romijni.* Russell (1987) described hooded, flared setae in notopodia of segments 3–6 from the paedomorphic ampharetid *Paedampharete acutiseries* Russell. He suggested that "the spatulate setae of *H. florida* and *A. galapagensis* may represent a type of "spatulate" setae distinctly different from that of *S. sovjeticus, A. acutifrons* and *P. acutiseries.*" A detailed examination of spatulate setae from larval *A. galapagensis, D. apalea,* and *H. florida* shows a similar 3-dimensional form to that described by Russell (1987). Notosetae, which are generally similar in appearance to ampharetid spatulate setae, have been described, respectively, by the bracketed authors on the first 6, 8 and 11 setigers of *Eupolymnia nebulosa* (Bhaud 1988 and Bhaud & Gremare 1988), *Thelepus setosus* (Duchêne 1983), and *Loima medusa* (Wilson 1928). Hooded, flared, notosetae eventually disappear, with the possible exception of *P. acutiseries,* in all of the species discussed above.

The initial formation of spatulate setae, capillary notosetae and uncini and their subsequent loss on anterior segments here, are generally similar to that described for the ampharetids *A. galapagensis* (Zottoli 1983), *M. palmata* (Grehan et al. 1991), *H. florida* (Zottoli 1974), and the terebellids *E. nebulosa* (Bhaud & Gremare 1988), *Loima conchilega* (Kessler 1963), *L. medusa* (Wilson 1928), and *Nicolea zostericola* (Eckelbarger 1974).

Larval and adult uncini are similar in *D. apalea,* in contrast to *A. galapagensis* (Zottoli 1983) and *H. florida* (Zottoli 1974) where multi-toothed larval uncini are replaced in most segments by uncini with a single row of teeth.

Branchial formation in *D. apalea* is similar to that of the ampharetids *A. galapagensis* (Zottoli 1983), *A. romjini* (Cazaux 1982), *H. florida* (Zottoli 1974), and possibly *P. acutiseries* (Russell 1987).

Tubes, similar to those of *D. apalea,* were formed by 3-setiger, 1.75–2 day old *H. florida* larvae (Zottoli 1974), by 4-setiger *M. palmata* larvae (Grehan et al. 1991) and by 8-setiger, 20 day old *Alkmaria romijni* larvae (Cazaux 1982), shortly after they had abandoned the interior of the maternal tube. Larvae of the terebellids, *E. nebulosa* (Bhaud & Gremare 1988), *L. conchilega* (Kessler 1963), *N. zostericola* (Eckelbarger 1974), and *T. setosus* (Duchêne 1983), formed similar tubes, respectively, at the 6-, 2-, 14- and 4-setiger stages. Tube formation at such an early stage suggests that *D. apalea* larvae are benthic, remaining in the same general area as their parents. This does not preclude the possibility of larval transport from place to place by bottom currents. Once larvae form their own tube, they most likely remain permanently affixed, reaching new feeding areas by tube elongation as described by Fauchald & Jumars (1979). Ecklebarger (1974) reported that juvenile and adult *N. zostericola,* forced from their tubes, moved by repeatedly folding the abdomen upon itself and then straightening out. These actions lifted worms off the bottom and into the water column, transporting them short distances. The author observed similar movements in juvenile and adult *H. florida* forced from their tubes. Because of the general similarity in body shape and structure of ampharetids and terebellids, it is assumed that most, including *D. apalea,* could move short distances in the manner described above if displaced from their tubes.

Panel N31 (DOS 2) was submerged for about 2 years from 5 Sep 1975 to 3 Aug 1977. There are more larvae and juveniles than adults (Fig. 1). Assuming that larvae and juveniles of *D. apalea* remain in the area where they were bred, Fig. 1 most likely reflects the distribution of the species as a whole. This assumption is supported by the fact that worms live in attached tubes in all but the earliest phases of their life and that their body shape is not conducive to sustained active locomotion in a pelagic environment. The presence of numerous larvae and adults with gametes in their body cavities suggests that breeding took place shortly before the time of retrieval. The small number of large adults suggests a life span of one year. This is also supported by the presence of gravid adults, juveniles and larvae in a panel (N68, DOS1) retrieved after approximately one year. If the life span of *D. apalea* were more than one year, one would expect a proportionately greater number of adults.

Acknowledgments

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A new species of *Spiochaetopterus* (Chaetopteridae: Polychaeta) from a cold-seep site off Hatsushima in Sagami Bay, central Japan

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Abstract.—*Spiochaetopterus sagamiensis,* a new species (Polychaeta: Chaetopteridae), is described from two specimens collected from a cold-seep site off Hatsushima in Sagami Bay, central Pacific side of Japan. In this species, the large chaetae on chaetiger 4 (A4) are distinctive in having a triangular profile of the head, a nearly straight ventral edge of the inflated distal part, and two dorsolateral grooves on the shaft. The species has trilobed notopodia on the first segment of the median region (B1), bilobed ones on the second (B2), and entire ones on the third (B3) and on all succeeding segments. Uncinal plates of neuropodium B2 have more than 30 teeth; the upper toothed edge is smoothly curved. Anterior eyespots are absent. *Spiochaetopterus sagamiensis* occurs in deep water (800–1100 m depth) and is the first member of this family to be recorded in a deep-sea chemosynthetic community.

Chaetopterid polychaetes commonly occur on mud and sandy mud bottoms from the intertidal to shallow shelf waters. In Japanese waters, two species of *Spiochaetopterus* are known: *S. okudai* Gitay, 1969 and *S. costarum* (Claparède, 1870) (Okuda 1935, Gitay 1969, Nishi & Arai 1996). Chaetopterids are poorly known from deep-sea bottoms: only one species, the type species *S. typicus* Sars, 1856, has been recorded from shallow water to a depth of 2700 meters off W. Greenland (Kirkegaard 1960), at depths of 20 to 1865 meters in Arctic Seas and the Atlantic Ocean (Fauvel 1914), and at depths of 35 to 2030 meters in the North Pacific and associated waterbodies (Uschakov 1955). Levin et al. (1991) listed unidentified chaetopterid polychaetes present in the fauna of seamounts from the eastern Pacific Ocean at depths of 1058 to 3353 meters. Other records from deep-sea bottoms are worthy of re-examination (e.g., Levenstein 1961; Hartman 1971; Hartman & Fauchald 1971). This paper describes a new species of *Spiochaetopterus* found in a deep sea cold–seep off Hatsushima in Sagami Bay (Miura 1988). It is the first chaetopterid polychaete found in a chemosynthetic community (cf. Desbruyères & Segonzac 1997) and the third species in the genus described from Japan.

Materials and Methods

During dive 115 of the Deep-sea Research Vehicle (DSRV) *Shinkai 2000* (observer: K. Egawa) in Sagami Bay, two chaetopterid specimens were collected with three *Calyptogena* shells at depths of about 800–1100 m (Sugiura & Egawa 1985). The specimens were fixed in 10% sea-water formalin on the mother ship and later transferred to 70% ethanol. The specimens were sent to the second author for further study of the faunal structure of the Hatsushima cold-seep site (Miura 1988).

Parts of the specimens, such as segment 7 of the anterior region and large (cutting) chaetae were removed dehydrated through an alcohol series, air-dried, and observed with scanning electron microscopy (Hitachi S-800). Type series were deposited in the Natural History Museum and Institute, Chiba (CBM-ZW). For the description, the terminology of Crossland (1904) and Bhaud et al. (1994) is followed. In these papers, three body regions are defined as region A (anterior), region B (middle) and region C (posterior); in each region, segments are numbered from anterior to posterior: for instance, the fourth segment of the anterior region is termed segment A4 or simply A4.

Family Chaetopteridae Malmgren, 1867

Genus *Spiochaetopterus* Sars, 1856

Spiochaetopterus sagamiensis, new species

Figs. 1–2

Spiochaetopterus sp.—Miura, 1988 (dive numbers 177 and 115 inadvertently switched in table 2).

Material examined.—Off Hatsushima, Sagami Bay, DSRV *Shinkai 2000* Dive 115, 5 Jun 1984, 35°01′N, 139°12′E, 800–1100 m, collected with *Calyptogena* shells, holotype (CBM-ZW-701), incomplete, with a fragment of tube and paratype (CBM-ZW-702).

Diagnosis.—*Spiochaetopterus* of small size, eyes absent, with one pair of long palps. Large (cutting) chaetae of segment A4 with inflated head. Distal end of A4 chaetae triangular ventrally; shaft without ventral groove, with two dorso-lateral grooves. Segment A7 with brownish ventral gland; A8 and A9 with whitish ventral glands observed in alcohol preserved specimens. Notopodia trilobed in segment B1, bilobed in B2, entire in B3 and following segments. Neuropodia entire in B1, bilobed in all other middle segments. Uncini with over 30, maximum 40 teeth on uncinal plates. Tube unbranched, smooth, not annulated, with serrated opening.

Description.—Both holotype and paratype incomplete, lacking posterior region (region C). Holotype 18 mm long excluding palps, about 1 mm wide. Paratype 24 mm long excluding palps, 0.8–1.0 mm wide. Regions A and B (anterior and middle) creamy white, dorsal side of region B light brown in alcohol apart from glandular regions.

Region A narrow, 3.5 mm long for nine segments in holotype; 9 mm in paratype. Prostomium ovoid. Peristomium horseshoe-shaped, plump with prostomium on dorsal side (Fig. 1B). Eyespots absent. Prostomial antennae absent (Fig. 1B, C). Paired palps long, grooved, 10 mm long in holotype (14 mm in paratype), arising from posterior border of peristomium, near posterolateral border of prostomium (Fig. 1A, B, C, E). Dorsal groove ciliated, extending from base of palpi in A1 to A9 (Fig. 1B, E). Ventrum of region A with a long slender plastron (ventral glandular area) (Fig. 1A, C, E), with longitudinal white stripes, separated into five portions (Fig. 1C); portion I, longer than others, overlaying from peristomium to segment A2, white in colour, portion II from A3 to A4, narrower at A4, cream-colored; portion III from A5 through anterior half of A6, dark brown; portion IV from posterior half of A6 through A7, white; portion V from A8 to A9, white. Segments A1–A3 short, parapodia with a single row of 25–40 lanceolate chaetae; A4 elongate, with two large (cutting) chaetae, and more than 20 lanceolate chaetae; A5–A9 longer and wider than anterior three segments, with single row of 35–40 lanceolate chaetae (Fig. 2E–H).

Large (cutting) A4 chaetae obliquely triangular, occurring singly on both side (Fig. 2A–F); overhang of ventral edge of head distinct but weak. Distal part 300 μm long, 230 μm wide, with blunt distal tip and nearly horizontal ventral edge 200 μm wide; shaft 1300 μm long, 10–15 μm wide in middle portion, asymmetrical, nearly oval in cross section, without ventral groove; neck between head and shaft as wide as shaft (Fig. 2A, B, E).

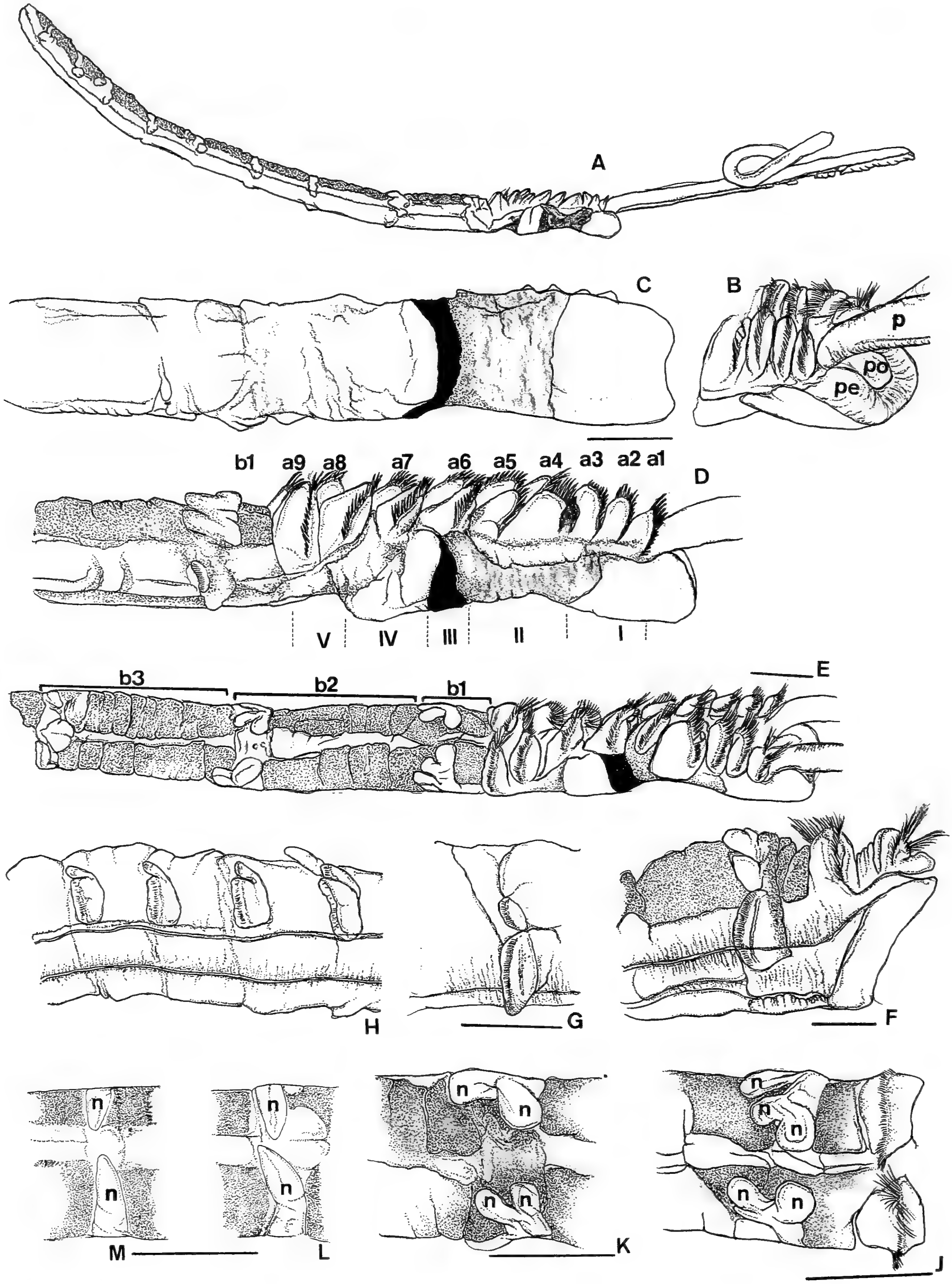

Fig. 1. *Spiochaetopterus sagamiensis* new species, drawn from holotype (A–E, J–M) and paratype (F–H). For all drawings (A to M) anterior part of the body is on the right. A. Whole body, lateral view. B. Anterior portion enlarged. C. Anterior portion including A, segment B1 and anterior B2, ventral view. D. Same, lateral view. E. Regions A and B, dorso-lateral view. F. A8 to B2, lateral view. G. B3 neuropodium, lateral view. H. A6 to B8 showing rami of neuropodia, ventrolateral view. J. Segments A9 and B1, dorsal view. K. Segment B2, dorsal view. L. Segment B3, dorsal view. M. Segment B4, dorsal view. Abbreviations.—I to V, indication

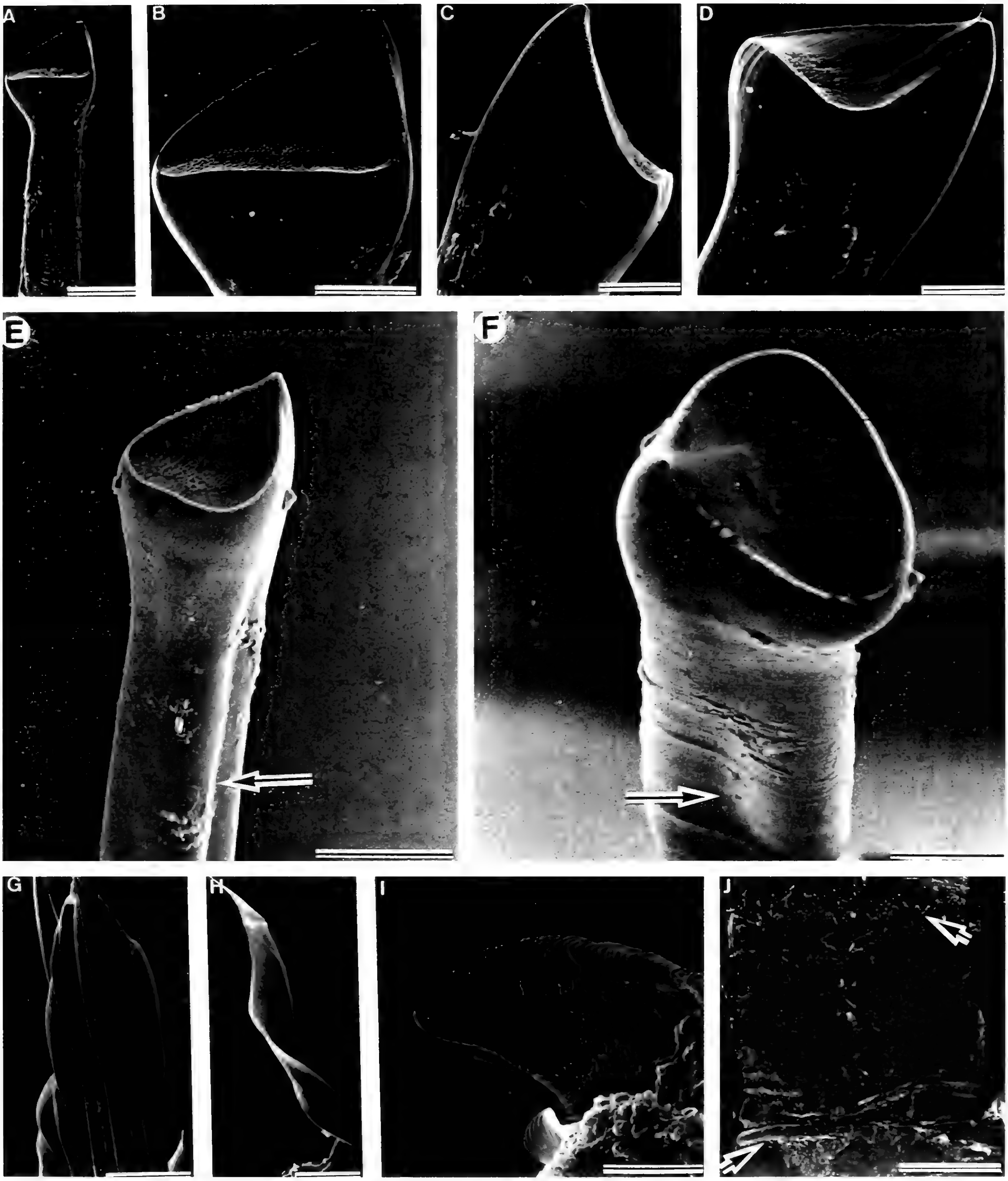

Fig. 2. *Spiochaetopterus sagamiensis* new species. Scanning electron micrographs of chaetae and tube of paratype. A–D. Distal part of A4 large (cutting) chaeta, ventral view (A, B) and lateral view (C, D); scales equal 200 μm (A) and 50 μm (B–D). E & F. Distal part of A4 large (cutting) chaeta, ventrolateral (E) and anterior dorsolateral view (F); unlabeled arrows point to dorsolateral groove on shaft; scale equal 100 μm (E) and 50 μm (F). G & H. Chaetae from region A, close-up view of thoracic setae; scales equal 75 μm (G) and 50 μm (H). I. Uncini of B2 neuropodium; scale equals 10 μm. J. Part of tube, lower arrow shows undulation, upper one serration; scale equals 750 μm.

←

of ventral parts of region A, i.e., separated portion of ventral plastron and posterior peristomium; a1 to a9, segments of region A; b1, first segment of region B; b2, b3, second or third segment of region B; n, notopodium; ne, neuropodium; p, palp; pe, peristomium; po, prostomium. All scales equal 0.5 mm.

Head of A4 chaetae inflated, obliquely truncate; upper tip of head tilted toward longitudinal axis of body; consequently external lateral oblique edge longer than internal edge. Horizontal edge smoothly circular without ventral sinus. Dorsolateral grooves on shaft (Fig. 2E, F). Ventral edge of oblique plane perpendicular to axis of shaft. Collar decreasing regularly in diameter.

Remaining anterior segments (A5–A9) large, inflated, shorter and wider ventrally; parapodia with 35–40 lanceolate chaetae in single rows; lanceolate chaetae asymmetrical, longitudinally folded, slightly brownish, with smooth surface and serrated edges (Fig. 2G, H).

Region B longer than anterior region, with eight elongate glandular segments (seven in paratype); paddle and cupule absent. B1 shorter than following segments (Fig. 1E). Middle parapodia biramous, along posterior margins of segments (Fig. 1E, E, H). Notopodia with one to three lobes; neuropodia bilobed except in segment B1, with inflated uncinal plates. Notopodia of segment B1 foliaceous, trilobed, medial lobes resulting from a subdivision of inner lobe; outer lobe cirriform (Fig. 1E, J). Notopodia of B2 bilobed, with single, entire inner lobes (Fig. 1E, K); those of segments B3 and following entire (Fig. 1L, M). Neuropodia of segment B1 entire, with only lower lobe developed (Fig. 1F); other neuropodia bilobed, with rounded upper lobes and elongate lower lobes (Fig. 1G, H). On neuropodia of B3, teeth on uncinal plate directed backward on anterior smaller dorsal lobe; that on larger ventral lobe directed forward.

Uncini bluntly triangular, with single row of 35 to 40 minute teeth ($n = 6$, average 38.2 ± 1.94) (Fig. 2I). Segment B4 of paratype with more than 40 uncini on outer lobe and more than 15 on inner one. Outer serrated edge of uncinal plate smoothly curved.

Posterior body region (region C) lacking in types.

Both examined specimens are mature, with segments of region B distended; the notopodia appear as distended, inflated transverse bags.

Tube is fragile, slender, straight, smooth, and not annulated. Collar folds occur at subequal intervals along tube length. Tube wall is thin, consisting of several layers of secretion, and regularly undulated externally (Fig. 2J).

Etymology.—The species epithet is derived from the type locality, Sagami Bay.

Remarks.—Among the 11 described species in *Spiochaetopterus,* 5 species lack eyespots: *S. sagamiensis, S. typicus* Sars, *S. bergensis* Gitay, *S. okudai* Gitay and *S. monroi* Gitay. These five species may be distinguished mainly on the shape of the ventral edge of the oblique section of A4 setae: straight without protuberances in *S. sagamiensis,* circular in *S. typicus,* with three protuberances in *S. bergensis* (Bhaud, 1998). In these three cases the ventral edge is horizontal, perfectly perpendicular to the shaft *Spiochaetopterus okudai* and *S. monroi* were reexamined. The ventral edge of A4 chaetae is oblique relative to the longitudinal axis of the shaft in both species. *S. okudai* lacks the sinus and *S. monroi* has a marked sinus. Secondarily, *Spiochaetopterus okudai* and *S. monroi* have bilobed notopodia in region B (Gitay 1969); however, most notopodia are entire in *S. sagamiensis.* From observations by the third author of Atlantic-Mediterranean and Pacific species, smoothly curved serrated edges of uncinal plates of *S. sagamiensis* may be regarded as a discriminatory character.

In conclusion, four diagnostic characteristics may be retained for this new species: eyes are absent; the morphology of A4 chaetae with a triangular profile of the head, a nearly straight ventral edge of the inflated distal part, and two dorsolateral, and not ventral, grooves on the shaft; the notopodia on B3 have only one lobe; and, outer serrated edges of uncinl plates smoothly curved.

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Two new subtribes, Stokesiinae and Pacourininae, of the Vernonieae (Asteraceae)

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Abstract.—New subtribes Stokesiinae and Pacourininae are established in the Vernonieae (Asteraceae) for the Southeastern United States genus *Stokesia* and the South American genus *Pacourina*

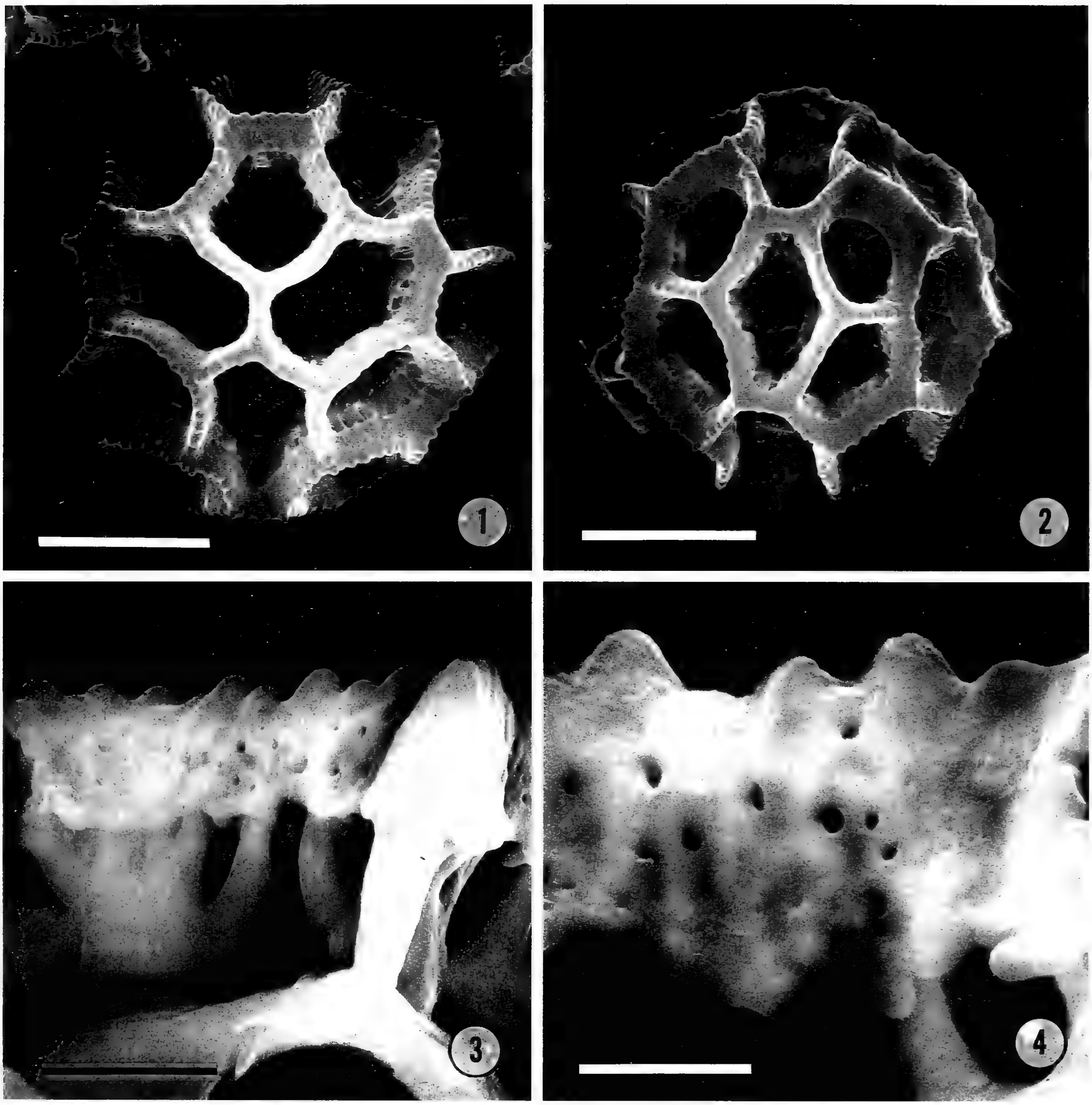
Revisions of the Vernonieae by the author have until recently involved mostly Western Hemisphere members (Robinson 1996). In the absence of studies of Old World members of the tribe, among which relatives might have been discovered, the monotypic Western Hemisphere genera *Stokesia* L'Hér. and *Pacourina* Aubl. were left unplaced as to subtribe. More recent studies of Old World Vernonieae by the author have made it clear that *Stokesia* and *Pacourina* are most closely related to other Western Hemisphere genera, but that they are deserving of separate subtribal status. The new subtribes are described below.

The genus *Stokesia* has long been noted for its mostly liguliform corollas, resembling those of the tribe Lactuceae, *Fitchia* Hook.f. of the Heliantheae, and some Mutisieae such as *Hyaloseris* Griseb. (Espinar 1973). The tribal position has sometimes been questioned, but placement has usually been in its correct position in the tribe Vernonieae (Bentham & Hooker 1873, Hoffmann 1890–1894). The genus contains a single species, and has been promoted as a possible crop plant useful as a source for epoxy resins (Gunn & White 1974). The plant is also widely cultivated as an ornamental. A drawing has been provided by Gunn and White (1974), and a color photograph can be seen in Rickett (1967). The pollen of the genus has a rather weak perforated tectum and a unique lophate pattern with trisected colpi meeting at the poles (Figs. 1–4). The genus has a chromosome number that differs from most other Vernonieae, especially other genera from the Western Hemisphere. A first count of n = 9 (Jones, 1968) has been corrected by a series of six subsequent counts of n = 7 (Jones 1974). Almost all other New World Vernonieae have n = 16 or 17. Most Old World Vernonieae have n = 9 or 10.

Stokesiinae H.Rob., subtribus nov.

Type: *Stokesia* L'Hér., Sertum Angl. 27. 1789.

Plantae herbaceae perennes ad 0.5 m altae, sparce pilosae, pilis longis simplicibus non septatis. Folia plerumque rosulata alterna base anguste petioliformia in nodis vaginata. Inflorescentiae pauce capitatae laxe cymosae. Capitula pedunculata; bracteae involucri 40–50 in seriebus 3–4, bracteae exteriores in appendicibus longe foliiformes margine spinosae, bracteae interiores angustiores in apicibus setiferae. Flores 60–70 homogami; corollae azurae vel albae plerumque late liguliformes in limbis 5-lobatae, corollae centrales ca. 3 actinomorphae; thecae antherarum base rotundatae, cellulis endothecialibus distincte lineatis, lineis in partibus longitudinalibus ceterum variabiliter arcuatis; appendices apicales antherarum breves glabrae in parietibus cellularum tenues; basi stylorum non noduliferi; rami stylorum glandulopunctati, papillis aciculiformibus argutis.

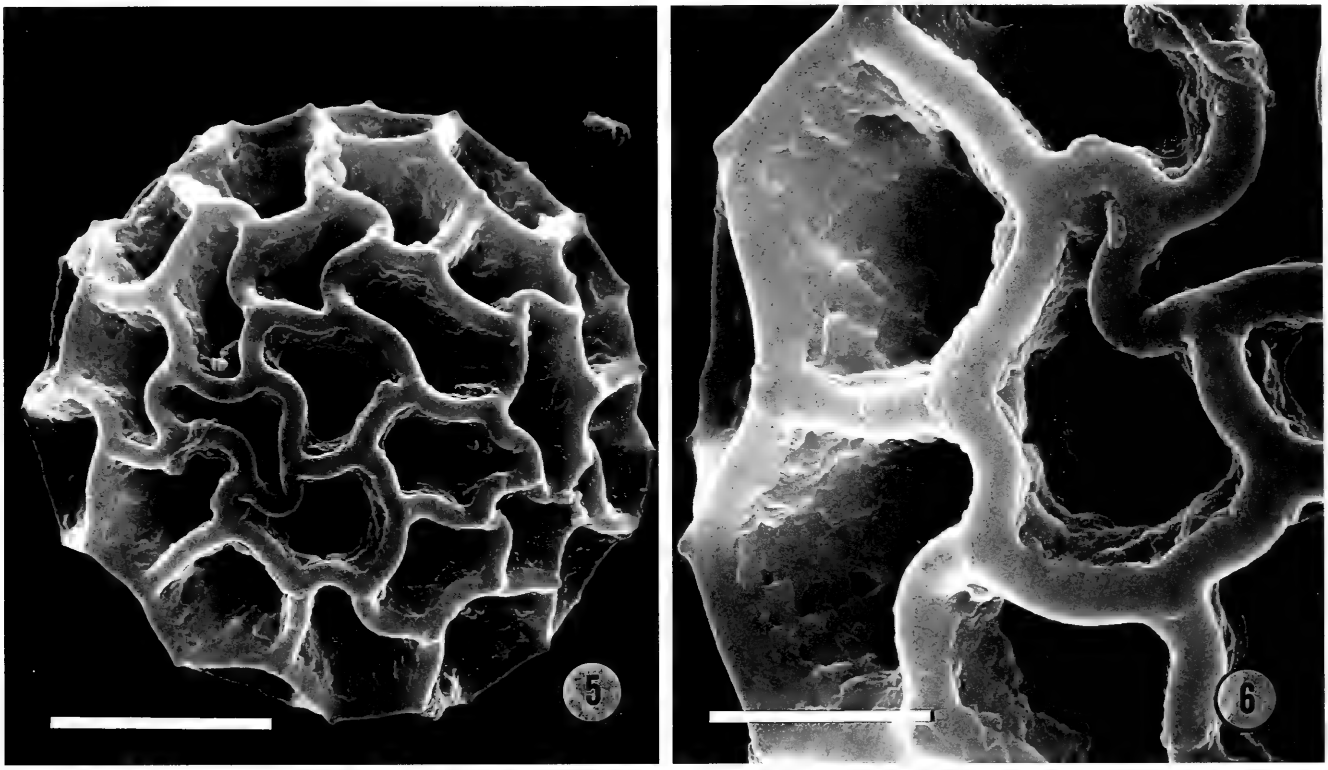


Figs. 1–4. *Stokesia laevis* (Hill) Greene, Knobloch 1426 (US), Mississippi. 1. Polar view, line = 20 µm. 2. Colpar view, line = 20 µm. 3, 4. Detailed views of muri with baculae and perforated tectum. 3. line = 3.8 µm. 4. line = 1.76 µm.

Achenia 3-4-angulata plerumque prope basem glandulo-punctata, cellulis subsuperficialibus porosis fibriformibus, raphidis subnullis minutis breviter oblongis; squamae pappi 4 aut 5 subulatae perfacile deciduae 8–9 mm longae. Grana pollinis triporata, lacunis colpi rhomboideis, muris minute crenulatis (Figs. 1–4). Numerus chromosomatum $n = 7$.

The single species in the subtribe is *Stokesia laevis* (Hill) Greene, which is native to the Southeastern United States in southern South Carolina, Georgia, Alabama and Mississippi, western Florida and eastern Louisiana.

Pacourina is a singularly distinctive emergent aquatic plant of tropical America. The inflorescence, with heads sessile in a series of leaf axils, is reminiscent of the *Lepidaploa* Group in the subtribe Vernoninae. The sclerified apical anther appendage, however, is totally foreign to that group and



Figs. 5, 6. *Pacourina edulis* Aubl., Killip and Smith 14576 (US), Colombia. 5. Whole grain, line = 15 μm. 2. Closer view showing lacuna with pore and lack of micropunctations on muri, line = 6.7 μm.

is extreme for even the Piptocarphinae and Lychnophorinae. Triporate, psilolophate pollen is known otherwise in the tribe Vernonieae only in the Paleotropical subtribe Erlangeinae, but the pollen of *Pacourina* is larger than pollen in any members of that group, and the inflorescence and anther appendages are totally different. Thus, the combination of characteristics precludes placement in any presently existing subtribe of the Vernonieae. Closest relationships of the new subtribe are not known, but they are presumed to be Neotropical. The distinctive nature of the plant may derive to considerable extent from is aquatic specialization.

Pacourininae H.Rob., subtribus nov.

Type: *Pacourina* Aubl., Hist. Pl. Guiane 2:800. 1775.

Plantae carnosae aquaticae, folia simplicia alterna valde dentata. Inflorescentiae seriate cymosae, bracteis foliiformibus; capitula sessilia axillaria solitaria late campanulata homogama; bracteae involucri ca. 50 latae virides et margine albae; receptacula epaleacea; flores ca. 50 in capitulo; corollae purpureae, lobis distaliter valde scleroideis; thecae antherharum base dentate appendiculatae; appendices apicales antherarum glabrae valde scleroideae; basi stylorum leniter latiores, pilis stylorum acicularibus. Achenia 10-costata suberose corticata in sulcis idioblastifera; setae pappi breves multiseriatae deciduae, squamellis persistentibus. Grana pollinis triporata psilolophata emicropunctata (Figs. 5, 6).

The single species in the subtribe in *Pacourina edulis* Aubl. of Central America and tropical South America. The species is well illustrated in Nash and Williams (1976, fig. 7, p. 461).

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Revisions in paleotropical Vernonieae (Asteraceae)

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Abstract.—The paleotropical subtribes Erlangeinae, Centrapalinae and Gymnantheminae are described as new. Fourteen paleotropical genera are described, raised from lower rank, resurrected, enlarged or reduced with 110 new combinations. *Cabobanthus* (2 spp.), *Hilliardiella* (8 spp.), *Orbivestus* (4 spp.), *Vernoniastrum* (8 spp.), *Koyamasia* (1 sp.), *Brenandendron* (3 spp.), *Myanmaria* (1 sp.) and *Manyonia* (1 sp.) are described as new. *Oocephala* (S. B. Jones) H. Rob. (2 spp.) and *Lampropappus* (O. Hoffm.) H. Rob. (3 spp.) are elevated to generic rank. Four genera are resurrected, the Asian *Acilepis* D. Don with 9 of 10 species newly combined, the African *Bechium* DC. (2 spp.), *Centrapalus* Cass. (9 spp.), *Linzia* Sch. Bip. ex Walp. with 5 of 7 species newly transferred, and *Polydora* Fenzl (8 spp.). One species is transferred to make a total of 27 in *Distephanus,* 4 species are transferred to total 7 in *Cyanthillium,* and 39 species are transferred to total 43 in *Gymnanthemum. Lamprachaenium* Benth. is synonymized with *Phyllocephalum* Blume with 1 species transferred.

The present paper provides a limited reorganization of the Eastern Hemisphere Vernonieae for purposes of a projected generic review of the tribe. The need to summarize the whole tribe presents a special problem. The half of the tribe in the Western Hemisphere has been rather well delimited into workable and phyletically acceptable genera (Robinson 1996). This includes an accurate delimitation of the type genus *Vernonia* Schreb. that is primarily found in eastern North America. The Eastern Hemisphere members of the tribe have thus been left in a particularly untenable position, with an excessively paraphyletic core genus and mostly paraphyletic or polyphyletic segregates, none of which are congeneric *Vernonia.* In fact, none of the existing subtribal names in the Vernonieae are applicable to the large elements that are endemic to the Eastern Hemisphere.

At the time of the summary of the New World Vernonieae (Robinson 1966), only a few Eastern Hemisphere elements have been revised by the author. The name *Baccharoides* was resurrected for the members of the *Stengelia* Group as early as Robinson et al. (1980), and transfers were made into *Baccharoides* and *Cyanthillium* (Robinson, 1990) mostly to accomodate species adventive in the Western Hemisphere. *Distephanus* was resurrected and partially revised as a last step in the removal of some of its species from the tribe Senecioneae (Robinson & Kahn 1986). In the latter study the opportunity was taken to provide the proper combination for the type species of *Gymnanthemum* Cass. that had originally been named as a *Eupatorium.* Nevertheless, no further work was planned in the Eastern Hemisphere members of the Vernonieae as recently as the time of the publication of the preliminary Western Hemisphere revision in the Kew International Compositae Conference volume (Robinson 1996).

The present study has built upon the reference works of many other authors. Humbert (1960), Wild (1977, 1978), Wild & Pope (1978a, 1978b), Jeffrey (1988), which cover all the genera of the tribe in various parts of Africa, have proven most useful in the present study. The study of Jones (1981), restricted to *Vernonia* sensu lato, and Lisowski (1992) that excludes *Vernonia,* have been less useful. The works of Kirkman (1981), Pope (1983), Koyama (1984), Isawumi (1993, 1995), and Isawumi et al. (1996) have added important information. The present study has used the summary of secondary metabolite chemistry of the Vernonieae by Bohlmann and Jakupovic (1990) and the various reports of chromosome numbers by Jones (1974, 1979, 1982). DNA studies are as yet limited to those mentioned by Keeley (1994, 1995) and Kim et al. (1996). The final conclusions of the present study are, nevertheless, ultimately based on examination of specimens in the United States National Herbarium (US) and on some specimens kindly sent on loan by Kew (K), British Museum (BM), Bruxelles (BR) and Paris (P).

Jones (1977, 1981) noted basic differences between the Vernonieae in the Eastern and Western Hemispheres, and this has been generally accepted by others such as Jeffrey (1988). These differences have been reviewed to some extent by Isawumi (1995). The Hemispheric trends noticed by Jones (1977) are in the chromosome numbers and chemistry. The Western Hemisphere species usually have a chromosome number of N = 17, and the Eastern Hemisphere species have mostly N = 9 or 10. The chemicals cited were terpenoids and flavonoids. Jones (1981) also stated that triporate pollen grains were known only from the Eastern Hemisphere. Since that time, some examples of triporate grains have been found in Latin America, *Acilepidopsis* (Robinson 1989), *Mesanthophora* (Robinson 1992a), *Pacourina* (Robinson 1992b), but at least the first two of these are considered to be related to Eastern Hemisphere members of the tribe. Robinson and Kahn (1986) and Isawumi et al. (1996) briefly noted the apparent restriction of glandular dots on the anthers and their appendages to New World members of the Vernonieae. In the present study, the raphids of the achene wall in the Eastern Hemisphere species have proven to be predominently elongate, with only a few entities such as *Gutenbergia* having characteristically subquadrate or short raphids. Most groups of Western Hemisphere Vernonieae have characteristically subquadrate raphids. In their chemical survey, Bohlmann and Jakupovic (1990) found the distinctive 5-alkyl coumarins only in Eastern Hemisphere genera and species, groups that are all placed in this study in the new subtribe Erlangeinae.

Inflorescences with scorpioid or well developed seriate cymes in the Vernonieae seem almost entirely restricted to the New World and New World genera like *Struchium* that have become Pantropical. A notable exception, *Manyonia,* described below as a new genus from East Africa, is considered to be a relative of New World genera, and it is described in the subtribe Vernoniinae.

Some doubts about the hemispheric differences were expressed by Keeley and Turner (1990). They mention some cases of Western Hemisphere "*Vernonia*" with chromosome numbers of N = 10 or 12, and they call attention to similarities between the groups referred to by the present author as Piptocarphinae in the Americas and the Gymnantheminae in the Eastern Hemisphere. The latter groups both tend to be woody, often have deciduous inner involucral bracts and usually have blunt-tipped sweeping hairs on their styles. Nevertheless, the possible relationship is considered here to be above the generic and subtribal levels. The doubts of Keeley & Turner (1990) are justified to the extent that *Vernonia* cannot be simply divided into two genera, one for each Hemisphere. Many segregates are needed for each hemisphere.

There is an important limitation to the use of pollen structure as a phyletic characteristic in the Vernonieae, a limitation already seen in both Western and Eastern Hemisphere members of the tribe (Robinson 1996). First, the simple non-lophate or sublophate pollen, Type A, often considered primitive in the tribe, was not considered primitive by the present author (Robinson 1996). Second, some pollen variations are of more importance than others. Differences between various lophate patterns seem to correlate well with other characters, but all groups seem able to revert erratically to non-lophate or sublophate forms, the Type A of Jones (1981). The truly triporate forms, with irregularly organized polar lacunae, are evidently not closely related to other lophate types with distinct colpi. However, they may be very closely related to colporate forms that are non-lophate. This does not mean that the difference between triporate and non-lophate tricolporate cannot be used as a key character when the character happens to correlate with other features, as in *Cyanthillium.*

The present study has been restricted by available time and specimens. The new subtribes are kept to a minimum, although that minimum seems to fit the Paleotropical material rather well. The new genera and taxa elevated to generic rank are those that seem inescapable, and no attempt is made here to dispose of some additional distinctive elements in the Eastern Hemisphere that do not fit in the genera presently recognized. Possibly, some smaller distinctive elements have been completely missed in the present survey. The number of species transferred into the various segregate genera is necessarily incomplete, but proper names are now available for many species that should not be retained in *Vernonia.* It is hoped that other authors will continue the process of making transfers. An attempt has been made to avoid overly broadening the concepts of the segregate genera. Even so, *Gymnanthemum* has been interpreted to include many elements that differ from the type by corolla lobe, style and achene characters. This has been done with the conviction that the broader concept of that genus will prevail.

The synonymy given for most of the African species follows Jeffrey (1988).

New Subtribes of the Eastern Hemisphere Vernonieae

All presently named subtribes of the Vernonieae are based on primarily Western Hemisphere groups. None of these subtribal names apply to the primarily Eastern Hemisphere groups. To rectify this situation, the following three new subtribes are named.

Erlangeinae H. Rob., subtribus nov. Type: *Erlangea* Sch. Bip., Flora 36:34. 1853. Type: *E. plumosa* Sch. Bip.

Vernonia sect. *Tephrodes* DC. Prodr. 5: 24. 1836. Type: *Conyza cinerea* L.
Bechium DC., 5:70. 1836. Type: *B. scapiforme* DC.
Vernonia sect. *Lepidella* Oliver & Hiern, Fl. Trop. Afr. 3:267. 1877. Type: *Vernonia petersii* Oliver & Hiern.
Vernonia subg. *Orbisvestus* S. B. Jones, Rhodora 83:60. 1981. Type: *Vernonia karaguensis* Oliver & Hiern.
Vernonia sect. *Orbisvestus* S. B. Jones, Rhodora 83:61. 1981. Type: as above.
Vernonia subsect. *Orbisvestus* S. B. Jones, Rhodora 83:61. 1981. Type: as above.
Vernonia subsect. *Hilliardianae* S. B. Jones, Rhodora 83:66. 1981. Type: *Webbia oligocephala* DC.
Vernonia subsect. *Tephrodes* (DC.) S. B. Jones, Rhodora 83:70. 1981.
Vernonia subsect. *Lepidella* (Oliver & Hiern) S. B. Jones, Rhodora 83:72. 1981.
Vernonia subsect. *Oocephalae* S. B. Jones, Rhodora 83:72. 1981. Type: *Vernonia oocephala* Baker
Vernonia subsect. *Bechium* (DC.) S. B. Jones, Rhodora 83:73. 1981.

Plantae herbaceae annuae aut perennes vel frutescentes, pilis saepe symmetriciter T-formibus. Folia alterna vel opposita vel ternata pinnatinervata. Receptaculum epaleaceum vel raro paleaceum. Flores 3 vel ca. 100 in capitulo; corollae lavandulae vel purpureae; thecae antherarum base non vel tenuiter caudatae; appendices apicales glabrae in parietibus cellularum tenues raro tenuiter ornatae; base stylorum noduliferi; rami stylorum aciculiformiter papillosi. Achenis 4–6 vel 8–10 costata; raphidis plerumque elongatis raro subquadratis; carpopodia anguste cylindrica; pappus longe setiformis vel abbreviatus vel coroniformis saepe facile deciduus. Grana pollinis non lophata et tricolporata vel lophata et triporata in formibus lophatis lacunis polaribus irregularibter dispositis, tectis micropunctatis vel emicropunctatis. Numerus chromosomatum N = 9, 10, 20.

The name is chosen to conform with the already established term "Erlangeoid" (Pope 1983). The subtribe is circumscribed to include all the Vernonieae presently known with triporate pollen (excluding *Pacourina* Aubl., Robinson 1992b) or 5-alkyl coumarins (Bohlmann & Jakupovic 1990). The unquestioned core of the subtribe includes genera with only 4–5 angled achenes and herbaceous habits, but, at present, additional forms with 10-ribbed achenes and woody habits are also included. All the included genera have acicular sweeping hairs of the style. The genera included are the New World *Acilepidopsis* H. Rob. (1989) and *Mesanthophora* H. Rob. (1992a), and Old World *Acilepis* D. Don, *Ageratinastrum* Mattf., *Ambassa* Steetz, *Bechium* DC., *Bothriocline* Oliv. ex Benth., *Brachythrix* Wild & G. V. Pope, *Cyanthillium* Blume, *Decastylocarpus* Humbert, *Dewildemania* O. Hoffm., *Diaphractanthus* Humbert, *Erlangea* Sch. Bip., *Ethulia* L. f., *Gossweilera* S. Moore, *Gutenbergia* Sch. Bip. ex Walp., *Hystrichophora* Mattf., *Iodocephalus* Thorel ex Gagnep., *Kinghamia* C. Jeffrey, *Lamprachaenium* Benth., *Msuata* O. Hoffm., *Phyllocephalum* Blume, *Omphalopappus* O. Hoffm., *Rastrophyllum* Wild & G. V. Pope, and six genera newly named or elevated below.

Centrapalinae H. Rob., subtribus nov. Type: *Centrapalus* Cass., Dict. Sci. Nat. ed. 2, 7:382. 1817. Type: *Centrapalus galamensis* Cass.

Vernonia subsect. *Stengelia* Sch. Bip. ex Walp., Repert. Bot. Syst. 2 [Suppl. 1]: 946. 1843. Type: *Vernonia adoensis* Sch. Bip. ex Walp.

Vernonia sect. *Stengelia* (Sch. Bip. ex Walp.) Benth. & Hook. f., Gen. Pl. 2: 227. 1873.

Vernonia subsect. *Centrapalus* (Cass.) S. B. Jones, Rhodora 83:69. 1981.

Vernonia sect. *Azureae* S. B. Jones, Rhodora 83:74. 1981. Type: *Vernonia glabra* Vatke.

Plantae herbaceae perennes vel raro annuae, pilis simplicibus multiseptatis vel asymmetriciter T-formibus vel nullis. Folia alterna pinnatinervata vel longitudinaliter nervata. Bracteae involucri apice saepe appendiculatae vel plerumque herbaceae. Flores numerosi in capitulo; corolla purpurea vel azurea; thecae antherarum base rotundatae; appendices apicales glabrae vel raro papilliferae in parietibus cellularum leniter incrassatae; base stylorum noduliferi vel non noduliferi; rami stylorum acute papilliferi. Achenis 10-costata, raphidis elongatis vel interdum subquadratis; pappus plerumque setiformis. Grana pollinis tricolporata lophata vel non lophata micropunctata vel non micropunctata in formibus lophatis lacunis polaribus solitariis interdum praesentibus. Numerus chromosomatum N = 9, 10.

The subtribe is typified by *Centrapalus* Cass., and includes *Adenoon* Dalz., *Aedesia* O. Hoffm, *Baccharoides* Moench, *Camchaya* Gagnep., *Lachnorhiza* A. Rich., *Linzia* Sch. Bip. ex Walp., *Muschleria* S. Moore, *Neurolakis* Mattf. and *Pleurocarpaea* Benth. The sesquiterpene constituents include elemanolides (Bohlmann & Jakupovic 1990).

The genera of the subtribe are herbaceous or weakly shrubby, and the sweeping hairs of the styles are acicular. The subtribe includes elements with the distinctive *Linzia*-type pollen cited by Jeffrey (1988) such as *Linzia* and *Aedesia* and one with polar lacunae on its pollen grains and a lack of basal stylar nodes like *Baccharoides* (Isawumi 1993; Isawumi et al. 1996).

Gymnantheminae H. Rob., subtribus nov. Type: *Gymnanthemum* Cass., Bull. Soc. Philom. Paris 1817:10. 1817. Type: *Gymnanthemum cupulare* Cass. [= *G. coloratum* (Willd.) H. Rob. & B. Kahn].

Distephanus Cass., Bull. Soc. Philom. Paris 1817:151. 1817. Type: *Distephanus populifolius* (Lam.) Cass.

Vernonia sect. *Strobocalyx* Blume ex DC., Prodr. 5:21. 1836. Type: *Vernonia arborea* Buch.-Ham.

Gongrothamnus Steetz *in* Peters., Reise Mossamb. Bot. 336. 1864. Type: *G. divaricatus* Steetz *in* Peters

Vernonia sect. *Distephanus* (Cass.) Benth. & Hook. f., Gen. pl. 2:228. 1873.

Vernonia sect. *Lampropappus* O. Hoffm., Bol. Soc. Broter. 13:14. 1896. Type: *Vernonia lampropappa* O. Hoffm.

Vernonia subsect. *Strobocalyx* (Bl. ex DC.) S. B. Jones, Rhodora 83:64. 1981.

Vernonia subsect. *Gongrothamnus* (Steetz) S. B. Jones, Rhodora 83:65. 1981.

Vernonia subsect. *Pawekianae* S. B. Jones, Rhodora 83:66. 1981. Type: *Vernonia angulifolia* DC.

Vernonia subsect. *Urceolatae* S. B. Jones, Rhodora 83:67. 1981. Type: *Vernonia sphaerocalyx* O. Hoffm.

Vernonia subsect. *Turbinella* S. B. Jones, Rhodora 83:67. 1981. Type: *Vernonia lampropappa* O. Hoffm.

Vernonia subsect. *Distephanus* (Cass.) S. B. Jones, Rhodora 83:68. 1981.

Vernonia subsect. *Glutinosae* S. B. Jones, Rhodora 83:73. 1981. Type: *Vernonia glutinosa* DC.

Plantae fruticosae vel arborescentes vel scandentes, pilus simplicibus et arachnoideis vel L-formibus vel T-formibus. Folia alterna pinnatinervata vel trinervata. Bracteae involucri 20–70 in seriebus 2–7 plerumque gradatae interiores interdum deciduae; receptacula epaleacea vel paleacea. Flores 1–40 (–75) in capitulo; corollae lavandulae vel roseae vel flavae, lobis plerumque erectis et longe triangularibus rariter elongatis et arcte revolutis; thecae antherarum base plerumque valde caudatae; appendices apicales induratae et glabrae in parietibus cellularum aliquantum ornate incrassatae; basi stylorum non noduliferi vel noduliferi interdum abrupte noduliferi; rami stylorum plerumque obtuse papilliferi. Achenia 5 aut 10-12-costata, raphidis plerumque elongatis interdum subquadratis vel nullis, carpopodia lata; pappus plerumque setiformis, Grana pollinis tricolporata non lophata vel sublophata vel raro lophata in formibus lophatis lacunis polaribus solitariis nullis; tectis micropunctatis. Numerus chromosomatum N = 10, 2N = 30.

The subtribe is typified by the genus *Gymnanthemum* Cass., but it also includes *Distephanus* Cass., *Centauropsis* Boj. *in* DC., *Oliganthes* Cass., and three genera named or elevated below. The sesquiterpene lactone constituents include elemanolides (Bohlmann & Jakupovic 1990).

The subtribe includes all of the true large shrub and tree Vernonieae in the Eastern Hemisphere. The sweeping hairs of the styles often have rather blunt tips. Inner involucral bracts are persistent or deciduous, and a few species of *Gymnanthemum* and *Brenandendron* have long coiled corolla lobes. These characteristics are generally shared by the Gymnantheminae and the American Piptocarphinae, but deciduous bracts and reflexed corolla lobes are much more consistently present and blunt sweeping hair much less consistently present, in the Piptocarphinae. The Gymnantheminae lack stellate hairs like those common in the Piptocarphinae.

New Genera and New Combinations of Eastern Hemisphere Vernonieae
Subtribe Vernoniinae

Manyonia H. Rob., gen. nov. (Vernoniinae).

Type: *Vernonia peculiaris* Verdc.

Plantae herbaceae perennes ad 1 m altae; caules brunnescentes striati sparce hispiduli, pilis simplicibus multiseptatis uniseriatis, internodis 4–6 cm longis. Folia alterna, petiolis 8–10 mm longis; laminae membranaceae ovatae 8–11 cm longae 3.2–5.0 cm latae base anguste cuneatae margine biserratae apice plusminusve acuminatae supra sparce pilosae subtus dense glandulo-punctatae, nervis secundariis utrinque 5 vel 6 supra et subtus puberulis. Inflorescentiae seriate cymosae, ramis ad 14 cm longis, pedunculis plerumque brevibus 2–3 (–15) mm longis dense puberulis. Capitula campanulata 6 mm alta et lata; bracteae involucri ca. 100; seriebus exterioribus 3–4 patentes longe subulatae 2.5 mm longae base dilatatae 0.1–0.2 mm latae inferne margine puberulae; bracteae intermediae oblongae 4 mm longae apice longe aristatae; bracteae interiores anguste oblongae 5 mm longae et 2 mm latae apice acuminatae; receptaculum glabrum in diametro ca. 1.8 mm. Flores ca. 35 in capitulo; corollae lilacinae ca. 5.5 mm longae, tubis angustis ca. 2.5 mm longis superne infundibularibus, faucibus ampliatis ca. 1 mm longis, lobis oblongis ca. 1.5 mm longis et 0.3 mm latis extus glanduliferis; thecae antherarum ca. 2 mm longae base non caudatae; appendices apicales ca. 0.4 mm longae in parietibus cellularum tenues glabrae; basi stylorum disciformiter nodati; rami stylorum in papillis aciculiformibus obsiti. Achenia oblonga 1.5 mm longa 5-costata inter costam breviter setulifera et longitudinaliter multiseriate idioblastifera, costis glabris prominentibus et induratis, raphidis perdense dispositis subquadratis vel polygonatis; setae pappi ca. 20 barbellatae ca. 4 mm longae; squamulae exteriores ca. 25 minute ciliatae. Grana pollinis in diametro ca. 35 μ sublophata tricolporata.

The genus *Manyonia* has been considered by the author as a relative of New World Vernonieae since he first saw the illustration of the seriate cymes accompanying the original description (Verdcourt 1956). This structure, otherwise lacking in native Old World Vernonieae, is confirmed in material borrowed from The Royal Botanic Gardens, Kew. This relationship seems confirmed by a poorly researched characteristic, the type of ornamentation of the endothecial cells of the anther. The cells in *Manyonia* have rather strong thickenings, longitudinal in some cell rows, and in other rows, arching across the lower end. This is a pattern seen in many Western Hemisphere Vernonieae. Eastern Hemisphere Vernonieae have weaker ornate thickenings if any. Further examination of specimens of *Manyonia* shows a strong resemblance to New World genera such as *Heterocypsela* H. Rob. and *Dipterocypsela* S. F. Blake, especially in the wall of the achene with extremely crowded subquadrate or polygonal raphids. The new genus differs from *Heterocypsela* and *Dipterocypsela* in lacking the heteromorphic achenes and the glanduliferous anther appendages of its American relatives. The pollen of *Manyonia* is sublophate, more like *Dipterocypsela* and unlike the lophate form in *Heterocypsela.*

The generic name is derived from the vernacular name Manyoni cited on Burtt 5119 (K). The needed combination is as follows:

Manyonia peculiaris (Verdc.) H. Rob., comb. nov. basionym: *Vernonia peculiaris* Verdc., Kew Bull. 1956:447. 1956. Tanzania.

New Genera and New Combinations of Eastern Hemisphere Vernonieae Subtribe Erlangeinae H. Rob.

Acilepis D. Don, Prodr. Fl. Nepal. 169. 1825. Type: *Acilepis squarrosa* D. Don.

Lysistemma Steetz *in* Peters, Reise Mossamb. Bot. 340. 1864. Type: *Lysistemma dendigulense* (DC.) Steetz.

Xipholepis Steetz *in* Peters, Reise Mossamb. Bot. 344. 1864. Type: *Xipholepis silhetensis* Steetz.

Vernonia sect. *Xipholepis* (Steetz) Benth. & Hook.f., Gen. pl. 2:229. 1873.

Erect perennial herbs; stems pentangular, with hairs multiseptate at base and often with long subfusiform apical cell. Leaves alternate, obovate to oblong-ovate. Inflorescences of single heads, spiciform cymes, or corymbose cymes with few to many heads. Involucres funnelform to campanulate; bracts 50–200 in 6–12 series, persistent, apiculate to subacute; receptacle epaleaceous. Heads with 25–80 florets; corollas lavender, tubes slender below, funnelform above into throat, throat half or less as long as anther thecae, lobes long and narrow, with glandular dots; anther bases blunt, not tailed; apical anther appendages glabrous, with thin-walled cells; style base with node, style branches with acicular sweeping hairs. Achenes 8–10 ribbed, setulae with one cell long, other cell short, raphids oblong with rhomboid tips; pappus whitish, both series rather easily deciduous, with many barbellate inner setae, outer setae shorter, scarcely broader. Pollen triporate, lophate, nearly psilate, emicropunctate, with ca. 20 lacunae.

The Asiatic *Acilepis* is distinct in the rather simple stem hairs, the pedunculate or separated heads, the triporate pollen and in such details as the often totally deciduous pappus and the highly unequal cells of the setulae of the achene. Jeffrey (1988) recognized the group for an African species, *Vernonia polysphaera,* treated below as the new genus *Cabobanthus.* The latter has basal tubers, sessile clustered heads, a more persistent pappus and the cells of the setulae of equal length.

The following ten species are recognized in the genus:

Acilepis aspera (Buch.-Ham.) H.Rob., comb. nov. basionym: *Vernonia aspera* Buch.-Ham., Trans. Linn. Soc. London 14:219. 1824.

Eupatorium pyramidale D. Don, Prodr. Fl. Nepal. 170. 1825.
Vernonia roxburgii Less., Linnaea 6:674. 1831.
Xipholepis aspera (Buch.-Ham.) Steetz *in* Peters, Reise Mossamb. Bot. 345. 1864.
Vernonia pyramidalis (D. Don) Mitra, Ind. For. 99:100. 1973. China, India, Myanmar, Nepal, Thailand.

Acilepis clivorum (Hance) H. Rob., comb. nov. basionym: *Vernonia clivorum* Hance, J. Bot. 7:164. 1869.

Aster coriaceiformis H. Lév. & Vaniot, Repert. Spec. Nov. Regni Veg. 8:358. 1910. China.

Acilepis dalzelliana (J. R. Drumm. & Hutch.) H. Rob., comb. nov. basionym: *Vernonia dalzelliana* J. R. Drumm. & Hutch., Kew Bull. 1909:261. 1909.
India.

Acilepis dendigulensis (DC.) H. Rob., comb. nov. basionym: *Decaneurum dendigulense* DC. *in* Wight, Contr. Bot. Ind. 7. 1834, not *Vernonia dendigulensis* DC.

Lysistemma dendigulense (DC.) Steetz *in* Peters, Reise Mossamb. Bot. 341. 1864.
Vernonia indica C. B. Clarke, Comp. Ind. 16. 1876. Western peninsular India.

Acilepis nantcianensis (Pamp.) H. Rob., comb. nov. basionym: *Vernonia bracteata* var. *nantcianensis* Pamp., Nouv. Giorn. Bot. Ital., n.s. 18:98. 1911.

Vernonia silhetensis var. *nantcianensis* (Pamp.) Hand.-Mazz., Symb. Sin. 7: 1084. 1936.
Vernonia nantcianensis (Pamp.) Hand.-Mazz., Noitsibl. Bot. Gart. Mus. Berl.-Dahl. 13:608. 1937.
China.

Acilepis saligna (DC.) H. Rob., comb. nov. basionym: *Vernonia saligna* DC., Prodr. 5:33. 1836.

Vernonia longicaulis DC., Prodr. 5:33. 1836.
Vernonia martinii Vaniot, Bull. Acad. Intern. Geogr. Bot. 12:124. 1903.
Vernonia sequinii Vaniot, Bull. Acad. Intern. Geogr. Bot. 12:241. 1903.
China, India, Myanmar.

Acilepis scariosa (DC.) H. Rob., comb. nov. basionym: *Decaneurum scariosum* DC., Prodr. 7:264. 1838.

Vernonia scariosa Arn., Nova Acta Phys. Med. Acad. Caes. Leop. Carol. Nat. Cur. 18:346. 1836, hom. illeg., not *V. scariosa* Poir., 1808.
Gymnanthemum scariosum (DC.) Sch. Bip. ex Walp., Rep. 2:949. 1843.
Centratherum scariosum C. B. Clarke, Comp. Ind. 4. 1876.
Vernonia lankana Grierson, Ceylon J. Sci., Biol. Sci. 10:43. 1972.
Sri Lanka.

Acilepis silhetensis (DC.) H. Rob., comb. nov. basionym: *Decaneurum silhetense* DC., Prodr. 5:67. 1836.

Eupatorium glabrum Heyne ex Wallich, Num. List. Dr. pl. 3283. 1831, nom. nud.
Decaneurum glabrum DC., Prodr. 5:67. 1836.
Gymnanthemum glabrum (DC.) Sch. Bip. ex Walp., Rep. 2:948. 1843.
Gymnanthemum silhetense (DC.) Sch. Bip. ex Walp., Rep. 2:948. 1843.
Xipholepis silhetensis (DC.) Steetz *in* Peters, Reise Mossamb. Bot. 344. 1864.
Vernonia bracteata Wall. ex C. B. Clarke, Comp. Ind. 17. 1876.
Vernonia silhetensis (DC.) Hand.-Mazz., Symb. Sin. 7:1084. 1936.
China, India, Thailand.

Acilepis spirei (Gandog.) H. Rob., comb. nov. basionym: *Vernonia spirei* Gandog., Bull. Soc. Bot. France 54:194. 1907.
China, Laos, Vietnam.

Acilepis squarrosa D. Don, Prodr. Fl. Nepal 169. 1825.

Vernonia squarrosa (D. Don) Less., Linnaea 6:627. 1831.
Vernonia rigiophylla DC., Prodr. 5:15. 1836.
Vernonia teres Wall. ex DC., Prodr. 5:15. 1836.
China, India, Nepal, Sikkim, Thailand, Vietnam.

Bechium DC., Prodr. 5:70. 1836. Type: *Bechium scapiforme* DC.

Erect or subhorizontally proliferating annual or biennial herbs, 1–4 dm high; hairs mostly of one long cell, appearing sericeous, red stipitate glands with multicellular tips on stems and bracts. Leaves alternate, rosulate or subrosulate, subsessile, blades oblong. Inflorescences scapiform with 1 to many corymbosely disposed heads. Heads shortly to longly pedunculate; involucral bracts ca. 30 in ca. 3 series, with red stipitate glandular hairs; receptacle epaleaceous. Florets 25–50; corollas reddish-violet, slender tubes funnelform above, throat very short, lobes with sparse biseriate nonglandular hairs, rarely with stipitate reddish gland at tip; anther bases rounded, without tails; apical appendage glabrous, with thin cell walls; style base with distinct wide node; style with sweeping hairs fat, pointed, few to many septate. Achenes 10-costate, with many unevenly pointed setulae, many idioblasts, raphids elongate with rhomboid tips; pappus with single series of easily deciduous to subpersistent bristles and short outer squamae, bristles narrowed below, some wider distally. Pollen tricolporate, non-lophate, echinate.

The genus is recognized primarily on the basis of the herbaceous annual or biennial habit, elongate raphids of the achene wall, slender white pappus bristles, type A pollen, and the rather broad, pointed sweeping hairs with few to many septations. The species placed in the genus here are two of the members of the Vernonieae in Madagascar that have reddish glands with multicellular caps on their peduncles and involucral bracts. Both species need new combinations since the oldest name for the type species has never been transferred to the genus.

Bechium nudicaule (Less.) H. Rob., comb. nov. basionym: *Vernonia nudicaulis* Less., Linnaea 6:637. 1831.

Bechium scapiforme DC., Prodr. 5:71. 1836.
Vernonia scapiformis (DC.) Drake, Bull.

Soc. Bot. France 46:244. 1889.
Madagascar.

Bechium rhodolepis (Baker) H. Rob., comb. nov. basionym: *Vernonia rhodolepis* Baker, J. Bot. 20:139. 1882.

Vernonia purpureo-glandulosa Klatt, Bot. Jahrb. Syst. 12 (Beibl. 27):21. 1890.
Madagascar.

Cabobanthus H. Rob., gen. nov. (Erlangeinae).
Type: *Vernonia polysphaera* Baker.

Plantae herbaceae perennes base tuberosae. Caules subglabri aut tomentosi, pilis simplicibus uniseriatis multiseptatis. Folia alterna sessilia vel subsessilia. Capitula in axillares superiores ad 5 aggregata; involucra infundibularia, bracteis ca. 35 in seriebus ca. 5 ovatis vel oblongis apiculatis; receptacula epaleacea. Flores ca. 10 in capitulo; corollae purpureae, tubis cylindricibus superne infundibularibus; faucibus quam theceis dimidiis brevioribus; thecae base breviter caudatae; appendices antherarum apicales in parietibus cellularibus tenues non glanduliferae; basi stylorum noduliferi; rami stylorum aciculiformiter papillosi. Achenia 8–10-costatae, setulis in cellulis aequales, raphidis minutis anguste oblongis; setae pappi arcte barbellatae. Grana pollinis triporata ca. 35 μm lacunosa emicropunctata.

The genus is notable for the erect stems bearing axillary clusters of heads and the triporate, emicropunctate pollen grains. The following two species are recognized:

Cabobanthus bullulatus (S. Moore) H. Rob., comb. nov., basionym: *Vernonia bullulata* S. Moore, J. Bot. 65, suppl. 2: 44. 1927.
Zambia.

Cabobanthus polysphaerus (Baker) H. Rob., comb. nov., basionym: *Vernonia polysphaera* Baker, Kew Bull. 1898:148. 1898.

Vernonia humblei De Wild., Repert. Spec. Nov. Regni Veg. 13:207. 1914.
Congo, Tanzania, Zambia.

Cyanthillium Blume, Bidjr. 889. 1826.
Type: *Cyanthillium villosum* Blume.

Isonema Cass., Bull. Soc. Philom. Paris 1817:152. 1817, hom. illeg., not *Isonema* R. Br., 1810. Type: *Isonema ovata* Cass.

Vernonia sect. *Tephrodes* DC., Prodr. 5: 24. 1836. Lectotype: *Conyza cinerea* Blume (Jones 1981).

Cyanopsis Blume ex DC., Prodr. 5:69. 1836, nom. illeg. et superfl., not Cass., 1817.

Claotrachelus Zoll. & Moritz ex Zoll., Natuur-Genrrsk. Arch. Ned. Indië 2: 263, 565. 1845. Type: *Claotrachelus rupestris* Zoll. & Moritz ex Zoll.

Seneciodes L. ex Post & O. Kuntze, Lex. Gen. Phan. 2:515. 1903. Type: *Conyza cinerea* L.

Triplotaxis Hutch., Bull. Misc. Inform. 1914:355. 1914. Lectotype: *Herderia stellulifera* Benth. in Hook.f. (Robinson 1990).

Vernonia subsect. *Tephrodes* (DC.) S. B. Jones, Rhodora 83:70. (1981).

Annual or short-lived perennial herbs ca. 1 m tall; stem hairs asymmetrically and symmetrically T-shaped. Leaves alternate, narrowly petiolate, blades thinly papery. Inflorescences terminal, corymbose to pyramidal cymes. Heads pedunculate; involucral bracts papery, green with pale or purplish margins, ca. 30 in 3(–5) gradate series, persistent; receptacle epaleaceous. Florets 15–94; corollas bluish to lavender, funnelform with slender lower tubes, throat a third as long to nearly as long as lobes, lobes with simple hairs especially near tips; anthers without tails; apical appendages glabrous, with thin cell walls; style base with broad node; sweeping hairs acicular. Achenes 5-angled or ribbed, or terete, with idioblasts, sometimes with glands, raphids elongate; pappus with many long, fragile, slender-tipped bristles or squamellae, persistent, with callose ring in one species. Pollen triporate, echinolophate. N = 9, 11, 18 (Jones 1979, 1982).

The synonymy follows that in Robinson

(1990a) with the removal of *Vernonia* subsections *Orbisvestus* and *Hilliardianae.* Attempts to interpret the genus more broadly to include *Gutenbergia* Sch.Bip. ex Walp. (Robinson, 1990b), are rejected here. At this time, other more closely related species, with shrubbier habits, non-lophate pollen, tailed anthers and T-shaped hairs or no hairs on the corolla lobes, are placed in separate genera (see *Hilliardiella* and *Orbivestus* below). The species of *Cyanthillium* are all annuals or weak perennial subshrubs with triporate lophate pollen, The following seven species are presently placed in the genus.

Cyanthillium albicans (DC. *in* Wight) H. Rob., comb. nov. basionym: *Vernonia albicans* DC. *in* Wight, Contrib. Bot. Ind. 6. 1834.
Western peninsular India.

Cyanthillium cinereum (L.) H. Rob., Proc. Biol. Soc. Wash. 103:252. 1990.

Conyza cinerea L., Sp. Pl. 862. 1753.
Vernonia cinerea (L.) Less., Linnaea 4: 291. 1829.
Seneciodes cinerea (L.) Post & O. Kuntze, Lex. Gen. Phan. 2:515. 1903.
Throughout paleotropical region, widely adventive in Neotropics.

Cyanthillium conyzoides (DC. *in* Wight) H. Rob., comb. nov. basionym: *Vernonia conyzoides* DC. *in* Wight, Contr. Bot. Ind. 6. 1834.
Western peninsular India.

Cyanthillium hookerianum (Arn.) H. Rob., comb. nov. basionym: *Vernonia hookeriana* Arn., Nov. Act. Nat. Cur. 18:346. 1836.
Sri Lanka.

Cyanthillium patulum (Ait.) H. Rob., Proc. Biol. Soc. Wash. 103:252. 1990.

The synonymy is as in Robinson (1990a) with the exclusion of *Conyza chinensis* Lam. and its combinations.
Tropical Asia, Indonesia, Madagascar, adventive in West Indies.

Cyanthillium stelluliferum (Benth.) H. Rob., Proc. Biol. Soc. Wash. 103:252. 1990.

Herderia stellulifera Benth. *in* Hook. f. & Benth., Niger Fl., 425. 1849.
Triplotaxis stellulifera (Benth.) Hutch., Bull. Misc. Inf. Kew 1914:356. 1914.
West and central tropical Africa, Uganda to Angola.

Cyanthillium vernonioides (Muschl.) H. Rob., comb. nov. basionym: *Erlangea vernonioides* Muschl., Bot. Jahrb. Syst. 46:62. 1911, not *Vernonia vernonioides* (A. Gray) Bacigalupo, 1931.
Vernonia meiostephana C. Jeffrey, Kew Bull. 43:225. 1988.

Hilliardiella H. Rob. gen. nov. (Erlangeinae). Type: *Vernonia pinifolia* Less.

Webbia DC., Prodr. 5:72. Oct. 1836, lectotype *Vernonia pinifolia* Less., hom. illeg., not *Webbia* Spach, Jun 1836.
Vernonia subsect. *Hilliardianae* S. B. Jones, Rhodora 83:66. 1981. Type: *Vernonia oligocephala* (DC.) Sch. Bip.

Plantae herbaceae perennes ad 1 m altae; caules pilosi, pilis aequaliter T-formibus. Folia alterna; laminae subtus saepe dense canescentiter pilosae. Inflorescentiae laxe vel subdense corymbose cymosae; capitula pedunculata; involucra campanulata; bracteae 25–40 ca. 3–4-seriatae persistentes; receptacula epaleacea. Flores 12–20 in capitulo; corollae purpureae extus pauce vel dense pilosae, pilis T-formibus leniter contortis; tubis superne infundibularibus, faucibus brevibus, lobis linearibus; thecae base non vel breviter appendiculatae; appendices apicales antherarum glabrae in parietibus cellularum tenuis; basi stylorum noduliferi, papillae ramorum aciculiformes. Achenia 4–5-costata dense setulifera et idioblastifera, raphidis elongatis; carpopodia anguste cylindrica; setae pappi albae barbatae tenues subpersistentes, seriebus exteriores breviter lanceolatis. Grana pollinis non lophata tricolporata echinata. Numerus chromosomatum N = 9, 10 (Jones 1942).

Chemistry reported for the genus includes germacranolides, hirsutanolides, quaianolides and bisabolene derivatives (Bohlmann & Jakupovic 1990). Most chromosome counts have reported N = 10.

Hilliardiella is closely related to *Cyanthillium,* but it seems consistently different by the more perennial habit, the non-lophate pollen, and especially the T-shaped hairs of the corolla. The group has been rather well defined at various levels by Candolle (1836) and Jones (1981).

The name is derived from the subsectional name of Jones (1981), but the genus is described as new to avoid any complications from spelling. The name, as indicated by Jones (1981), honors Dr. Olive M. Hilliard, student of the Asteraceae of Natal. The following eight species are credited to the genus.

Hilliardiella aristata (DC.) H. Rob., comb. nov. basionym: *Webbia aristata* DC., Prodr. 5:73. 1836, not *Vernonia aristata* Less., 1829.

Vernonia natalensis Sch. Bip. ex Walp., Rep. 2:947. 1843.
South Africa.

Hilliardiella calyculata (S. Moore) H. Rob., comb. nov. basionym: *Vernonia calyculata* S. Moore, J. Linn. Soc. Bot. 35:316. 1902.
Congo, Tanzania, Malawi, Mozambique, Zambia.

Hilliardiella hirsuta (Sch. Bip. ex Walp.) H. Rob., comb. nov. basionym: *Vernonia hirsuta* Sch. Bip. ex Walp., Rep. 2:947. 1843.
South Africa.

Hilliardiella leopoldii (Vatke) H. Rob., comb. nov. basionym: *Vernonia leopoldii* Vatke, Linnaea 39:478. 1878.
Ethiopia.

Hilliardiella nudicaulis (DC.) H. Rob., comb. nov. basionym: *Webbia nudicaulis* DC., Prodr. 5:73. 1836.

Vernonia dregeana Sch. Bip. ex Walp., Rep. 2:947. 1843.
South Africa.

Hilliardiella oligocephala (DC.) H. Rob., comb. nov. basionym: *Webbia oligocephala* DC., Prodr. 5:73. 1836.

Webbia elaegnoides DC., Prodr. 5:73. 1836, not *Vernonia elaegnoides* H.B.K., 1818.
Vernonia oligocephala (DC.) Sch. Bip. ex Walp., Rep. 2:947. 1843.
Vernonia krausii Sch. Bip. ex Walp., Rep. 2:947. 1843.
Tanzania south to the Cape Province.

Hilliardiella pinifolia (Less.) H. Rob., comb. nov. basionym: *Vernonia pinifolia* Less., Linnaea 4:257. 1829.

Webbia pinifolia (Less.) DC., Prodr. 5:72. 1836.
South Africa.

Hilliardiella smithiana (Less.) H. Rob., comb. nov. basionym: *Vernonia smithiana* Less., Linnaea 6:638. 1831.
West and Central Tropical Africa.

Orbivestus H. Rob., gen. nov. (Erlangeinae). Type: *Vernonia karaguensis* Oliv. & Hiern.

Vernonia subg. *Orbisvestus* S. B. Jones, Rhodora 83:60. 1981. Type: *Vernonia karaguensis* Oliv. & Hiern.

Plantae suffrutescentes vel frutescentes; caules pilosi, pilis T-formibus. Folia alterna breviter petiolata; laminae sparse pilosae. Inflorescentiae laxe corymbose cymosae. Capitula pedunculata; involucra campanulata; bracteae 25–30 ca. 4-seriatae persistentes; receptacula epaleacea. Flores 8–16 in capitulo; corollae purpureae extus non vel perpauce pilosae, pilis raris sub-T-formibus, tubis superne leniter infundibularibus, faucibus et lobis subaequilongis, lobis longe triangularibus; thecae antherarum base breviter vel longe caudatae; appendices antherarum apicales glabrae in parietibus cellularum tenues; basi stylorum breviter et distincte noduliferi; papillae ramorum aciculiformes. Achenia 4–5-costata setulifera multo idioblastifera, raphidis elongatis; carpopodia anguste cylindrica; setae pappi barbellatae facile deciduae, squamis exterioribus brevis persistentibus. Grana pollinis non lophata tricolporata echinata. Numerus chromosomatum N = 9, 20 (Mangenot & Mangenot 1962, Mehra et al. 1965, Jones 1982).

The genus *Orbivestus* is distinct from the related *Cyanthillium* by the more shrubby habit, the lack of simple hairs on the corolla lobes, and the non-lophate pollen. It is distinct from *Hilliardiella* by the longer corolla throats and more triangular lobes that bear few or no hairs. The few hairs seen on the corolla lobes in the type species are asymmetrically T-shaped, quite different from those in *Hilliardiella.* The genus has more prominent tails on the anthers than in either of the related genera. Chemical constituents include 5-alkyl coumarins, bisabolene derivatives and glaucolides (Bohlmann & Jakupovic 1990).

Although the subgeneric name by Jones (1981) is the inspiration for the generic name, the genus has been described as new to avoid the consistent extra "s" in the Jones spelling. Jones did not explain his spelling, and the reason for his choice is unknown. The spelling used here is that found in Jeffrey (1988) and Bohlmann & Jakupovic (1990). Still, it seems unnecessary to completely abandon the name coined by Jones.

The following four species are placed in the genus.

Orbivestus cinerascens (Sch. Bip. *in* Schweinf.) H. Rob., comb. nov. basio– nym: *Vernonia cinerascens* Sch. Bip. *in* Schweinf., Beitr. Fl. Aeth. 162. 1897.

Vernonia tephrodioides Chiov., Fl. Somal. 2:255. 1932.
Senegal east to western India, south to Angola and Botswana.

Orbivestus homilanthus (S. Moore). H. Rob., comb. nov. basionym: *Vernonia homilantha* S. Moore, J. Bot. 41:138. 1903.

Vernonia sennii Chiov., Fl. Somal. 2:256. 1932.
Kenya, Somalia.

Orbivestus karaguensis (Oliv. & Hiern) H. Rob., comb. nov. basionym: *Vernonia karaguensis* Oliv. & Hiern, Trans. Linn. Soc. London 29:91. 1873.

Vernonia cistifolia O. Hoffm., Engl. Pflanzenw. Ost-Afr. C 404. 1895.
Vernonia elliotii S. Moore, J. Linn. Soc. Bot. 35:315. 1902.
Vernonia bothrioclinoides C. H. Wright, Bull. Misc. Inf. 1906:108. 1906.
Vernonia porphyrolepis S. Moore, J. Bot. 46:39. 1908.
Vernonia campanea S. Moore, J. Bot. 54: 251. 1916.
Vernonia melanacrophylla Cufod., Nouv. Giorn. Bot. Ital., n.s. 50:102. 1943.
Sudan south to Mozambique and Zimbabwe, west to Nigeria.

Orbivestus undulatus (Oliv. & Hiern) H. Rob., comb. nov. basionym: *Vernonia undulata* Oliv. & Hiern, Fl. Trop. Afr. 3: 276. 1877.

West and central tropical Africa, north to Sudan, south to Angola.

Oocephala (S. B. Jones) H. Rob., stat. nov. (Erlangeinae).

Vernonia subsect. *Oocephalae* S. B. Jones, Rhodora 83:72. 1981.

Type species: *Vernonia oocephala* Baker.

Low much-branched shrubs to 1 m high, stems with weakly L-shaped simple hairs and with multiseptate simple hairs. Leaves alternate, subsessile, linear to elliptical, sometimes serrate. Inflorescences corymbose cymes with usually shortly pedunculate heads or with heads sessile in apical clusters of leaves. Involucre ovoid or cylindrical; bracts 20–40 in 4–7 gradate series, ovate to oblong, appressed; receptacle without pales. Florets ca. 15 in a head; corollas white or lavender, tubular to narrowly funnelform, throat as long as lobes, tips without hairs or with few short biseriate hairs; anther bases rounded, apical appendages glabrous, with thin-walled cells; style base with indistinct ring; style branches with acicular sweeping hairs. Achenes weakly 8-ribbed, sericeous with many setulae, idioblasts numerous, raphids narrowly elongate; pappus biseriate, outer shorter and broader, inner setiform, subplumose, glabrous near base. Pollen triporate, lophate, minutely papillate on murae, emicropunctate or weakly micropunctate.

The genus is distinquished by subplumose inner pappus, triporate pollen and stems with weakly L-shaped hairs. *Vernonia* sect. *Oocephala* is based on a single species with pedunculate ovoid heads containing few tubular florets. The additional species here referred to *Oocephala* was described by Jeffrey (1988) in his Group 3 subgroup A with *Centrapalus,* but the achene is most like *Oocephala* and *Vernoniastrum,* and a small corolla remnant shows triporate pollen. The species is not related to the *Centraplinae,* and is placed here on the basis of its subplumose pappus, in spite of considerable difference in general appearance.

The genus contains the following two species.

Oocephala agrianthoides (C. Jeffrey) H. Rob., comb. nov. basionym: *Vernonia agrianthoides* C. Jeffrey, Kew Bull. 43: 227. 1988.
Burundi, Congo, Tanzania.

Oocephala stenocephala (Oliv.) H. Rob., comb. nov. basionym: *Vernonia stenocephala* Oliv. *in* Hook., Ic. Pl. 14:35, t. 1349A. 1881.

Vernonia oocephala Baker, Bull. Misc. Inf. 1895:68. 1895.
Vernonia luteoalbida De Wild., Repert. Spec. Nov. Regni Veg. 13:207. 1913.
Nigeria east to Tanzania and south to Mozambique.

Polydora Fenzl, Flora 27:312. 1844. Type species: *Polydora stoechadifolia* Fenzl = *Webbia serratuloides* DC.

Crystallopollen Steetz *in* Peters, Reise Mossamb. Bot. 363. 1864. Type species: *Crystallopollen angustifolium* Steetz.

Mostly annuals; stems with one-armed T-shaped hairs. Leaves alternate. Inflorescence a lax thyrsoid panicle with corymbosely cymose branches with pedunculate heads or with single terminal head. Involucral bracts ca. 80 in ca. 7 series, often with widely scarious margins and awned often black tips, receptacles epaleaceous. Florets ca. 30 in a head; corollas whitish to purplish, tube longly funnelform, throat as long as the narrow glabrous lobes; anther bases plain, not tailed; apical appendage glabrous, with cell walls thin, sometimes weakly ornate; style base with distinct annular node; branches with acicular sweeping hairs. Achenes 5 or 8–10 ribbed, setuliferous, raphids narrowly elongate; pappus with copious barbellate setae, greenish, yellowish or tawny, rarely white; outer pappus short, squamiform. Pollen triporate, scarcely echinolophate to psilolophate, with or without micropunctations. Chromosome number N = 9 (Jones 1979, 1982). Reported sesquiterpene lactones are germacranolides, hirsutanolides and furanheliangolides (Bohlmann & Jakupovic 1990).

The genus is distinct in the annual habit, chromosome number of N = 9, the one-armed T-shaped hairs, untailed anthers and triporate pollen.

Some of the species of the *Vernonia chloropappa* group are keyed by Pope (1986).

The genus is here credited with the following eight species.

Polydora angustifolia (Steetz *in* Peters) H. Rob., comb. nov. basionym: *Crystallopollen angustifolium* Steetz *in* Peters, Reise Mossamb. Bot. 366. 1864, not *Vernonia angustifolia* Michx., 1803 or *V. angustifolia* D. Don ex Hook. & Arn., 1835.

Vernonia erinacea H. Wild, Kirkia 11:2. 1978.
Tanzania and Mozambique, east to Zambia and Zimbabwe.

Polydora bainesii (Oliv. & Hiern) H. Rob., comb. nov. basionym: *Vernonia bainesii* Oliv. & Hiern *in* Oliv., Fl. Trop. Afr. 3: 272. 1877.
Tanzania and Mozambique, east to Zambia and Zimbabwe.

Polydora chloropappa (Baker) H. Rob., comb. nov. basionym: *Vernonia chloropappa* Baker, Bull. Misc. Inf. 1898:146. 1898.

Vernonia kassneri De Wild. & Muschl., Bull. Soc. Bot. Belg. 49:242. 1912.

Vernonia smaragdopappa S. Moore, J. Linn. Soc. Bot. 47:284. 1925.
Congo, Malawi, Tanzania, Zambia.

Polydora jelfiae (S. Moore) H. Rob., comb. nov. basionym: *Vernonia jelfiae* S. Moore, J. Linn. Soc. Bot. 47:262. 1925.
Angola, Burundi, Congo, Malawi, Tanzania, Zambia, Zimbabwe.

Polydora poskeana (Vatke & Hildebr.) H. Rob., comb. nov. basionym: *Vernonia poskeana* Vatke & Hildebr., Oesterr. Bot. Zeitschr. 25:324. 1875.
Angola, Botswana, Nambia, Transvaal, Zimbabwe.

Polydora serratuloides (DC.) H. Rob., comb. nov. basionym: *Webbia serratuloides* DC., Prodr. 5:72. 1836, not *Vernonia serratuloides* H. B. K., 1818.

Vernonia perrottetii Sch. Bip. ex Walp., Rep. 2:947. 1843.

Polydora stoechadifolia Fenzl, Flora 27: 312. 1844.
West and central tropical Africa from Sudan and Ethiopia south to Angola and Zambia.

Polydora steetziana (Oliv. & Hiern) H. Rob., comb. nov. basionym: *Vernonia steetziana* Oliv. & Hiern *in* Oliv., Fl. Trop Afr. 3:278. 1877.
South Africa.

Polydora sylvicola (G. V. Pope) H. Rob., comb. nov. basionym: *Vernonia sylvicola* G. V. Pope., Kew Bull. 41:395. 1986.
Angola, Congo, Malawi, Mozambique, Tanzania, Zambia, Zimbabwe.

Vernoniastrum H. Rob., gen. nov. (Erlangeinae) Type: *Crystallopollen latifolium* Steetz *in* Peters

Vernonia sect. *Lepidella* Oliv. & Hiern, Fl. Trop. Afr. 3:267. 1877. Type: *Vernonia petersii* Oliv. & Hiern, not *Lepidella* Tiegh., 1912 or *Lepidella* E. J. Gilbert, 1925.

Vernonia subsect. *Lepidella* (Oliv. & Hiern) S. B. Jones, Rhodora 83:72. 1981.

Plantae herbaceae perennes 0.3–1.0 m altae; caules pilosi, pilis simplices in cellulis apicalibus elongatis base leniter inaequalibus. Folia alterna. Inflorescentiae uni- vel multo capitatae. Involucra campanulata; bracteae ca. 50 in ca. 3 series gradatae persistentes; receptacula epaleacea. Flores ca. 50 in capitulo; corollae rubro-purpurascentes, tubis anguste infundibularibus, faucibus quoad lobis et thecis brevioribus, lobis distaliter pilosis; thecae antherarum base acuminate vel acute caudatae; appendices antherarum apicales glabrae in parietibus cellarum tenues; base stylorum noduliferi; rami stylorum aciculariter piliferi. Achenia 4–5-angulata, idioblastis saepe in seriebus transversalibus aggregatis, raphidis elongatis; setae pappi interiores margine dense barbellatae subpersistentes, squamae exteriores lateriores persistentes. Grana pollinis triporata lophata micropunctata vel emicropunctata. Numerus chromosomatum N = 10 (Jones 1979, 1982).

Vernoniastrum seems closely related to the foregoing *Polydora* Fenzl, but differs by the perennial habit, the non-T-shaped hairs, the tailed anther bases and the chromosome number of N = 10. The core element of the genus also has the idioblasts of the achene in distinct transverse bands, a feature not seen outside of the genus *Vernoniastrum.*

The genus is credited here with the following eight species:

Vernoniastrum aemulans (Vatke) H. Rob., comb. nov. basionym: *Vernonia aemulans* Vatke, Oesterr. Bot. Zeitschr. 27:195. 1877.
Kenya, Tanzania.

Vernoniastrum ambiguum (Kotschy & Peyr.) H. Rob., comb. nov. basionym: *Vernonia ambigua* Kotschy & Peyr., Pl. Tinn., 35, t. 17B. 1867.
West tropical Africa to Sudan and Tanzania and south to Angola.

Vernoniastrum latifolium (Steetz *in* Peters) H. Rob., comb. nov. basionym: *Crystallopollen latifolium* Steetz *in* Peters, Reise Mossamb. Bot. 364, t. 48a. 1864, not *V. latifolia* Lem., 1855.

Vernonia petersii Oliv. & Hiern, Trans. Linn. Soc. London 29:90. 1873.
Vernonia eriocephala Klatt, Bull. Herb. Boiss. 4:826. 1896.
Angola and Congo east to Mozambique and Tanzania.

Vernoniastrum musofense (S. Moore) H. Rob., comb. nov. basionym: *Vernonia musofensis* S. Moore, J. Bot. 56:206. 1918.

Vernonia lappoides O. Hoffm., Bol. Soc. Brot. 13:19. 1896, hom. illeg., not Baker, 1873.
Vernonia miamensis S. Moore, J. Bot. 64:304. 1926.
Vernonia hoffmanniana Hutsch. & Dalz., Fl. W. Trop. Afr. 2:167. 1931, nom. nov. for *V. lappoides* O. Hoffm.
Vernonia philipsoniana Lawalree, Expl. Hydrobiol. Lac. Tanganyika (1946–47) Rés. Sc. 4, 2:59. 1955; nom. nov. superfl. for *V. lappoides* O. Hoffm.
Tropical Africa from Nigeria to Tanzania, south to Angola and Zimbabwe.

Vernoniastrum nestor (S. Moore) H. Rob., comb. nov. basionym: *Vernonia nestor* S. Moore, J. Linn. Soc. Bot. 35:317. 1902.

Vernonia chariensis O. Hoffm., Bull. Soc. Bot. France 55, mém. 8:40. 1908.
Vernonia cannabina Muschl., Bot. Jahrb. Syst. 46:94. 1911.
West Africa east to Tanzania south to Natal.

Vernoniastrum ugandense (S. Moore) H. Rob., comb. nov. basionym: *Vernonia ugandensis* S. Moore, J. Linn. Soc. Bot. 35:314. 1902.

Vernonia caput-medusae S. Moore, J. Linn. Soc. Bot. 37:166. 1905.
Vernonia fontinalis S. Moore, J. Bot. 52: 90. 1914.
Vernonia punctulata S. Moore, J. Linn. Soc. Bot. 47:262. 1925.
Vernonia proclivicola S. Moore, J. Linn. Soc. Bot. 47:262. 1925.
Vernonia mgetae Gilli, Ann. Naturhist. Mus. Wien 78:164. 1974.
Congo, Burundi and Tanzania south to Angola, Zambia and Mozambique.

Vernoniastrum uncinatum (Oliv. & Hiern ex Oliv.) H. Rob., comb. nov. basionym: *Vernonia uncinata* Oliv. & Hiern ex Oliv., Fl. Trop Afr. 3:277. 1877.

Vernonia amplexicaulis Baker, Kew Bull. 1895:216. 1895.
Ethiopia, Kenya, Somalia.

Vernoniastrum viatorum (S. Moore) H. Rob., comb. nov. basionym: *Vernonia viatorum* S. Moore, J. Linn. Soc. Bot. 35: 315. 1912.
Malawi.

Koyamasia H. Rob., gen. nov. (Erlangeinae). Type: *Camchaya calcarea* Kitam.

Plantae herbaceae perennes ad 0.5 m altae pauce ramosae; caules pilis simplicibus multiseptatis obsiti. Folia alterna anguste petiolata. Inflorescentiae terminales et axillares. Capitula longe pedunculata late campanulata; bracteae involucri ca. 90 ca. 4–5-seriatae persistentes in partibus majoribus herbaceae et reflexae; receptaculm glabrum. Flores ca. 90 in capitulo; corollae tenuiter carnosae, tubis angustis, faucibus abrupte campanulatis, lobis quoad faucibus leniter longioribus non reflexis extus glanduliferis; thecae antherarum valde exertae saepe nigricans base rotundatae, cellulis endothecialibus elongatis, in apicibus noduliferis; appendices apicales antherarum non longiores quam lateriores glabrae in parietibus cellularum firmis; basi stylorum non noduliferi. Achenia 10-costata glabra; raphidis minutis anguste oblongis; setae pappi paucae breves facile deciduae. Grana pollinis triporata emicropunctata. Numerus chromosomatum 2N = 54 (Koyama 1984).

The genus *Koyamasia* is established for a single Southeast Asian species occurring in limestone areas. It was originally described in *Camchaya* Gagnep., but was excluded from it by Koyama (1984). The species is similar to *Camchaya* in its geography and reduced pappus, but it differs in the triporate rather than tricolporate lophate pollen and the simple rather than T-shaped hairs. The genus may be more closely related to *Kinghamia* C. Jeffrey, which contrary to its original description, has triporate rather than tricolporate pollen, and is not closely related to *Linzia.* The West African *Kinghamia* is similar, but is a less robust plant with narrower leaf blades and much smaller heads. *Kinghamia* may represent convergent evolution in many of its similarities, but it seems to differ from *Koyamasia* by only some technical characteristics such as the reflexed mature corolla lobe tips, the presence of a basal stylar node, the pale and only partially exerted anthers, the longer anther appendages and the subquadrate endothecial cells without nodular thickenings.

The single species is as follows:

Koyamasia calcarea (Kitam.) H. Rob., comb. nov. basionym: *Camchaya calcarea* Kitam., Acta Phytotax. Geobot. 23: 71. 1968.
Thailand.

Phyllocephalum Blume, Bidjr. Fl. Ned. Ind. 888. 1826. Type: *Phyllocephalum frutescens* Blume

Decaneurum DC. ex Wight, Contr. Bot. Ind. 7–8. (1833), not *Decaneurum* DC., 1836. Type: *Decaneurum reticulatum* DC. ex Wight [= *Phyllocephalum indicum* (Less.) Kirkman]

Rolfinkia Zenker, Pl. Ind. 13. 1837. Type: *Rolfinkia centaureoides* Zenker [= *Phyllocephalum indicum* (Less.) Kirkman].

Lamprachaenium Benth, in Benth. & Hook. f., Gen. pl. 2:225. (1873). Type: *Decaneurum microcephalum* Dalzell

The herbaceous genera *Phyllocephalum* Blume of India and Indonesia, with three species (Kingham, 1981), and *Lamprachaenium* Benth. of India, with one species, have been examined and found to differ mostly by the costate achenes of the former versus the shiny dark ecostate achenes of the latter. In both genera, the achenes are oblong and glabrous, somewhat obcompressed, abruptly rounded above to the narrow attachment of the corolla, the pappus is of short highly deciduous setae and the raphids in the achene wall are subquadrate. Both genera have lophate triporate pollen with minutely spinulose margins of the muri as seen in Kirkman (1981) and Robinson & Marticorena (1986). Both have foliose lower involucral bracts or foliose tips on the bracts. The genera are here considered the same and the needed combination is as follows:

Phyllocephalum microcephalum (Dalzell) H. Rob., comb. nov. basionym: *Decaneurum microcephalum* Dalzell, Hooker's J. Bot. Kew Gard. Misc. 3:231. 1851. India.

New Genera and New Combinations of Eastern Hemisphere Vernonieae Subtribe Centrapalinae H. Rob.

Centrapalus Cass., Bull. Soc. Philom. Paris 1817:10. 1817. Type: *Centrapalus galamensis* Cass.

Vernonella Sond., Linnaea 23:62. 1850. Type: *Vernonella africana* Sond.

Annual or perennial, scapose or subscapose herbs, with or without brown woolly hair on crown of rootstock, anthesis often prior to leaf emergence; stem hairs simple, multiseptate. Leaves basal or cauline, alternate, sessile. Inflorescences terminal on stems and branches. Involucre hemispherical; bracts 125–150 in ca. 5 gradate series, linear, green, often with small teeth on distal margin; receptacle epaleaceous. Florets ca. 100 in a head; corollas light blue to bluish purple, tube funnelform above, throat nearly half as long as thecae, lobes sometimes fringed with long papillae; anther base not tailed; apical anther appendage glabrous, often colored, with slightly thickened cell walls; style base with broad node. Achenes weakly 10-costate, setuliferous, raphids narrowly oblong; pappus setae long, subpersistent, outer series setiform, short. Pollen tricolporate, echinate, lophate or non-lophate, without muri projecting into colpi, micropunctate. Chromosome number N = 9 (Jones 1974, 1979, 1982). Sesquiterpene lactones include elemanolides (Bohlmann & Jakupovic 1990).

The name *Centrapalus* has been used most recently within the broad concept of *Vernonia* for a group of coarse annual or perennial African herbs. The genus is of some potential commercial importance for the extraction of epoxy resins (Ayorinde et al., 1990). The proper combination has not previously been provided for the type species, and an additional eight species are placed in the genus here.

Centrapalus acrocephalus (Klatt) H. Rob., comb. nov. basionym: *Vernonia acrocephala* Klatt, Ann. Hofmus. Wien 7:100. 1897.
Sierra Leone, Nigeria and Congo south to Angola and Zimbabwe.

Centrapalus africanus (Sond.) H. Rob., comb. nov. basionym: *Vernonella africana* Sond., Linnaea 23:62. 1850.
South Africa.

Centrapalus chthonocephalus (O. Hoffm.) H. Rob., comb. nov. basionym: *Vernonia chthonocephala* O. Hoffm., Bol. Soc. Brot. 13:17. 1896.
Sierra Leone and Sudan south to Angola and Malawi.

Centrapalus denudatus (Hutch. & Burtt) H. Rob., comb. nov. basionym: *Vernonia denudata* Hutch. & Burtt, Rev. Zool. Bot. Afr. 23:37. 1932.
Congo, Tanzania, Zambia.

Centrapalus kirkii (Oliv. & Hiern *in* Oliv.) H. Rob., comb. nov. basionym: *Vernonia kirkii* Oliv. & Hiern *in* Oliv., Fl. Trop. Afr. 3:274. 1877.

Vernonia swynnertonii S. Moore, J. Linn. Soc. Bot. 40:107. 1911.
Vernonia zambesiaca S. Moore, J. Bot. 55:102. 1917.
Tanzania south to Zambia and Mozambique.

Centrapalus pauciflorus (Willd.) H. Rob., comb. nov. basionym: *Conyza pauciflora* Willd., Sp. Pl. 3:1927. 1803.

Centrapalus galamensis Cass., Dict. Sci. Nat., ed. 2, 7:383. 1817.
Vernonia pauciflora (Willd.) Less., Linnaea 4:292. 1829, not (Pursh.) Poir., 1817.
Vernonia afromontana R. E. Fr., Acta. Hort. Berg. 9:116. 1929.
Vernonia zernyi Gilli, Ann. Naturhist. Mus. Wein 78:165. 1974.
Vernonia petitiana A. Rich., Tent. Fl. Abyss. 1:373. 1848.
Sudan, Ethiopia, Somalia, Kenya, Uganda, Tanzania, Malawi, Zambia, Mozambique and West Africa.

Centrapalus praemorsus (Muschl.) H. Rob., comb. nov. basionym: *Vernonia praemorsa* Muschl., Bot. Jahrb. Syst. 46: 68. 1911.
Angola, Congo, Malawi, Tanzania, Zambia.

Centrapalus purpureus (Sch. Bip. ex Walp.) H. Rob., comb. nov. basionym: *Vernonia purpurea* Sch. Bip. ex Walp., Rep. 2:946. 1843.

Vernonia inulifolia Steud. ex Walp., Rep. 2:946. 1843.
Vernonia jaceoides A. Rich., Tent. Fl. Abyss. 1:376. 1848.
Vernonia rigorata S. Moore, J. Bot. 41: 155. 1903.
Vernonia scabrida C. H. Wright, Bull. Misc. Inf. Kew 1906:21. 1906.
Vernnonia duemmeri S. Moore, J. Bot. 52:91. 1914.
Vernonia pascuosa S. Moore, J. Linn. Soc. Bot. 47:163. 1925.
Vernonia keniensis R. E. Fr., Acta Hort. Berg. 9:114. 1929.
West, central and south tropical Africa north to Sudan and Ethiopia.

Centrapalus subaphyllus (Baker) H. Rob., comb. nov. basionym: *Vernonia subaphylla* Baker, Bull. Misc. Inf. Kew 1895: 290. 1895.

Nigeria, Cameroon, Congo, Tanzania, Angola, Malawi, Zambia.

Linzia Sch. Bip. ex Walp., Rep. 2:948. 1843. Type: *Linzia vernonioides* Sch. Bip. ex Walp.

Vernonia sect. *Azureae* S. B. Jones, Rhodora 83:74. 1981. Type: *Linzia glabra* Steetz *in* Peters

Perennial herbs; stems with simple multiseptate hairs. Leaves alternate, subsessile to short-petiolate. Inflorescences corymbiform cymes or single heads with short to long pecuncles. Involucre funnelform to campanulate; bracts 50–150 in 5–6 series, often pectinate-denticulate along distal margins, outer tips often elongate, green and recurved; receptacle epaleaceous. Florets ca. 20–50 in a head; corollas bluish, tube very long, funnelform near throat, throat very short, lobes apically stiffly hairy; anther base rounded; apical anther appendage glabrous, triangular, with thickened ornamentation in center; style base with small annulus. Achenes strongly 10-costate, usually with rows of idioblasts along sides of costae, setuliferous, raphids subquadrate to short-oblong; pappus of many somewhat persistent, long bristles, with short outer series. Pollen tricolporate, lophate, with muri intruding into short colpi, single polar lacunae often present, with or without micropunctations. Chromosome number N = 10 (Jones 1979, 1982). Sesquiterpene lactones include germacranolides and hirsutanolides (Bohlmann & Jalupovic 1990).

Linzia has been recognized rather accurately in recent literature because of the rather characteristic bluish flowers (Jones 1981) or distinctive pollen (Jeffrey 1988). The species are related to *Centrapalus,* but they differ by the more perennial habit, the very short throats of the corollas, the stronger ribs on the achenes, the idioblasts that are positioned along those ribs in most species and the chromosome number of N = 10.

The following seven species are credited to the genus.

Linzia gerberiformis (Oliv. & Hiern *in* Oliv.) H. Rob., comb. nov. basionym: *Vernonia gerberiformis* Oliv. & Hiern *in* Oliv., Fl. Trop. Afr. 3:285. 1877.

Vernonia macrocyanus O. Hoffm., Bol. Soc. Brot. 13:20. 1896.
Vernonia nandensis S. Moore, J. Linn. Soc. Bot. 35:323. 1902.
Vernonia towaensis De Wild., Bull. Jard. Bot. Brux. 5:96. 1915.
Angola, Burundi, Cameroon, Congo, Malawi, Nigeria, Sudan, Tanzania, Uganda, Zambia, Zimbabwe.

Linzia glabra Steetz *in* Peters, Reise Mossamb. Bot. 353. 1864.

Vernonia glabra (Steetz) Vatke, Oesterr. Bot. Zeitschr. 27:194. 1877.
Vernonia obconica Oliv. & Hiern *in* Oliv., Fl. Trop. Afr. 3:286. 1877.
Vernonia pogosperma Klatt, Ann. K.K. Naturhist. Hofmus. 7:99. 1892.
Vernonia hindei S. Moore, J. Bot. 41: 155. 1903.
Vernonia piovanii Chiov., Racc. Bot. Miss. Cons. Kenya 61. 1935.
Vernonia roseopapposa Gilli, Ann. Naturhist. Mus. Wien 78:165. 1974.
Congo, Burundi, Kenya, Tanzania, south to Angola, Namibia, Mozambique, Transvaal, Swaziland, Natal, Madagascar.

Linzia infundibulariformis (Oliv. & Hiern *in* Oliv.) H. Rob., comb. nov. basionym: *Vernonia infundibulariformis* Oliv. & Hiern *in* Oliv., Fl. Trop. Afr. 3:285. 1877.

Vernonia saussureoides Hutch., Bull. Misc. Inf. Kew 1921:378. 1921.
Burundi, Congo, Cameroon, Nigeria, Sudan, Tanzania, Uganda.

Linzia ituriensis (Muschl.) H. Rob., comb. nov. basionym: *Vernonia ituriensis* Muschl., Wiss. Ergebn. Deutsch. Zent.-Afr. Exped. 1907–8 (2):364. 1911.

Vernonia hillii Hutch. & Dalz., Fl. W. Trop. Afr. ed. 1, 2:165, 168. 1931.
Vernonia muhiensis Kalanda, Bull. Jard. Bot. Nat. Belg. 52:125. 1982.

Burundi, Cameroon, Congo, Ethiopia, Nigeria, Rwanda, Sudan, Tanzania.

Linzia melleri (Oliv. & Hiern *in* Oliv.) H. Rob., comb. nov. basionym: *Vernonia melleri* Oliv. & Hiern *in* Oliv., Fl. Trop. Afr. 3:282. 1877.

Vernonia superba O. Hoffm., Engl. Pflanzenw. Ost-Afr. C. 406. 1895.

Vernonia scabrifolia O. Hoffm., Bot. Jahrb. Syst. 30:424. 1901, nom. illeg., not Hieron., 1897.

Vernonia paludigena S. Moore, J. Bot. 52:91. 1914.

Vernonia vanmeelii Lawalrée, Expl. Hydrobiol. Lac Tanganyika. Rés. Sc. 6, 2: 59. 1955, nom. nov. for *V. scabrifolia* O. Hoffm.

Angola, Congo, Malawi, Mozambique, Rwanda, Tanzania, Zambia, Zimbabwe.

Linzia vernonioides Sch. Bip. ex Walp., Rep. 2:948. 1843.

Vernonia quartiniana A. Rich., Tent. Fl. Abyss. 1:379. 1848.

Vernonia congolensis De Wild. & Muschl., Bull. Soc. Bot. Belg. 49:237. 1912.

Vernonia vernonioides (Sch. Bip. ex Walp.) Cufod., Bull. Jard. Bot. Brux. 36, suppl.:1078. 1966, hom. illeg., not (A. Gray) Bacigal, 1931.

Burundi, Congo, Ethiopia, Tanzania.

Linzia usafuensis (O. Hoffm.) H. Rob., comb. nov. basionym: *Vernonia usafuensis* O. Hoffm., Bot. Jahrb. Syst. 30:425. 1901.

Vernonia candelabricephala Gilli, Ann. Naturhist. Mus. Wien 78:161. 1974.

Tanzania.

New Genera and New Combinations of Eastern Hemisphere Vernonieae Subtribe Gymnantheminae H. Rob.

Distephanus Cass., Bull. Soc. Philom. Paris 1817. 151. 1817. Type: *Conyza populifolia* Lam.

The genus characterization, synonymy, and many of the species are given by Robinson & Kahn (1986), who stressed the yellow flowers and trinervate leaves as important generic characteristics. The type species has been redescribed and illustrated particularly well by Hind (1996), and it is suggested in Scott (1993) and Hind (1996) that the number of species in the genus should be nearer to 40 instead of the 26 transferred by Robinson & Kahn (1986). During the present study only the following single additional species is transferred.

Distephanus henryi (Dunn.) H. Rob., comb. nov. basionym: *Vernonia henryi* Dunn., J. Linn. Soc. Bot. 35:500. 1903. China.

Gymnanthemum Cass., Bull. Soc. Philom. Paris 1817:10. 1817. Type: *G. cupulare* Cass. = *Baccharis senegalensis* = *Gymnanthemum coloratum* (Willd.) H. Rob. & BKahn

Bracheilema R. Br. ex Salt., Abyss. Append. 65. 1814, nom. nud.

Decaneurum DC., Arch. Bot. (Paris) 2: 516. 1833, nom. superfl. Type: as in *Gymnanthemum.*

Monosis DC. *in* Wight, Contrib. Bot. Ind. 5. 1834. Type: *Monosis wightiana* DC. *in* Wight [= *Vernonia arborea* Buch.-Ham.].

Vernonia sect. *Strobocalyx* Blume ex DC., Prodr. 5:21. 1836. Type: *Vernonia arborea* Buch.-Ham.

Plectreca Rafin., Fl. Tellur. 4:119. 1838 ("1836"). Type: *Staehelina corymbosa* Thunb.

Keringa Rafin., Sylva Tellur. 144. 1838. Type: *Vernonia amygdalina* Del.

Cheliusia Sch. Bip., Flora 24, 1. Intell. 26. 1841. Type: *Cheliusia abyssinica* Sch. Bip. = *Gymnanthemum amygdalinum* (Del.) Sch. Bip. ex Walp.

Strobocalyx (Bl. ex DC.) Spach, Hist. Nat. Veg. Phan. 10:39. 1841.

Punduana Steetz *in* Peters, Reise Mossamb. Bot. 345. 1864. Type: *P. volkameriifolia* (DC.) Steetz

Vernonia subsect. *Urceolata* S. B. Jones, Rhodora 83:67. 1981. Type: *Vernonia sphaerocalyx* O. Hoffm.

Shrubs or trees, moderately to densely branching; hairs often forming felt, with large often contorted cap cells basally or nearly basally attached. Leaves alternate, with short or winged petioles to rather long-petiolate. Inflorescences terminal on stems and branches, densely corymbiform. Heads with involucres campanulate to ovoid; bracts appressed, coriaceous to subcoriaceous, 25–35 in 4–5 series, inner bracts persistent or easily deciduous; receptacle epaleaceous. Florets 1–50; corollas white to violet; tube cylindrical, throat longer than thecae or very deeply cut, lobes with glands or spicules; anther base broadly tailed, often long; apical anther appendages glabrous, with rather thick-walled cells; style with or without node. Achenes 5–10-costate, with or without setulae or uniseriate hairs, raphids short to elongate or lacking; pappus of many rather persistent capillary bristles, often broad-tipped, with short outer squamellae. Pollen grains tricolporate, non-lophate or rarely lophate, echinate, micropunctate. Chromosome numbers N = 7?, 10, 20, 2N = 30 (Jones 1979, 1982). Sesquiterpene lactones include elemanolides (Bohlmann & Jakupovic 1990).

A broad interpretation of the *Gymnanthemum* is accepted here. The type species lacks a basal node on the style, but other closely related species have such nodes. The number of ribs on the achene varies from 5 to 10 within many subgroups. At least some of the species with persistent inner involucral bracts seem very closely related to species in which they are deciduous. The leaves also seem to vary in size, texture and margin. The corolla throat is usually long, but a number of species in Madagascar have sinuses cut nearly to the base of the throat. The corolla lobes usually show a characteristic long-triangular erect form, but a few species have long narrow lobes that are rolled back with age. The sweeping hairs are usually blunt, but those of *G. amygdalinum* are more pointed. The pollen is almost always non-lophate or Type A, but rarely, as in the type of *Punduana, Vernonia volkameriaefolia,* the pollen is lophate. The genus is limited within the subtribe in the present paper by only the most obvious differences in inflorescence shape, involucral bracts, leaf nervation, corolla symmetry and color, and lack of pales on the receptacle.

The genus is credited here with the following 43 species:

Gymnanthemum amygdalinum (Del.) Sch. Bip. ex Walp., Rep. 2:948. 1843.

Vernonia amygdalina Del., Cent. Pl. Afr. Voy. Méroé 41. 1826.
Gymnanthemum abyssinicum Sch. Bip. ex Walp., Rep. 2:948. 1843.
Vernonia vogeliana Benth. *in* Hook., Niger Fl. 427. 1849.
Vernonia condensata Baker., J. Bot. 8: 202. 1875.
Vernonia eritreana Klatt, Bull. Herb. Boiss. 4:826. 1896.
Vernonia randii S. Moore, J. Bot. 37:369. 1899.
Vernonia giorgii De Wild., Bull. Jard. Bot. Brux. 5:92. 1915.
Vernonia bahiensis Toledo, Arq. Bot. Estado Sao Paulo, n.s. 1:52. 1939.
Vernonanthura condensata (Baker) H. Rob., Phytologia 73:69. 1992.
Yemen and Ethiopia, South Uganda, Kenya and Tanzania, Brazil, widely cultivated.

Gymnanthemum anceps (C. B. Clarke ex Hook.f.) H. Rob., comb. nov. basionym: *Vernonia anceps* C. B. Clarke ex Hook. f., Fl. Brit. Ind. 3:233. 1881.
Sri Lanka.

Gymnanthemum andersonii (C. B. Clarke) H. Rob., comb. nov. basionym: *Vernonia andersonii* C. B. Clarke, Comp. Ind. 27. 1852.

Vernonia chevalieri Gagnap., Bull. Mus. Hist. Nat. Paris 25:488. 1919, hom. illeg., not O. Hoffm., 1908.
Assam, Myanmar, China.

Gymnanthemum andrangovalense (Humbert) H. Rob., comb. nov. basionym: *Vernonia andrangovalensis* Humbert, Notul. Syst. (Paris) 13:311. 1948.
Madagascar.

Gymnanthemum antanalus (Humbert) H. Rob., comb. nov. basionym: *Vernonia antanala* Humbert, Notul. Syst. (Paris) 13:314. 1948, in part., emend., Humbert, Not. Syst. (Paris). 15:361. 1959.
Madagascar.

Gymnanthemum appendiculatum (Less.) H. Rob., comb. nov. basionym: *Vernonia appendiculata* Less., Linnaea 6:636. 1831.
Madagascar.

Gymnanthemum arboreum (Buch.-Ham.) H. Rob., comb. nov. basionym: *Vernonia arborea* Buch.-Ham., Trans. Linn. Soc. London 14:218. 1824.

Monosis wightiana DC. *in* Wight, Contrib. Bot. Ind. 5. 1834, not *Vernonia wightiana* Arn.

Vernonia celebrica DC., Prodr. 5:21. 1836.

Vernonia javanica DC., Prodr. 5:22. 1836.

Vernonia blumeana DC., Prodr. 5:22. 1836.

Strobocalyx arborea (Buch.-Ham.) Sch. Bip., Jahres. Pollichia 18–19:171. 1861.

Vernonia monosis Benth. ex C. B. Clarke, Comp. Ind. 24. 1852, nom. nov. for *Monosis wightiana* DC. *in* Wight, 1834.

Vernonia vaniotii Lévl., Repert. Spec. Nov. Regni Veg. 12:531. 1913.
SE. Asia, Indonesia.

Gymnanthemum baronii (Baker) H. Rob., comb. nov. basionym: *Vernonia baronii* Baker, J. Linn. Soc. Bot. 20:173. 1885.

Vernonia campenoni Drake, Bull. Soc. Bot. France 46:241. 1899.
Madagascar.

Gymnanthemum bellinghamii (S. Moore) H. Rob., comb. nov. basionym: *Vernonia bellinghamii* S. Moore, J. Bot. 38:155. May 1900.

Vernonia goetzeana O. Hoffm., Bot. Jahrb. Syst. 28:503. July 1900.

Vernonia elizabethvilleana De Wild., Repert. Spec. Nov. Regni Veg. 13:20. 1941.
Congo and Tanzania south to Mozambique.

Gymnanthemum bockianum (Diels) H. Rob., comb. nov. basionym: *Vernonia bockiana* Diels, Bot. Jahrb. Syst. 29:608. 1900.

Pluchea rubicunda Schneid. *in* Sarg., pl. Wils. 3:418. 1916. China.

Gymnanthemum chapelieri (Drake) H. Rob., comb. nov. basionym: *Vernonia chapelieri* Drake, Bull. Soc. Bot. France 46:234. 1899.
Madagascar.

Gymnanthemum coloratum (Willd.) H. Rob. & B. Kahn, Proc. Biol. Soc. Wash. 99:501. 1986.

Eupatorium coloratum Willd., Sp. Pl. 3: 1768. 1803.

Baccharis senegalensis Pers., Syn. Pl. 2: 424. 1807.

Gymnanthemum cupulare Cass., Dict. Sc. Nat., ed. 2, 20: 109. 1821.

Vernonia senegalensis (Pers.) Less., Linnaea 4:265. 1829.

Decaneurum grande DC., Prodr. 5:67. 1836.

Decaneurum senegalense (Pers.) DC., Prodr. 5:68. 1836.

Gymnanthemum grande (DC.) Sch. Bip. ex Walp., Rep. 2:948. 1843.

Gymnanthemum senegalense (Pers.) Sch. Bip. ex Walp., Rep. 2:948. 1843.

Gymnanthemum quercifolium Steetz *in* Peters, Reise Mossamb. Bot. 334. 1864.

Vernonia oxyura O. Hoffm., Engl. Pflanzenw. Ost.-Afr. C. 403. 1895.

Vernonia polyura O. Hoffm., Bot. Jahrb. Syst. 30:422. 1901.

Vernonia cirrhifera S. Moore, J. Linn. Soc. Bot. 35:320. 1902.

Vernonia longipetiolata Muschl., Bot. Jahrb. Syst. 46:74. 1911.

Vernonia aldabrensis Hemsl., J. Bot. 54, suppl. 2:20. 1916.

Vernonia grandis (DC.) Humb., Fl. Madag. 189:44. 1960.

West tropical Africa east to Kenya, south to Mozambique and Madagascar.

Gymnanthemum corymbosum (Thunb.) H. Rob., comb. nov. basionym: *Staehelina corymbosa* Thunb., Prodr. pl. Cap. 2:143. 1800.

Vernonia corymbosa (Thunb.) Less., Linnaea 6:647. 1831.

Plectreca corymbosa (Thunb.) Rafin., Fl. Tellur. 4:119. 1838 ("1836").

South Africa.

Gymnanthemum coursii (Humbert) H. Rob., comb. nov. basionym: *Vernonia coursii* Humbert, Notul. Syst. (Paris) 13: 310. 1948.

Madagascar.

Gymnanthemum crataegifolium (Hutch.) H. Rob., comb. nov. basionym: *Vernonia crataegifolia* Hutch., Bull. Misc. Inf. Kew 7:330. 1912.

South Africa.

Gymnanthemum cumingianum (Benth. *in* Hook.f.) H. Rob., comb. nov. basionym: *Vernonia cumingiana* Benth., Hooker's J. Bot. Kew Gard. Misc. 4:232. 1852.

China, Philippines.

Gymnantheum cylindriceps (C. B. Clarke) H. Rob., comb. nov. basionym: *Vernonia cylindriceps* C. B. Clarke, J. Linn. Soc. Bot. 25:35. 1880.

India, Nepal.

Gymnanthemum dissolutum (Baker) H. Rob., comb. nov. basionym: *Vernonia dissoluta* Baker, J. Linn. Soc. Bot. 20: 174. 1883.

Vernonia sparsiflora Baker, J. Linn. Soc. Bot. 20:172. 1883.

Vernonia capreaefolia Baker, J. Linn. Soc. Bot. 22:487. 1887.

Madagascar.

Gymnanthemum esculentum (Hemsl. ex F. B. Forbes & Hemsl.) H. Rob., comb. nov. basionym: *Vernonia esculenta* Hemsl. ex F. B. Forbes & Hemsl., J. Linn. Soc. Bot. 23:401. 1888.

Vernonia papillosa Franch., J. Bot. 10: 368. 1896.

Vernonia arbor Lévl., Repert. Spec. Nov. Regni Veg. 11:304. 1912.

China.

Gymnanthemum exsertiflorum (Baker) H. Rob., comb. nov. basionym: *Vernonia exsertiflora* Baker, Bull. Misc. Inf. Kew 1898:147. July 1898.

Vernonia kreismannii Welw. ex Hiern, Cat. Afr. Pl. Welw. 1, 3:517. Dec 1898.

Vernonia sphaerocalyx O. Hoffm., Bot. Jahrb. Syst. 30:423. 1901.

Angola and Congo to Malawi and Tanzania.

Gymnanthemum exsertum (Baker) H. Rob., comb. nov. basionym: *Vernonia exserta* Baker, J. Linn. Soc. Bot. 22:488. 1887.

Vernonia grisea Baker, J. Linn. Soc. Bot. 22:488. 1887, hom. illeg., not Baker, 1873.

Vernonia trichodesma Baker, J. Linn. Soc. Bot. 25:325. 1890.

Vernonia lantziana Drake, Bull. Soc. Bot. France 46:235. 1899.

Madagascar.

Gymnanthemum glaberrimum (Welw. ex O. Hoffm.) H. Rob., comb. nov. basionym: *Vernonia glaberrima* Welw. ex O. Hoffm., Bol. Soc. Brot. 13:15. Sept 1896.

Vernonia hensii Klatt, Bull. Herb. Boiss. 4:828. Dec. 1896.

Vernonia mashonica N. E. Br., Bull. Misc. Inf. Kew 1906:108. 1906.

West, central and south tropical Africa north to Sudan.

Gymnanthemum hildebrandtii (Vatke) H.

Rob., comb. nov. basionym: *Vernonia hildebrandtii* Vatke, Osterr. Bot. Zeit. 25: 323. 1875.

Vernonia taylorii S. Moore, J. Bot. 38: 154. 1900.
Kenya, Somalia, Tanzania.

Gymnanthemum humblotii (Drake) H. Rob., comb. nov. basionym: *Vernonia humblotii* Drake, Bull. Soc. Bot. France 46:235. 1899.

Vernonia beforonensis Humbert, Notul. Syst. (Paris) 13:320. 1948.
Madagascar.

Gymnanthemum louvelii (Humbert) H. Rob., comb. nov. basionym: *Vernonia louvelii* Humbert, Notul. Syst. (Paris) 15: 247. 1958.
Madagascar.

Gymnanthemum mespilifolium (Less.) H. Rob., comb. nov. basionym: *Vernonia mespilifolia* Less., Linnaea 6:641. 1831.
South Africa.

Gymnanthemum myrianthum (Hook.f.) H. Rob., comb. nov. basionym: *Vernonia myriantha* Hook.f., J. Linn. Soc. Bot. 7: 198. 1864.

Vernonia podocoma Sch. Bip. ex Vatke, Linnaea 39:476. 1875.
Vernonia subuligera O. Hoffm., Engl., Pflanzenw. Ost.-Afr. C. 403. 1895.
Vernonia stipulacea Klatt, Bull. Herb. Boiss. 4:457. 1896.
Vernonia lujae De Wild., Pl. Nov. Herb. Hort. Then. 2:119, t. 96. 1900.
Vernonia ampla O. Hoffm., Bot. Jahrb. Syst. 30:423. 1901.
Vernonia myrianthoides Muschl., Bot. Jahrb. Syst. 46:84. 1911.
Vernonia uhligii Muschl., Bot. Jahrb. Syst. 46:79. 1911.
Vernonia oliveriana Pichi-Serm., Webbia 7:345. 1950, nom. illegit. superfl. for *V. podocoma* Sch. Bip. ex Vatke.
Vernonia chlarugii Pich-Serm., Miss. Stud. Lago Tana 7, Ricerche Bot. 1: 155, t. 30. 1951.
West Africa from Guinea and Sierra Leone to Cameroon, Congo, Sudan, Ethiopia, Kenya, Tanzania, Uganda to south tropical Africa.

Gymnanthemum obovatum Gaudich., Voy. Uran. Bot. 471. 1830.

Vernonia cuneata Less., Linnaea 6:644. 1831.
Vernonia vagans DC., Prodr. 5:32. 1836.
Vernonia scandens DC., Prodr. 5:32. 1836.
Decaneurum obovatum (Gaudich.) DC., Prodr. 5:67. 1836.
Gymnanthemum scandens (DC.) Steetz *in* Peters, Reise Mossamb. Bot. 338. 1864.
Gymnanthemum vagans (DC.) Steetz *in* Peters, Reise Mossamb. Bot. 338. 1864.
Gymnanthemum affine Steetz *in* Peters, Reise Mossamb. Bot. 338. 1864.
Vernonia obovata (Gaudich.) Boerl., Handl. Fl. Ned. Indié 2:1. 1891, not *Vernonia obovata* Less., 1829.
India, Myanmar, Indonesia.

Gymnanthemum pectiniforme (DC. *in* Wight) H. Rob., comb. nov. basionym: *Vernonia pectiniformis* DC. *in* Wight, Contr. Bot. Ind. 2. 1834.

Vernonia puncticulata DC., 7:264. 1838.
Lysistemma pectiniforme (DC. *in* Wight) Steetz *in* Peters, Reise Mossamb. Bot. 343. 1864.
India, Sri Lanka.

Gymnanthemum pectorale (Baker) H. Rob., comb. nov. basionym: *Vernonia pectoralis* Baker, J. Bot. 20:139. 1882.
Madagascar.

Gymnanthemum pleistanthum (Humbert) H. Rob., comb. nov. basionym: *Vernonia secundifolia* subsp. *pleistantha* Humbert, Bull. Soc. Bot. France 94:380. 1947.
Madagascar.

Gymnanthemum rueppellii (Sch. Bip. ex Walp.) H. Rob., comb. nov. basionym: *Vernonia rueppellii* Sch. Bip. ex Walp., Rep. 2:946. 1864.

Vernonia francavillana Oliv. & Hiern *in*

Oliv., Fl Trop. Afr. 3:296. 1877.
Ethiopia.

Gymnanthemum secundifolium (Boj. ex DC.) H. Rob., comb. nov. basionym: *Vernonia secundifolia* Boj. ex DC., Prodr. 5: 22. 1836.

Vernonia quadriflora Baker, J. Linn. Soc. Bot. 20:173. 1884.
Madagascar.

Gymnanthemum solanifolium (Benth.) H. Rob., comb. nov. basionym: *Vernonia solanifolia* Benth., Hooker's J. Bot. Kew Gard. Misc. 1:486. 1842.
China, Myanmar, Thailand, Vietnam.

Gymnanthemum subcrassulescens (Humbert) H. Rob., comb. nov. basionym: *Vernonia subcrassulescens* Humbert, Notul. Syst. (Paris) 13:309. 1948.
Madagascar.

Gymnanthemum theophrastifolium (Schweinf. ex Oliv. & Hiern) H. Rob., comb. nov. basionym: *Vernonia theophrastifolia* Schweinf. ex Oliv. & Hiern, *in* Oliv., Fl. Trop. Afr. 3:294. 1877.

Vernonia myriocephala A. Rich., Tent. Fl. Abyss. 1:374. 1848, hom. illeg., not DC., 1836.
Cacalia richardiana O. Kuntze, Rev. Gen. Pl. 2:969. 1891, nom. nov. for *V. myriocephala* A. Rich.
Vernonia seretii De Wild., Ann. Mus. Congo V, 11:207. 1907.
Vernonia macrophylla Chiov., Ann. Bot. Roma 9:70. 1911.
Vernonia richardiana (O. Kuntze) Pichi-Serm., Webbia 7:340. 1950.
Congo and Nigeria east to Uganda, Kenya and Ethiopia.

Gymnanthemum thomsonianum (Oliv. & Hiern *in* Oliv.) H. Rob., comb. nov. basionym: *Vernonia thomsoniana* Oliv. & Hiern *in* Oliv., Trans. Linn. Soc. London 29:91. 1873.

Vernonia livingstoniana Oliv. & Hiern *in* Oliv., Fl. Trop. Afr. 3:295. 1877.
Vernonia cruda Klatt, Bull. Herb. Boiss. 4:456. 1896.
Vernonia densicapitulata De Wild., Bull. Jard. Bot. Brux. 5:92. 1915.
West, central and south tropical Africa.

Gymnanthemum urticifolium (A. Rich.) H. Rob., comb. nov. basionym: *Vernonia urticifolia* A. Rich., Tent. Fl. Abyss. 1:378. 1848.

Vernonia antinoriana Avetta, Nouv. Giorn. Bot. Ital. 21:348. 1889.
Vernonia mellifera Muschl., Bot. Jahrb. Syst. 46:90. 1911.
Congo, Ethiopia, Kenya.

Gymnanthemum vidalii (G. Merr.) H. Rob., comb. nov. basionym: *Vernonia vidalii* G. Merr., Philipp. Is., Bur. Gov. Lab. Bull. 6:6. 1904 ("1903").
Philippines.

Gymnanthemum volkameriifolium (DC.) H. Rob., comb. nov. basionym: *Vernonia volkameriaefolia* DC., Prodr. 5:32. 1836.

Vernonia acuminata DC., Prodr. 5:32. 1836.
Vernonia punduana DC., Prodr. 5:32. 1836.
Vernonia esqirolii Lévl., Repert. Spec. Nov. Regni Veg. 11:304. 1912.
China, India, Myanmar.

Gymnanthemum wightianum (Arn.) H. Rob., comb. nov. basionym: *Vernonia wightiana* Arn., Pugill. pl. Ind. Or. 27. 1836.
Sri Lanka.

Gymnanthemum zanzibarense (Less.) H. Rob., comb. nov. basionym: *Vernonia zanzibarensis* Less., Linnaea 6:637. 1831.
Kenya, Tanzania.

Gymnanthemum zeylanicum (L.) H. Rob., comb. nov. basionym: *Eupatorium zeylanicum* L., Sp. pl. 837. 1753.

Vernonia zeylanica (L.) Less., Linnaea 4: 344. 1829.
Sri Lanka.

A number of additional species have been placed in the genus that are excluded here. These include *G. congestum* Cass., = *Critoniopsis triflosculosa* (H. B.

K.) H. Rob. (Robinson 1993), *G. frutescens* (Bl.) Sch. Bip. ex Walp., *G. molle* (DC.) Sch. Bip. ex Walp., *G. phyllolaenum* (DC.) Sch. Bip. ex Walp. and *G. reticulatum* (Wight) Sch. Bip. ex Walp. which belong to *Phyllocephalum* (Kirkman 1981).

Brenandendron H. Rob., gen. nov. (Gymnantheminae).

Type: *Vernonia titanophylla* Brenan

Plantae arborescentes ad 8 m altae mediocriter ramosae; caules velutini, pilis fusiformibus vel leniter asymmetricis. Folia alterna petiolata vel subsessilia, laminis magnis interdum lobatis. Inflorescentiae frondiformes in ramulis racemosae vel spiciformes. Capitula sessilia vel breviter pedunculata; involucra campanulata; bracteae involucri usque ad 110 in seriebus 7–9 appressae interiores leniter deciduae subcoriaceae vel coriaceae; receptacula epaleacea. Flores 30–50 in capitulo; corollae plerumque tubiformes in faucibus elongatae, lobis erectis vel interdum recurvatis; thecae antherarum base longe obtuse caudatae; appendices apicales in parietibus cellularum firmae; basi stylorum annulate noduliferi. Achenia 8–10-costata glabra idioblastifera, raphidis rhomboideis breviter vel mediocriter elongatis; setae pappi interiores subplanae subpersistentes exteriores squamiformes vel nullae. Grana pollinis tricolporata echinata non lophata. Numerus chromosomatum N = 9 Mangenot & Mangenot (1957).

Germacranolides have been reported from the genus (Bohlmann and Jakupovic 1990).

Brenandendron is closely related to *Gymnanthemum,* but it differs by the distinctive frondiform inflorescence. Brenan (1953) provided a key to the three species. In addition to the differences given by Brenan, the three species differ in their corolla lobes. *Brenandendron donianum* has erect lobes much shorter than the corolla throat, *B. frondosum* has narrow erect lobes, and *B. titanophyllum* has strongly recurved narrow lobes.

The three species are as follows:

Brenandendron donianum (DC.) H. Rob., comb. nov. basionym: *Vernonia doniana* DC., Prodr. 5:23. 1836.

Vernonia conferta Benth. *in* Hook., Niger Fl. 427. 1849.

West and central tropical Africa from Angola to Liberia and Sudan.

Brenandendron frondosum (Oliv. & Hiern *in* Oliv.) H. Rob., comb. nov. basionym: *Vernonia frondosa* Oliv. & Hiern *in* Oliv., Fl. Trop. Afr. 3:294. 1877.

West Africa from Guinea to Cameroon.

Brenandendron titanophyllum (Brenan) H. Rob., comb. nov. basionym: *Vernonia titanophylla* Brenan, Kew Bull. 1953:116. 1953.

Cameroon, Congo, Equatorial Guinea.

Myanmaria H. Rob., gen. nov. (Gymnantheminae).

Type: *Vernonia calycina* DC.

Plantae frutescentes ca. 1 m altae mediocriter ramosae; caules puberuli, pilis simplicibus uniseriatis multiseptatis. Folia alterna breviter petiolata, laminis oblongo-ovatis apice obtusis. Inflorescentiae corymbiformae. Capitula in ramis terminalia pedunculata; bracteae involucri exteriores ca. 20 ca. 2–3-seriatae late ovatae virides foliiformes; bracteae interiores lineares acutae; receptacula epaleacea. Flores 35–50 in capitulo; corollae puberulae, tubis elongatis, faucibus quoad lobis longioribus, lobis 2–3-plo longioribus quam latioribus extus glanduliferis et pauce breviter pilosulis; thecae antherarum base distincte late caudatae; appendices apicales antherarum distincte induratae; basi stylorum non noduliferi; rami stylorum obtuse papilliferi. Achenia 10-costata idioblastifera in costis setulifera, raphidis subquadratis; setae pappi barbellatae numerosae 2–3-seriatae persistentes exteriores breviores vel nullae. Grana pollinia ca. 50 μm in diametro tricolporata echinata lophata micropunctata, lacunis polaribus triplicibus intercolpatis.

Myanmaria is endemic to Myanmar. The genus is easily distinguished by the ca. 20

large, broad, green outer involucral bracts that completely conceal the inner bracts. The species is often described as herbaceous, and it apparently commonly turns black when dry.

The single known species is as follows:

Myanmaria calycina (DC.) H. Rob., comb. nov. basionym: *Vernonia calycina* DC., Prodr. 5:60. 1836.
Myanmar.

Lampropappus (O. Hoffm.) H. Rob., stat. nov. (Gymnantheminae). *Vernonia* section *Lampropappus* O. Hoffm., Bol. Soc. Broter. 13:14. 1896. Type: *Vernonia lampropappus* O. Hoffm. *Vernonia* subsect. *Turbinella* S. B. Jones, Rhodora 83:67. 1981. Type: *Vernonia lampropappus* O. Hoffm.

Subshrubs to 0.6 m high; stems costate, tomentose, hairs with basally or slightly excentrically attached contorted capcells. Leaves alternate, shortly petiolate to more or less amplexicaul, blades densely tomentose abaxially. Inflorescence densely corymbose, with many heads. Heads hemispherical to turbinate; involucral bracts ca. 30, ca. 4–5-seriate, strongly gradate, outer bracts ovate, apices acute to shortly apiculate; receptacle epaleaceous. Flowers ca. 20 in a head; corollas white with purple tips to pale purple, actinomorphic or slightly zygomorphic, with lobe or sinus centered on outer side, longest lobe centered toward inside. Bases of anther thecae rounded, without tails; apical appendage with somewhat thickened and ornamented cell walls; base of style with broadened node; sweeping hairs of style branches with obtuse tips. Achenes 5-costate, densely villous with uniseriate hairs, with few septae near base, with few idioblasts; raphids subquadrate to short-oblong; pappus setae persistent, 3-seriate, broad and flat, densely scabrid on margins smooth on surfaces, outer segments shorter and narrower. Pollen grains tricolporate, non-lophate, echinate.

Lampropappus, as a section, was originally compared with the American *Stilpnopappus* Mart. ex DC. and the Eastern Hemisphere *Vernonia* sect. *Stengelia* (= *Baccharoides* Moench) by Hoffmann (1896) because of the broad flat pappus segments, but was distinguished at least from the *Vernonia* sect. *Stengelia* by the exappendiculate involucral bracts. *Lampropappus* does not have the subulate tips on the pappus elements seen in *Stilpnopappus.* The African genus is further distinguished by the uniseriate rather than biseriate hairs densely covering the achene and by the non-lophate pollen. One species of the present genus, *L. turbinella,* proves to be distinct in the slightly zygomorphic corollas that are rotated or resupinate by 1/10 so that a sinus is centered to the outside and a lobe centered to the inside. This is not seen in the other two species of the genus. This feature occurs elsewhere in the Vernonieae in the American genus *Mattfeldanthus* H. Rob. & R. M. King (1979), which also has zygomorphic corollas. The latter genus is related to *Lepidaploa* (Cass.) Cass. with lophate pollen and seriate-cymose inflorescences. Such resupination of the corolla also seems to occur in the Gorteriinae of the Arctoteae.

The following three species are placed in the genus:

Lampropappus eremanthifolia (O. Hoffm.) H. Rob., comb. nov. basionym: *Vernonia eremanthifolia* O. Hoffm., Bol. Soc. Broter. 13:15. 1896.
Angola.

Lampropappus hoffmannii H. Rob., nom. nov. basionym: *Vernonia lampropappus* O. Hoffm., Bol. Soc. Broter. 13:14. 1896.
Angola.

Lampropappus turbinellus (S. Moore) H. Rob., comb. nov. basionym: *Vernonia turbinella* S. Moore, J. Linn. Soc. Bot. 47:266. 1925.
Congo, Malawi, Zambia. Zygomorphy of the corollas is not mentioned in the original description of the species (Moore 1925).

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INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Applications published in the *Bulletin of Zoological Nomenclature*

The following Applications were published on 30 September 1998 in Vol. 55, Part 3 of the *Bulletin of Zoological Nomenclature.* Comment or advice on any of these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary (I.C.Z.N.), c/o The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Case No.	
3050	*Pachylops* Fieber, 1858 (Insecta, Heteroptera): proposed designation of *Capsus chloropterus* Kirschbaum, 1856 (currently *Orthotylus virescens* (Douglas & Scott, 1865)) as the type species.
3087	*Hydrobia* Hartmann, 1821 and *Cyclostoma acutum* Draparnaud, 1805 (currently *Hydrobia acuta*; Mollusca, Gastropoda): proposed conservation by replacement of the lectotype of *H. acuta* with a neotype; *Ventrosia* Radoman, 1977: proposed designation of *Turbo ventrosus* Montagu, 1803 as the type species; and HYDROBIINA Mulsant, 1844 (Insecta, Coleoptera): proposed emendation of spelling to HYDROBIUSINA, so removing the homonymy with HYDROBIIDAE Troschel, 1857 (Mollusca).
3051	*Scarus chrysopterus* Bloch & Schneider, 1801 (currently *Sparisoma chrysopterum*; Osteichthyes, Perciformes): proposed conservation of the specific name and designation as the type species of *Sparisoma* Swainson, 1839.
3071	*Osphronemus deissneri* Bleeker, 1859 (currently *Parosphromenus deissneri*; Osteichthyes, Perciformes): proposed replacement of holotype by a neotype.
1647	*Cacatua* Vieillot, 1817 and CACATUINAE Gray, 1840 (Aves, Psittaciformes): proposed conservation.
3004	LORISIDAE Gray, 1821 and GALAGIDAE Gray, 1825 (Mammalia, Primates): proposed conservation as the correct original spellings.

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 30 September 1998 in Vol. 55, Part 3 of the *Bulletin of Zoological Nomenclature.* Copies of these Opinions can be obtained free of charge from the Executive Secretary, I.C.Z.N., c/o The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Opinion No.

1902. *Anomalina* d'Orbigny, 1826 (Foraminiferida): *Anomalina ariminensis* d'Orbigny in Fornasini, 1902 designated as the type species.
1903. *Umbellula* Cuvier, [1797] (Cnidaria, Anthozoa): conserved as the correct original spelling, and corrections made to the entries relating to *Umbellularia* Lamarck, 1801 on the Official Lists and Indexes of Names in Zoology.
1904. *Aporcelaimus* Thorne & Swanger, 1936 (Nematoda): *Dorylaimus superbus* de Man, 1880 designated as the type species.
1905. S.D. Kaicher (1973–1992), *Card Catalogue of World-Wide Shells:* not suppressed for nomenclatural purposes.
1906. *Euchroeus* Latreille, 1809 (Insecta, Hymenoptera): conserved; *Chrysis purpurata* Fabricius, 1787 (currently *Euchroeus purpuratus*): specific name conserved; and *Chrysis gloriosa* Fabricius, 1793: specific name suppressed.
1907. *Nothosaurus* Münster, 1834 (Reptilia, Sauropterygia): given precedence over *Conchiosaurus* Meyer, [1833]
1908. *Hemidactylus garnotii* Duméril & Bibron, 1836 (Reptilia, Squamata): specific name conserved.
1909. *Holotropis herminieri* Duméril & Bibron, 1837 (currently *Leiocephalus herminieri*), *Proctotretus bibronii* T. Bell, 1842 (currently *Liolaemus bibronii*) (Reptilia, Squamata): specific names conserved, and *Liolaemus bellii* Gray, 1845 placed on the Official List.

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A revision of the Antarctic genus *Chlanidota* (Gastropoda: Neogastropoda: Buccinulidae)

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Abstract.—The genus *Chlanidota* is revised to contain two subgenera, *Chlanidota* sensu stricto and *Chlanidota* (*Pfefferia*). *Chlanidota* s.s. has a broad distribution throughout the Antarctic region, and contains five species: *Chlanidota* (*Chlanidota*) *vestita* (Martens, 1881), *C.* (*C.*) *densesculpta* (Martens, 1885), *C.* (*C.*) *paucispiralis* Powell, 1951, *C.* (*C.*) *pilosa* Powell, 1951, and *C.* (*C.*) *signeyana* Powell, 1951. The subgenus *Pfefferia*, which differs from *Chlanidota* primarily in the morphology of its operculum, is endemic to South Georgia Island, and is known from three species: *Chlanidota* (*Pfefferia*) *chordata* (Strebel, 1908), *C.* (*P.*) *palliata* (Strebel, 1908), *C.* (*P.*) *invenusta*, new species. With its bulliform shell lacking a siphonal canal, the monotypic, circum-Antarctic genus *Neobuccinum* is conjectured to be the sister taxon of *Chlanidota*, but is readily distinguished by its smoother, higher-spired shell, radula in which the central cusp of the lateral teeth is medially placed, and a penis lacking a papilla.

The genus *Chlanidota* Martens, 1878, is one of the more diverse and wide-ranging members of the antiboreal buccinoidean radiation comprising the family Buccinulidae. As is true of nearly all buccinoidean higher taxa, this genus has been defined primarily on the basis of shell morphology, occasionally supplemented with observations of the radula and operculum. Consequently, neither the limits of this genus nor its relationships to other buccinoidean taxa have been well established.

Martens (1878) first proposed *Chlanidota* as a monotypic subgenus of *Cominella*, but later (Martens 1881) transferred the subgenus to *Buccinum* Linné, 1758. Watson (1886) included the type species of *Chlanidota* in the genus *Neobuccinum* Smith, 1877. Thiele (1912) erected the monotypic *Ficulina* as a subgenus of *Cominella*. Later, he discovered this taxon to be a junior synonym of *Ficulina* Gray, 1867, and proposed *Notoficula* Thiele, 1917, as a new name. Still later, Thiele (1929:315) treated *Chlanidota* as a genus, and included *Notoficula*, *Pfefferia* Strebel, 1908, and *Bathydomus* Thiele, 1912, as subgenera. Powell (1951) elevated each of these subgenera to generic status, but regarded them to be closely related. Oliver (1983) showed *Notoficula* to be a neotenous eratoid rather than a buccinoidean.

Chlanidota has been treated most recently by Dell (1990), who included 13 species (Table 1), some tentatively, and noted that this genus has undergone an explosive radiation in Antarctic waters. He commented that the distributions, both geographic and bathymetric, "show puzzling patterns, especially through the Scotia Arc and adjacent regions of the Antarctic continent." The closely related taxon *Pfefferia* (see Ta-

Table 1.—Listing of species attributed to *Chlanidota* and *Pfefferia* and their present taxonomic placement. Taxa listed in **bold** are valid species referable to these subgenera of *Chlanidota.*

Chlanidota bisculpta Dell, 1990	Not a *Chlanidota.* Belongs in an as yet undescribed genus.
***Chlanidota* (*Chlanidota*) *densesculpta* (Martens, 1885)**	
Chlanidota elongata (Lamy, 1910)	Junior homonym of *Cominella elongata* Dunker, 1857; *Chlanidota lamyi* Dell, 1990 is a replacement name.
Chlanidota eltanini Dell, 1990	Not a *Chlanidota.* Belongs in an as yet undescribed genus.
Chlanidota gaini Lamy, 1910	Belongs in the conoidean genus *Belaturricula.*
Chlanidota lamyi Dell, 1990	Synonym of *Chlanidota signeyana* Powell, 1951
Chlanidota cf. *lamyi* Dell, 1990	Synonym of *Chlanidota signeyana* Powell, 1951
***Chlanidota* (*Chlanidota*) *paucispiralis* Powell, 1951**	
***Chlanidota* (*Chlanidota*) *pilosa* Powell, 1951**	
Chlanidota polysperia Dell, 1990	Not a *Chlanidota.* Belongs in an as yet undescribed genus.
Chlanidota pyriformis Dell, 1990	Synonym of *Chlanidota signeyana* Powell, 1951
Chlanidota smithi Powell, 1958	Synonym of *Neobuccinum eatoni* (Smith, 1875)
***Chlanidota* (*Chlanidota*) *signeyana* Powell, 1951**	
***Chlanidota* (*Chlanidota*) *vestita* (Martens, 1881)**	
***Chlanidota* (*Pfefferia*) *chordata* (Strebel, 1908)**	
Pfefferia cingulata Strebel, 1908	Synonym of *Chlanidota* (*Pfefferia*) *palliata* (Strebel, 1908)
Pfefferia elata Strebel, 1908	Synonym of *Chlanidota* (*Pfefferia*) *palliata* (Strebel, 1908)
***Chlanidota* (*Pfefferia*) *palliata* (Strebel, 1908)**	
***Chlanidota* (*Pfefferia*) *invenusta,* new species.**	

ble 1), endemic to South Georgia Island, was last reviewed by Powell (1951), who selected a type species and added several new records for two of the four species described by Strebel (1908).

The present revision of the genus *Chlanidota,* which includes the subgenus *Pfefferia,* is based on a study of the large collections of these taxa sampled under the auspices of the United States Antarctic Program (USAP), as well as the type material of all species described or subsequently assigned to these taxa. The objectives of this study are: to assess the relationships among nominal taxa of *Chlanidota* and *Pfefferia* based on anatomical as well as conchological characters; to discern biogeographic patterns in the distribution of these taxa; and to begin to build a framework of anatomical data that can be used to resolve phylogenetic relationships of and among the buccinoidean taxa of the Southern Hemisphere.

Materials and Methods

This report is based primarily on the extensive collections of *Chlanidota* and *Pfefferia* (including dry shells and alcohol preserved anatomical material) collected by the United States Antarctic Program (USAP) and housed at the National Museum of Natural History, Smithsonian Institution (USNM). Additional material, including type specimens housed in the following institutions, were examined: BMNH—The Natural History Museum, London; MNHN—Muséum national d'Histoire naturelle, Paris; MNH-U—Museum für Naturkunde der Humboldt-Universität zu Berlin; SAM—The South Australian Museum, Adelaide; SMNH—Swedish Museum of Natural History, Stockholm; ZMH—Zoologisches Institut und Zoologisches Museum der Universitat Hamburg.

In the material examined sections, "specimen" denotes alcohol preserved material,

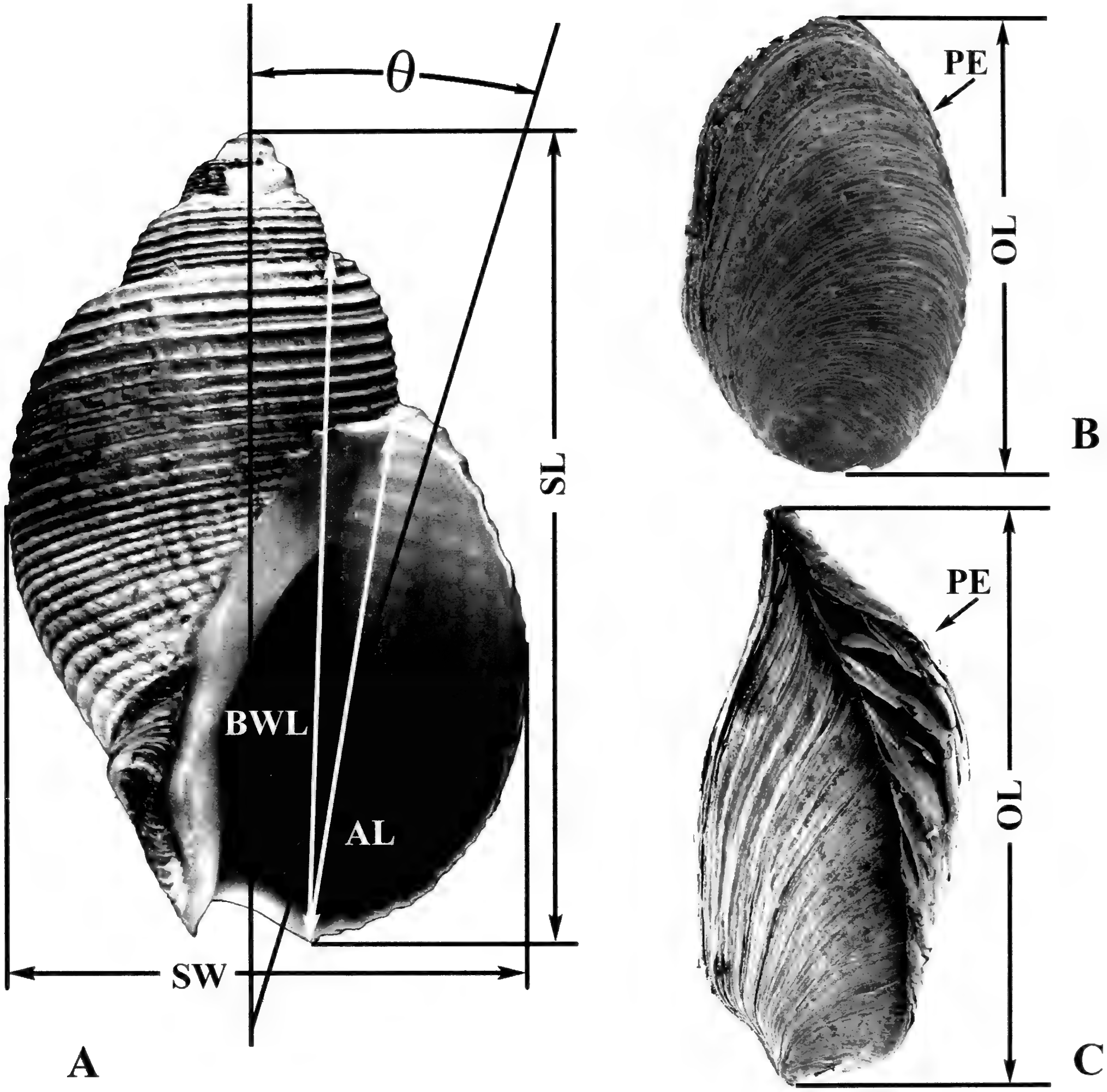

Fig. 1. Measurements of shell and operculum features. AL, aperture length; BWL, body whorl length; OL, operculum length; PE, posterior edge; SL, shell length; SW, shell width; θ, deflection of aperture from shell axis.

while "shell" refers to records containing only the empty shell.

Shell and operculum measurements were obtained for representative specimens of each species (n = 10, when available), as detailed in Figure 1. Shell ultrastructure was observed along freshly fractured surfaces parallel to the growing edge of the shell. Anatomical descriptions are based on gross dissections of preserved material. As the apex of the shell was strongly eroded in all specimens of *Chlanidota*, the aperture length (AL) rather than the shell length was used as the reference when reporting the relative size of anatomical features. 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).

Images were digitized using a Leaf Lumina Digital Scanning Camera. Optical and SEM images were processed using Photoshop Version 4.01 (Adobe).

Systematics

Order Neogastropoda Wenz, 1938

Superfamily Buccinoidea Rafinesque, 1815

The buccinoidean whelks comprise one of the few uncontroversial, monophyletic groups within the order Neogastropoda. While buccinoideans are readily identified on the basis of shell, radular, and alimentary system morphology (e.g., weakly sculptured shells lacking spines or columellar folds, lateral teeth with ≥2 cusps, absence of accessory salivary glands and rectal gland), there is no consensus as to the rank or inter-relationships of the group as a whole, or its constituent higher taxa (e.g., Thiele 1929; Wenz 1938; Bouchet & Warén 1985; 1986; Ponder & Warén 1988; Ponder & Lindberg 1996; Kantor 1996). As a result, most current classifications are of a typological rather than phylogenetic nature.

Based primarily on shell, radular, and opercular characters, Powell (1929) divided the Buccinoidea into the families Buccinidae, Neptuneidae, Buccinulidae, Cominellidae and Fasciolariidae. In the same year, Thiele (1929) published an alternative and more widely accepted higher classification of the Buccinoidea, comprising the families Columbellidae, Buccinidae, Melongenidae, Nassariidae, and Fasciolariidae. Powell (1951) subsequently revised his classification, regarding the Southern Hemisphere Buccinulidae (now including the subfamily Cominellinae) to be more closely related to the boreal family Neptuneidae than to Buccinidae. Ponder (1971) reviewed the New Zealand species of *Buccinulum* and concluded that anatomical differences did not justify their segregation from Buccinidae. Ponder (1974) and subsequently Ponder & Warén (1988) reduced the Buccinoidea to a family within Muricoidea, and also reduced in rank or synonymized most of the previously recognized families and subfamilies. Powell (1976) partially incorporated these demotions in taxonomic rank into revisions of his earlier work (e.g., Powell 1961), but (Powell 1979:192) clearly continued to regard the Southern Hemisphere Buccinulinae to be distantly related to the Northern Hemisphere Buccininae. Other authors have revised the higher systematics of the buccinoidean fauna of the Northern Hemisphere (Habe & Sato 1973) without treating austral representatives.

Pending a phylogenetic revision of the higher taxa within Buccinoidea, we provisionally retain the taxon Buccinulidae and its subdivisions, as understood by Powell (1951), to encompass the austral radiation of buccinoidean taxa.

Family Buccinulidae Finlay, 1928

Finlay (1928:250) proposed the family Buccinulidae (with subfamilies Buccinulinae and Siphonaliinae) and enumerated the included genera, but provided no diagnosis or differentiating characters. Powell (1929: 57) suggested that Finlay's work was based on protoconch and teleoconch characters, and provided a modified classification "based primarily on the dentition." Powell (1951:151) further refined his concept of Buccinulidae, noting that the chief characteristics of the group were tricuspid rachidian teeth and an operculum with a terminal or subterminal nucleus. He subdivided the family into three subfamilies, the Cominellinae, Buccinulinae and Prosiphiinae based on the number of cusps on the lateral teeth.

Subfamily Buccinulinae Finlay, 1928

As refined by Powell (1951:151) the Buccinulinae are characterized by radulae with tricuspid rachidian teeth and tricuspid lateral teeth. The subfamily ranges from Antarctica to New Zealand, Australia, and along the eastern Pacific coast as far north as California.

Genus *Chlanidota* Martens, 1878

Powell speculated that *Chlanidota*, *Pfefferia* and *Neobuccinum* may represent a transitional stage between the short-canalled Cominellinae and the long-canalled Buccinulinae, the latter including the Antarctic genera *Probuccinum*, *Cavineptunea*, and *Bathydomus*. He included *Chlanidota*, *Pfefferia*, and *Neobuccinum* within Buccinulinae primarily on the basis of their tricuspid lateral teeth, but noted that in these taxa the intermediate cusp was likely the result of a bifurcation of the inner cusp.

Subgenus *Chlanidota* Martens, 1878

Cominella (*Chlanidota*) Martens, 1878: [Type (by monotypy): *Cominella (Chlanidota) vestita* Martens, 1878].

Chlanidota Thiele, 1929:314–315; Powell, 1951:139; Dell, 1990:177.

Description—Shell medium-sized for family, reaching 25.5 to 42.6 mm, depending on species. Shell usually thin, fragile, ovate to elongate in outline, spire short to very short. Shell covered with thin to thick, smooth or hirsute periostracum. Spiral sculpture of either thin to very thin threads or of prominent cords. Aperture high, oval. Operculum very small (0.18–0.37 AL), ovate, coiled, with nucleus terminal, rotated to left, nearly perpendicular to long axis of operculum. Siphonal notch broad, dorsally recurved, siphonal fasciole with ridges along margins. Shell composed of 3 crystalline layers, outermost layer prismatic, middle layer of crossed-lamellar crystals with crystal faces comarginal (oriented parallel to growing edge), innermost layer of crossed lamellar crystals radial (oriented perpendicular to growing edge).

Digestive system generally typical of buccinids. Proboscis of medium length or long. Radular ribbon long, triserial. Rachidian tooth with arched base, straight sides, 3 large, robust cusps, usually of equal length. Lateral teeth with 3 cusps, outer cusp longest, middle cusp shortest, closely adjacent to innermost cusp. Salivary glands small, fused or separate. Valve of Leiblein large, well defined, lacking ciliary cone. Gland of Leiblein long, tubular, convoluted anteriorly, straightening and tapering posteriorly. Oesophagus wide, muscular, with posterior crop-like enlargement lined with tall longitudinal folds. Stomach broadly U-shaped, without caecum.

Penis long, dorsoventrally flattened, with long, cylindrical terminal papilla, surrounded by deep circular fold at its base.

Remarks.—This subgenus is endemic to the Antarctic region. The highest diversity is in the Weddell Quadrant, especially in the vicinity of South Georgia Island. There are no records from the Ross Quadrant. Only *Chlanidota vestita*, the type species, extends northward beyond the Antarctic Convergence. The bathymetric range of *Chlanidota* sensu stricto is from 3 to 1116 m.

Chlanidota (*Chlanidota*) *vestita*
(Martens, 1878)
Figs. 2–3; Table 2

Cominella (*Chlanidota*) *vestita* Martens, 1878:23; Martens, 1904:63; Thiele, 1904: 168, Taf. IX, fig. 56 (radula); Lamy, 1911:pl. I, fig. 5.

Buccinum (*Chlanidota*) *vestitum* Martens, 1881:43–44, Taf. 9, Fig. 3a–c.

Chlanidota vestita Tryon, 1881:201, pl. 79, fig. 391; Smith, 1902:203; Powell, 1951: 139; Carcelles, 1953:191, pl. 3, fig. 58; Powell, 1957:133; Powell, 1960:150; Dell, 1964:288; Gaillard, 1971:100; Cantera & Arnaud, 1984:68; Dell, 1990:184, fig. 311.

Neobuccinum vestitum Watson, 1886:216.

Description.—Shell (Fig. 2) small for genus (to 29 mm), thin, translucent, but strong, ovate in outline, with low, rounded spire. Protoconch unknown, upper teleoconch whorls heavily eroded. Teleoconch of up to 3½ evenly-rounded, convex whorls, deeply eroded where periostracum damaged or missing. Suture strongly impressed, forming extremely narrow channel between adapical spiral cord and previous whorl. Spiral sculpture of prominent but unequal cords, intervening spaces 2–4 times as broad as cords. Lectotype with 23 cords on body whorl, 8 on penultimate whorl. Para-

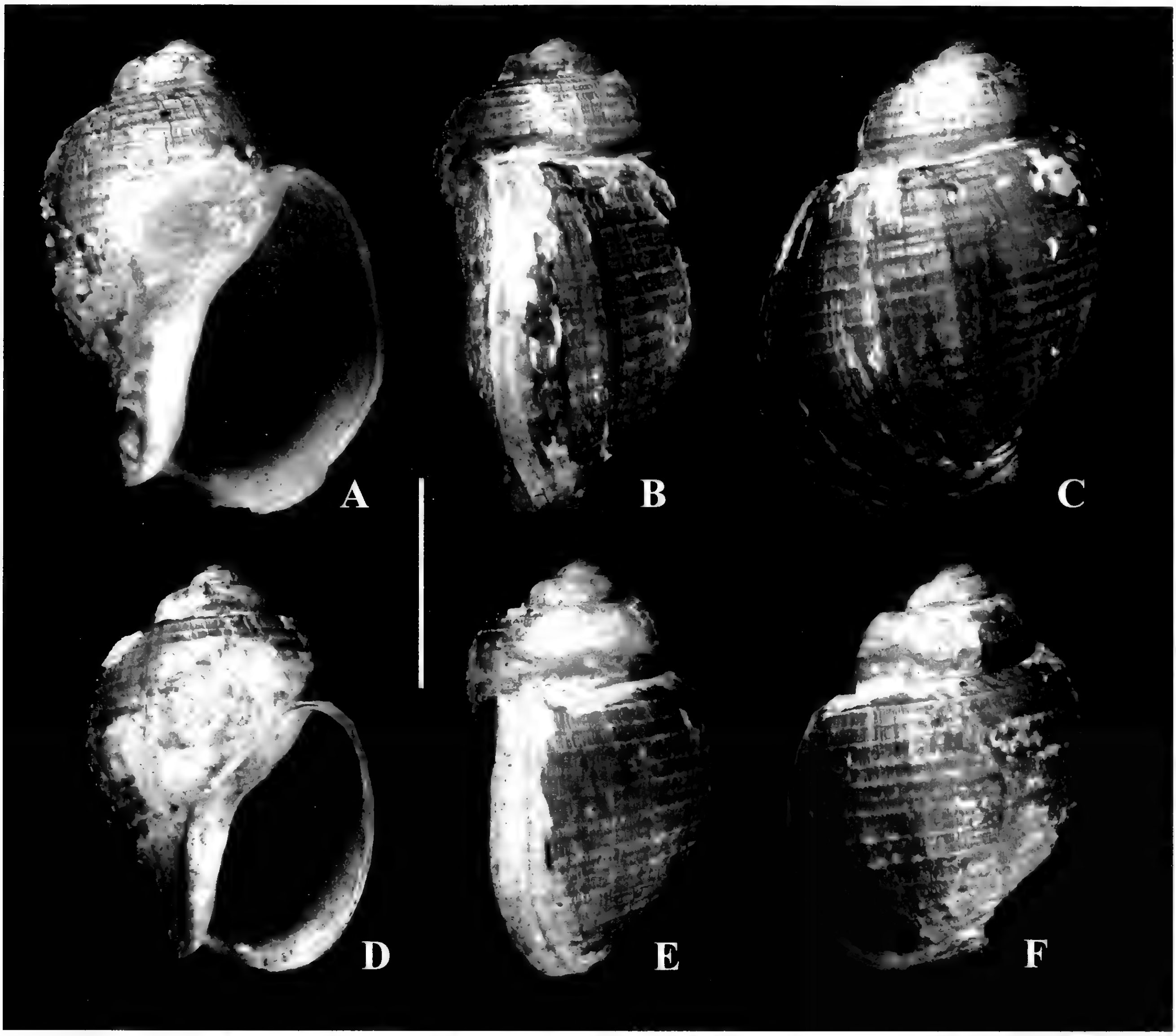

Fig. 2. *Chlanidota (Chlanidota) vestita* (Martens, 1878). A-C. Lectotype, MNH-U 25613-a (here designated). D–F. Paralectotype, MNH-U 25613-b. Both from Kerguelen Island. Scale bar = 1 cm.

lectotype with 22 cords on body whorl, 7 on penultimate whorl. Numerous fine, sinuated spiral threads between cords. Axial sculpture limited to growth lines, producing finely cancellate surface sculpture. Aperture broadly ovate, deflected from shell axis by 14–18°. Outer lip thin, evenly rounded, simple. Columella ≈½ AL, weakly concave, with strong siphonal fold. Parietal region, siphonal fasciole overlain by thin, grayish callus. Siphonal notch broad, dorsally recurved, with straight columellar, rounded apertural margins forming borders of fasciole. Ridge margin of fasciole runs from apertural margin of siphonal notch. Shell color chalky white, aperture weakly glazed. Periostracum thin, straw-colored, smooth, glossy. Operculum, as illustrated by Dell (1990:fig. 311), very small (0.28 AL), ovate. Radula (Thiele 1904:fig. 56) with tricuspid rachidian and lateral teeth, as described for other species of *Chlanidota* illustrated herein.

Type locality.—Kerguelen Island.

Type material.—Two lots of syntypes, MNH-U 25613 (2 shells), MNH-U 25626 (3 shells). One specimen from MNH-U 25613, corresponding in size to the original description, is here designated as the lectotype (Fig. 2A–C). The remaining four specimens are paralectotypes.

Material examined.—The lectotype (MNH-U 25613-a) and one paralectotype (MNH-U 25613-b).

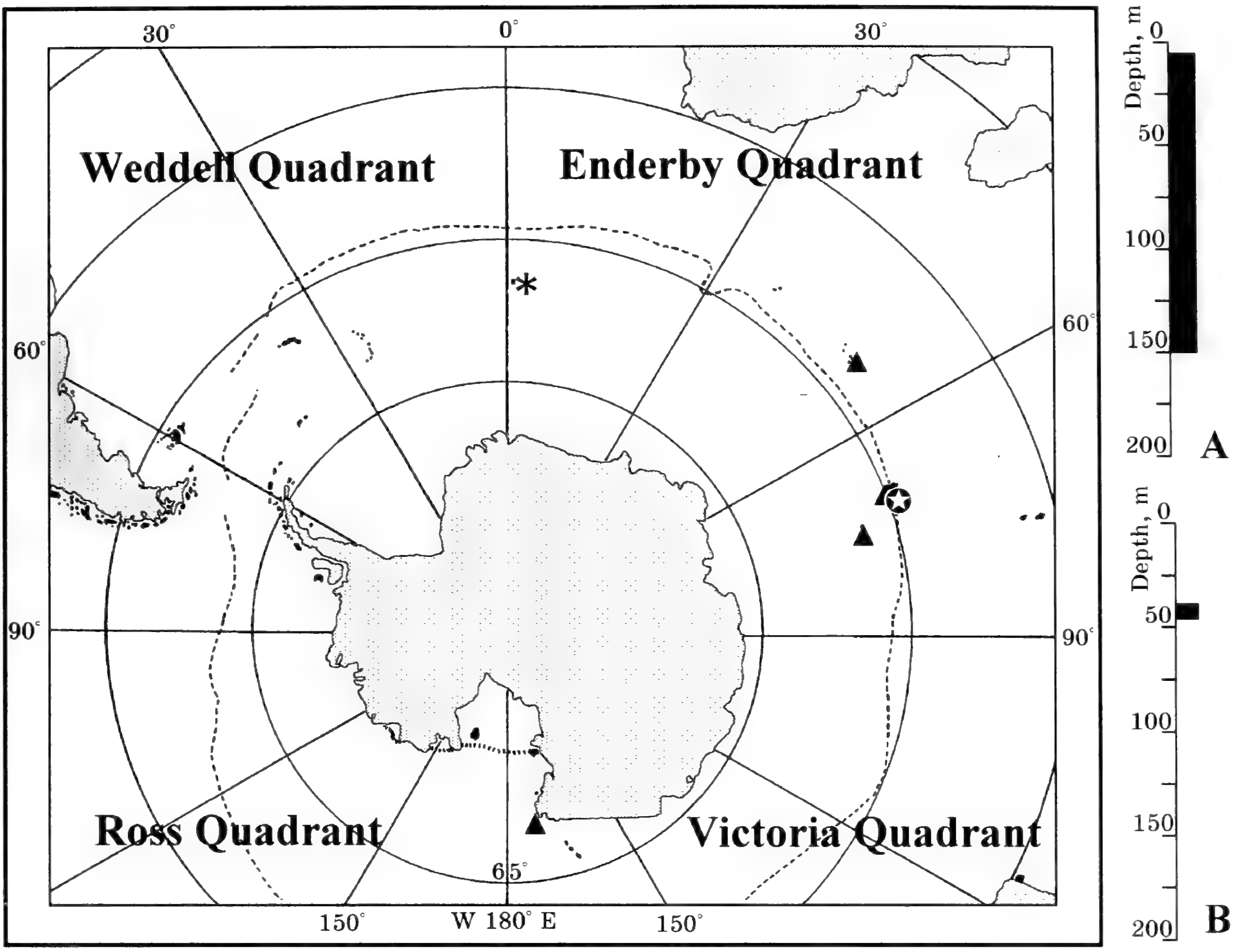

Fig. 3. Geographic distribution and bathymetric ranges of *Chlanidota* (*Chlanidota*) *vestita* (Martens, 1878). ✪ = type locality, ▲ = published records, and *Chlanidota* (*Chlanidota*) *pilosa* (Powell, 1951). ✳ = type locality. A. Bathymetric range of *C.* (*C.*) *vestita* (Martens, 1878). B. Bathymetric range of *C.* (*C.*) *pilosa* (Powell, 1951). Antarctic quadrants follow terminology of Markham (1912). Dashed line indicates Antarctic Convergence.

Table 2.—*Chlanidota* (*Chlanidota*) *vestita* (Martens, 1878). Shell measurements of lectotype and paralectotype 1. Linear measurements in mm.

Character	Lectotype	Paralectotype 1
Shell Length (SL)	22.5	19.4
Body Whorl Length (BWL)	20.1	16.8
Aperture Length (AL)	17.1	13.3
Shell Width (SW)	17.1	14.5
BWL/SL	0.89	0.87
AL/SL	0.76	0.69
SW/SL	0.76	0.75
No. spiral cords on:		
Penultimate whorl	8	7
Body whorl	23	22

Published records.—H.M.S. Challenger: Sta. 149, Accessible Bay, Kerguelen, 49°08′S, 70°12′E, in 20–25 fm volcanic mud; Sta. 149B, off Royal Sound, Kerguelen, 49°28′S, 70°30′W, 25 fm, volcanic mud; Sta. 149D, off Royal Sound, Kerguelen, 49°28′S, 70°13′W, 28 fm, volcanic mud; Sta. 151, off Heard Island, 52°59′30″S, 73°33′30″W, 75 fm, volcanic mud (Watson, 1886). British, Australian and New Zealand Antarctic Research Expedition (BANZARE): Sta. 12, Off Grave Island, Island Harbor, Kerguelen, 5 m in red and brown algae; Sta. 58, Hydrography Channel, SE of Green Island, Kerguelen, in 50 m (Powell 1951). R/V *Southern Cross*: Cape Adare, Ross Sea, 43–47 m, BMNH (Smith 1902:203, see Dell 1990:fig. 311).

Table 3.—*Chlanidota* (*Chlanidota*) *densesculpta* (Martens, 1885). Measurements of shell characters. Linear measurements in mm (n = 10, holotype not included).

Character	Mean	σ	Range	Holotype
Shell Length (SL)	34.3	2.22	29.5–36.6	31.2
Body Whorl Length (BWL)	29.8	1.90	25.9–32.3	27.8
Aperture Length (AL)	24.4	2.18	20.6–27.8	24.4
Shell Width (SW)	23.2	2.20	18.7–27.2	24.5
Operculum Length (OL)	6.2	0.87	4.4–7.5	—
BWL/SL	0.87	0.01	0.85–0.88	0.89
AL/SL	0.71	0.03	0.67–0.75	0.78
SW/SL	0.68	0.04	0.63–0.74	0.79
OL/AL	0.25	0.04	0.18–0.31	—

Distribution:—Kerguelen, the Crouzets, Heard Island and the Ross Sea, in 5–150 m (Fig. 3).

Remarks.—*Chlanidota vestita* is readily distinguished from all congeners by its small, broadly shouldered shell, stepped spire, high body whorl, and moderately strong spiral cords.

In addition to the Kerguelen and Crozet Plateaus, records include a single report from Cape Adare on the Antarctic continent (Smith 1902). Dell (1990:184, fig. 311) examined and figured the Cape Adare specimen [BMNH], and confirmed it to be *C. vestita*, and not *C. smithi* as reported by Powell (1958). Dell (1964:288) reported *C. vestita* from Heard Island.

Chlanidota (*Chlanidota*) *densesculpta* (Martens, 1885)
Figs. 4–7; Table 3

Cominella (*Chlanidota*) *densesculpta* Martens, 1885:91; Martens & Pfeffer, 1886: 71, pl. 1, fig. 3a–f.

Chlanidota densesculpta Thiele, 1912:263; David, 1934:128; Powell, 1951:140, pl. 8, figs. 31–33; Carcelles, 1953:192, pl. 3, fig. 60; Powell, 1960:150; Dell, 1990 (partim):183, fig. 305, non fig. 306.

Description.—Shell (Fig. 4) large for genus (to 40.3 mm), thin, translucent, fragile, ovate in outline, with low, rounded spire. Protoconch unknown, early whorls heavily eroded. Teleoconch of up to 6 evenly-rounded convex whorls, deeply eroded where periostracum damaged or missing. Suture impressed, obscured by thick periostracum. Spiral sculpture of numerous extremely fine spiral threads, broader than the spaces between them. Spiral threads sinuated, equal in strength, closely spaced (4–5 per mm), ~40 on penultimate whorl, >80 on body whorl. Axial sculpture limited to growth lines, producing finely cancellate surface sculpture appearing in places more like a rectangular array of fine pits. Aperture broadly ovate, deflected from shell axis by 9–13°. Outer lip thin, evenly rounded, slightly reflected. Columella <½ AL, weakly concave, with strong siphonal fold. Callus consisting of thin, silver-edged glaze overlying parietal region, siphonal fasciole. Siphonal notch broad, dorsally recurved, with straight columellar and rounded apertural margins that form borders of fasciole. Ridge margin of fasciole runs from apertural margin of siphonal notch, may be evident beneath columellar callus in some specimens. Shell color chalky white, aperture weakly glazed. Periostracum (Fig. 6C) thick, orange-tan, hirsute. Hair-like projections emanating from edges of lamellae at intersections of spiral threads with axial growth lines. Operculum (Fig. 4G–I, K) small (0.18–0.31 AL), broadly ovate, weakly coiled, with terminal nucleus (usually abraded) rotated nearly perpendicular to long axis. Attachment area nearly circular, spanning ¾ of inner surface, posterior, left margins thickened, glazed, abraded.

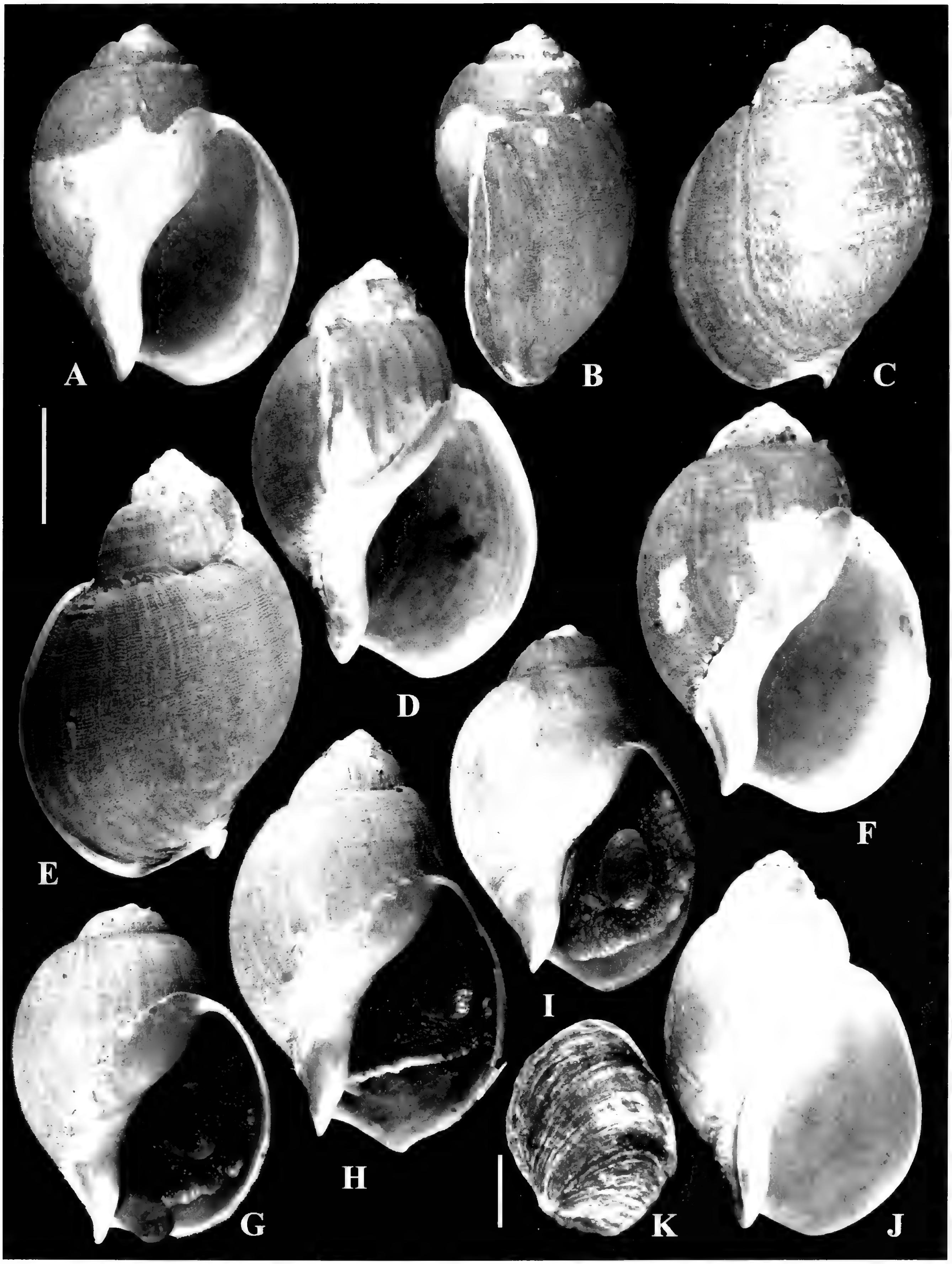

Fig. 4. *Chlanidota* (*Chlanidota*) *densesculpta* (Martens, 1875). A–C. holotype, MNH-U 37478. South Georgia Island. D–E, H, J. R/V *Islas Orcadas*, Sta. 20, Off South Georgia Island, 54°00′06″S, 37°40′36″W, in 68–80 m, USNM 906152. Periostracum of specimen in figure J removed with bleach to reveal spiral sculpture. F, G, I. R/V *Eltanin*, Sta. 1533, South Georgia Island, 54°00′S, 37°27′W, in 3–6 m. F. USNM 870722, G, I. USNM 896097. K. Operculum of specimen in fig. D. Scale bar = 1 cm for A–J, 2 mm for K.

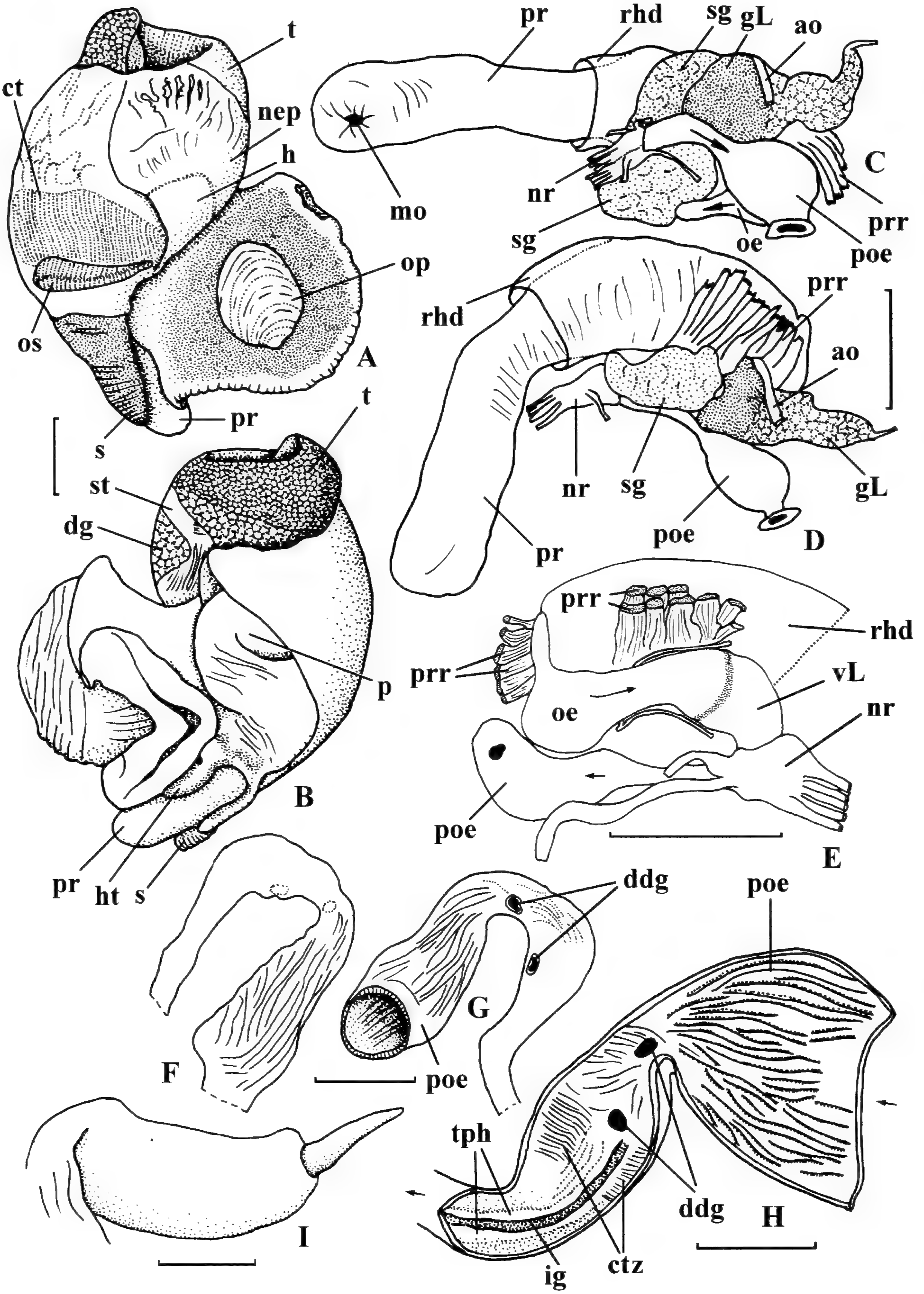

Fig. 5. *Chlanidota* (*Chlanidota*) *densesculpta* (Martens, 1875). R/V *Islas Orcadas*, Sta. 19, Off South Georgia Island, 54°01′42″S, 37°40′00″W, in 46–70 m, USNM 901651. A. Left, and B. right lateral views of ♂ animal removed from shell. C. Ventral and D. left lateral views of anterior alimentary system. E. Posterior portion of the proboscis, with salivary glands removed to show the valve of Leiblein. F. Dorsal, and G. ventral views of stomach. H. Stomach, opened mid-dorsally. I. Penis. Scale bars = 5 mm. Abbreviations: ao, anterior aorta; ct, ctenidium; ctz, compacting zone of the stomach; ddg, duct of the digestive gland; dg, digestive gland; gL, gland

Ultrastructure.—(Fig. 6D) Outermost layer prismatic (≈90 μm), middle layer comarginal crossed-lamellar (≈140 μm), inner layer radial crossed-lamellar (≈32 μm).

External anatomy.—(Fig. 5A–B). Soft tissues comprise approximately 2½ whorls. Mantle cavity spans just under ½ whorl, kidney ¼ whorl, digestive gland and gonad 1¾ whorls. Columellar muscle short, broad, attached to shell at rear of mantle cavity. Foot large, broadly rectangular (L/W ≈ 1–1.3). Body base color yellowish tan, dorsal surfaces of the head, tentacles, siphon, foot mottled with dark grayish black. Head small, with broad, tapering tentacles, black eyes.

Mantle cavity.—Mantle edge smooth. Siphon of medium length (≈⅓ AL), muscular, extending substantially beyond mantle edge. Osphradium greenish, bipectinate, with narrow axis, spanning about ½ mantle cavity length. Ctenidium large, wide, spanning about ¾ mantle cavity length. Hypobranchial gland formed of few, distinct, widely spaced folds.

Alimentary system.—Proboscis smooth, unpigmented, of moderate length when retracted (≈0.6 AL), but long in semiprotracted position (≈1.1 AL; Fig. 5C, D). Proboscis sheath very thin-walled, translucent. Mouth opening forming triangular slit. Buccal mass muscular, large, filling retracted proboscis. Odontophoral cartilages paired, fused anteriorly, spanning ⅔ of buccal mass. Radular ribbon long, 10.9–13.2 mm (0.47–0.52 AL), ≈540 μm wide (≈0.023 AL), triserial (Fig. 6A, B), consisting of 75–80 rows of teeth, posteriormost 5–7 teeth nascent. Rachidian teeth with 3 cusps on central portion of broad, anteriorly arched basal plate. Central cusp slightly longer, narrower than lateral cusps. Lateral teeth with 3 cusps. Outer cusp stouter, nearly twice as long as inner cusp. Intermediate cusp slightly shorter than, immediately adjacent to inner cusp. Salivary glands small (Fig. 5C, D; sg), fused, dorsal to nerve ring, right salivary gland totally covering valve of Leiblein. Salivary ducts pass loosely along both sides of esophagus, becoming embedded in esophageal walls near rear of buccal mass. Valve of Leiblein well defined, large (Fig. 5E; vL), pyriform, without ciliary cone. Gland of Leiblein convoluted anteriorly, tapering posteriorly (Fig. 5C, D; gL), opening without constriction to mid-esophagus, just anterior to, left of crop (Fig. 5C; poe). Esophagus wide, muscular, enlarging posteriorly (Fig. 5C; poe) to form a crop-like structure lined with tall longitudinal folds. Stomach U-shaped, without caecum (Fig. 5F, H). Paired ducts of digestive gland closely spaced (Fig. 5H; ddg). Typhlosoles present (Fig. 5H; tph), poorly defined. Digestive gland clearly divided into 2 lobes. Zone of compaction well pronounced (Fig. 5H; ctz). Rectum terminates with well-defined anal papilla.

Female reproductive system.—Typically buccinoidean. Oviduct opens into medium-sized albumen gland. Ingesting gland single. Capsule gland large, occupies ≈½ of mantle cavity. Bursa copulatrix present, simple, hemispherical.

Male reproductive system.—Seminal vesicle of medium size, highly coiled. Prostate narrow, running along posterior half of mantle cavity wall. Penis dorsoventrally compressed, long (0.8 × mantle cavity length), with smooth walls, long, cylindrical papilla surrounded by deep circular fold around its base (Fig. 5I).

Type locality.—South Georgia Island.

←

of Leiblein; h, heart; ht, cephalic tentacles; ig, intestinal groove; mo, mouth; nep, nephridium; nr, circumoesophageal nerve ring; oe, oesophagus; op, operculum; os, osphradium; p, penis; poe, posterior oesophagus; pr, proboscis; prr, proboscis retractors; rhd, proboscis sheath; s, siphon; sg, salivary gland; st, stomach; t, testes; vL, valve of Leiblein.

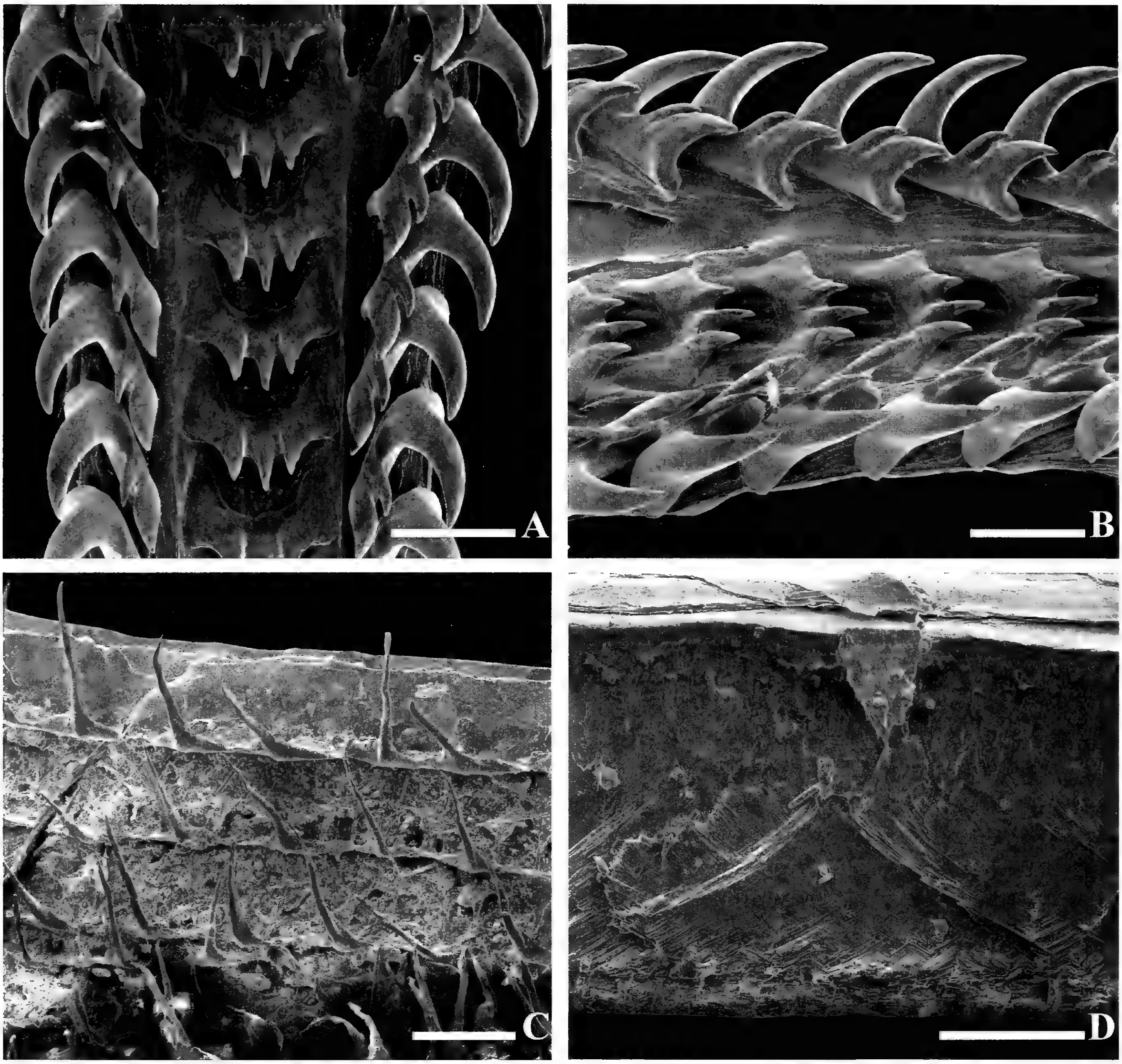

Fig. 6. *Chlanidota* (*Chlanidota*) *densesculpta* (Martens, 1875). A. Dorsal, and B. left lateral (45°) views of the central portion of the radular ribbon taken from animal in Fig. 5. C–D. R/V *Eltanin*, Sta. 1533, South Georgia Island, 54°00′S, 37°27′W, in 3–6 m, USNM 896097. C. Periostracum. D. Shell ultrastructure, fracture surface parallel to growing edge. Scale bar = 200 μm for A–C, 100 μm for D.

Type material.—Holotype, MNH-U 37478 (fig. 4A–C).

Material examined.—Holotype. R/V *Eltanin*: Sta. 1533, South Georgia Island, 54°00′S, 37°27′W, in 3–6 m, 7 Feb 1966, 1 shell, USNM 870722, 6 specimens, USNM 896097. R/V *Islas Orcadas:* Sta. 18, Off South Georgia Island, 54°02′30″S, 37°39′36″W, in 60–71 m, 15 May 1975, 4 specimens, USNM 901650; Sta. 19, Off South Georgia Island, 54°01′42″S, 37°40′00″W, in 46–70 m, 15 May 1975, 10 specimens, USNM 901651 (anatomical descriptions are based on specimens from this lot); Sta. 20, Off South Georgia Island, 54°00′06″S, 37°40′36″W, in 68–80 m, 15 May 1975, 7 specimens, USNM 901652; Sta. 21, Off South Georgia Island, 53°57′30″S, 37°20′42″W, in 27–40 m, 16 May 1975, 1 specimen, USNM 901653; Sta. 95, Off South Georgia Island, 54°11′48″S, 37°41′06″W, in 68–80 m, 9 Jun 1975, 3 specimens, USNM 901654. R/V *Prof. Siedlecki*, Sta. 81, Off South Georgia Island, 54°43′S, 35°13′W, in 300–306 m, 11 Dec 1986, 1 broken shell, USNM 897523.

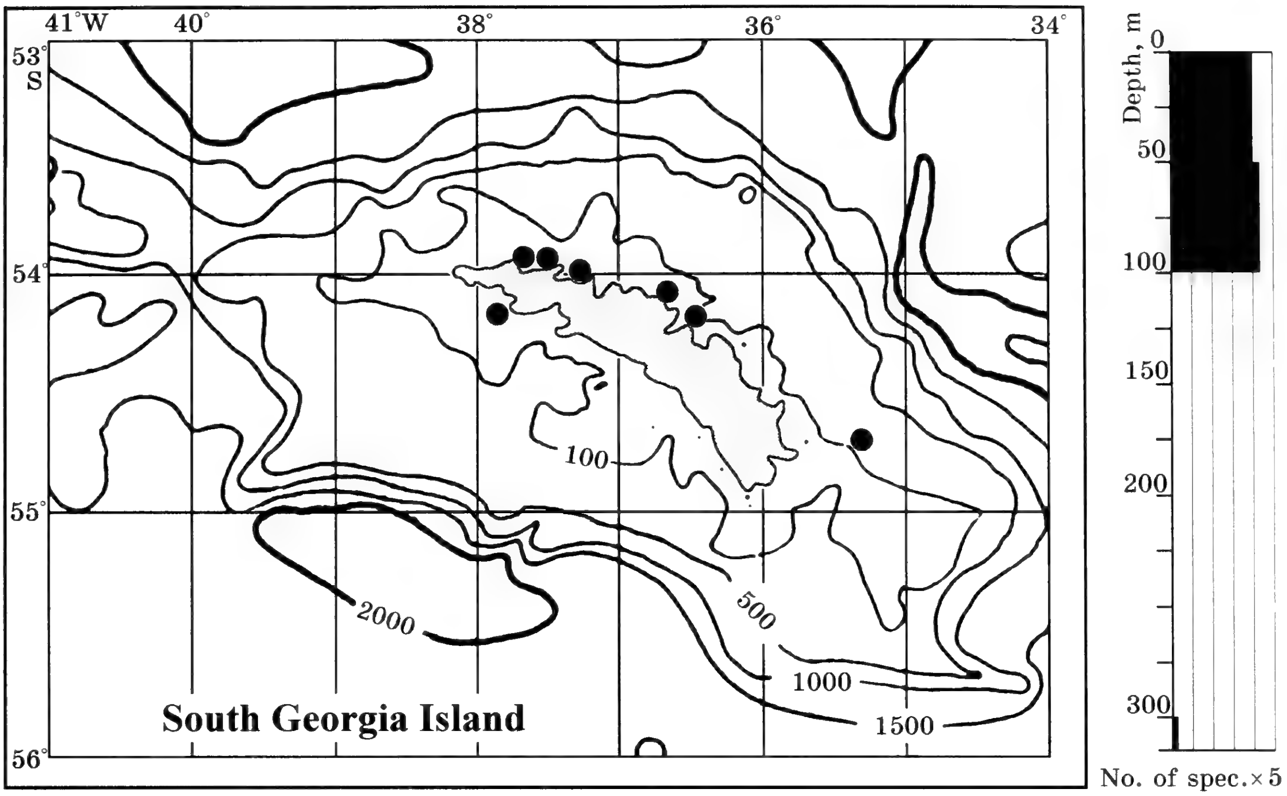

Fig. 7. Geographic distribution and bathymetric range of *Chlanidota* (*Chlanidota*) *densesculpta* (Martens, 1875). The type locality is "South Georgia Island."

South Georgia, Bay of Islands, in 7.5 m, 3 specimens, USNM 252874.

Published records.—R/V *Discovery II*: Sta. 45, 2.7 miles S 85°E of Jason Light, South Georgia, in 238–270 m; Sta. 141, East Cumberland Bay, South Georgia, 200 yards from shore under Mt. Duse, in 17–27 m; Sta. 145, Stromness Harbour, South Georgia, between Grass Island and Tonsberg Point, in 26–35 m; Sta. 1941, Leith Harbour, South Georgia, in 55–22 m; Sta. WS 62, Wilson Harbour, South Georgia, in 26–83 m; Sta. MS 6, East Cumberland Bay, ¼ mile south of Hope Point to 1¼ cables S × E of King Edward Point Light, South Georgia, in 24–30 m; Sta. MS 10, East Cumberland Bay, ¼ mile south of Hope Point to ¼ mile south of Government Flagstaff, South Georgia, in 26–18 m (Powell 1951). SW of Snow Hill Island, 64°36′S, 57°42′W, in 125 m (Strebel 1908). Kerguelen (22–345 m) and Crozet (22–505 m) Islands (Cantera & Arnaud 1984).

Distribution.—All of the specimens that we examined were from South Georgia Island. There have been several published reports of *C. densesculpta* occurring at other localities. According to Powell (1951), Martens (1903) record of *C. densesculpta* from Bouvet Island is *Notoficula bouveti* (Thiele, 1912). Strebel (1908:33) neither discussed nor figured the single specimen of *C. densesculpta* he reported from off the Antarctic Peninsula. Similarly, the recent reports of this species from the Kerguelen (22–345 m) and Crozet (22–505 m) Islands (Cantera & Arnaud 1984:68) lack descriptions or illustrations. Pending confirmation of the identification of these records, we provisionally regard *Chlanidota densesculpta* to be endemic to South Georgia Island (Fig. 7). Live-collected specimens were all taken at depths ranging from 3 to 80 m. The only record outside this range is a single dead and broken specimen (R/V *Prof. Siedlecki* Sta. 81) taken in 300–306 m. Dell (1990) misidentified two lots of the bathyal species *Chlanidota* (*Pfefferia*) *invenusta* (described below) as *C.* (*C.*) *densesculpta*, which led to his incorrect report

Table 4.—*Chlanidota* (*Chlanidota*) *pilosa* Powell, 1951. Shell measurements of holotype. Linear measurements in mm.

Character	Holotype
Shell Length (SL)	25.3
Body Whorl Length (BWL)	23.3
Aperture Length (AL)	21.1
Shell Width (SW)	20.0
BWL/SL	0.92
AL/SL	0.83
SW/SL	0.79
No. spiral cords on:	
Penultimate whorl	21
Body whorl	57

of a very broad bathymetric range (0–1400 m) for the latter species.

Remarks.—This species has a striking conchological resemblance to *Chlanidota* (*Pfefferia*) *palliata* Strebel, which is also endemic to South Georgia Island, but can be discriminated most easily on the basis of its small operculum (18–0.31 AL, vs. 0.67–0.83 AL in *C. palliata*), which lacks the "feathered" posterior edge diagnostic of the subgenus *Pfefferia*. *Chlanidota densesculpta* is readily distinguished from other species of *Chlanidota* s.s. by its extremely fine and indistinct spiral sculpture as well as by the presence of a thick, finely hirsute periostracum.

Skeletal ossicles of holothurians were found in the rectum of one of the specimens dissected.

Chlanidota (*Chlanidota*) *pilosa*
Powell, 1951
Figs. 3, 8; Table 4

Chlanidota pilosa Powell, 1951:139, 194, fig. L73, pl. 8, figs. 29–30; Kaicher 1990: 5807.

Description.—Shell (Fig. 8) small for genus (to 25.5 mm), very thin, translucent, fragile, globose, with very low, rounded spire. Protoconch unknown, early whorls heavily eroded. Teleoconch of evenly rounded, highly convex whorls. Spiral sculpture of numerous fine spiral threads, broader than intervening spaces. Spiral threads sinuated, equal in strength, closely

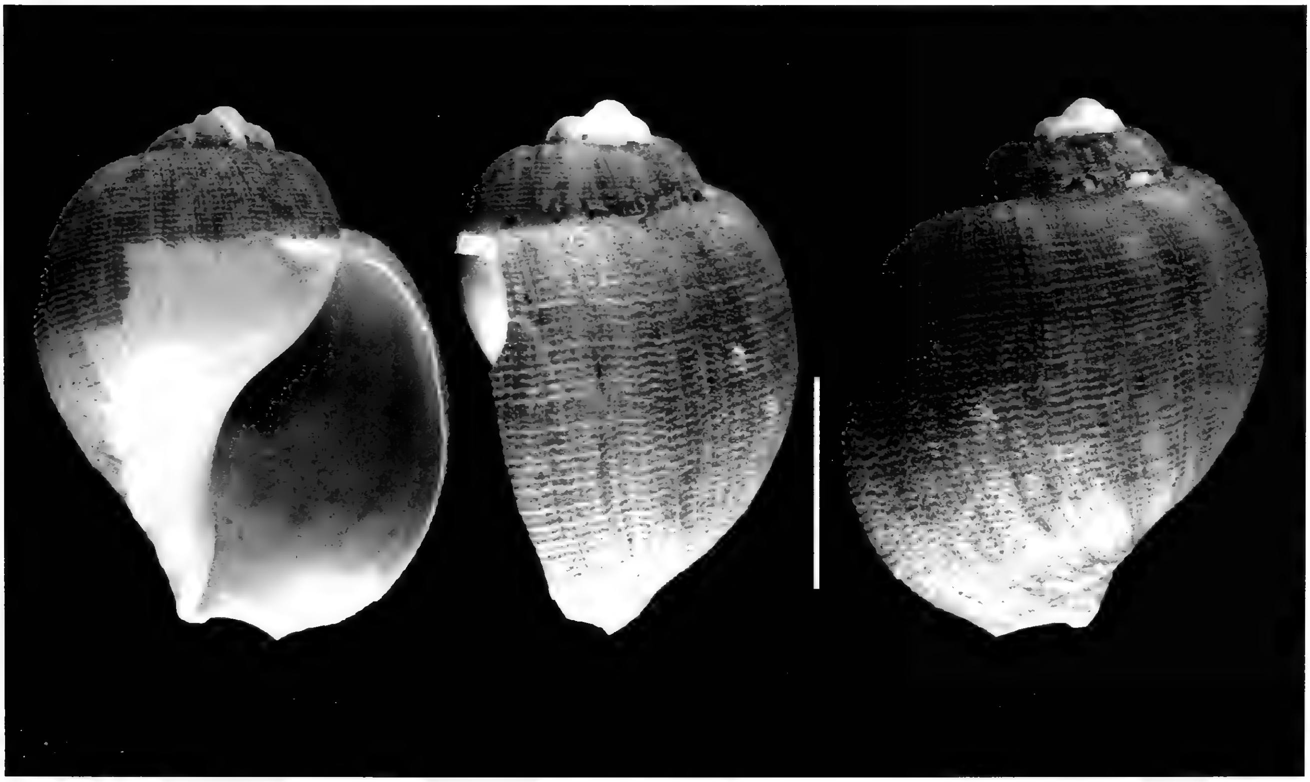

Fig. 8. *Chlanidota* (*Chlanidota*) *pilosa* Powell, 1951. Holotype, BMNH 1961500. R/V *Discovery II*, Sta. 456, 1 mile east of Bouvet Island, in 40–45 m. Scale bar = 1 cm.

Table 5.—*Chlanidota* (*Chlanidota*) *signeyana* (Powell, 1951). Measurements of shell characters. Linear measurements in mm (n = 10, holotype not included).

Character	Mean	σ	Range	Holotype of *C. signeyana*	Holotype of *C. pyriformis*	Holotype of *C. elongata* (from Lamy, 1911)
Shell Length (SL)	29.8	6.7	21.4–42.2	37.4	28.6	30.0
Body Whorl Length (BWL)	24.5	5.1	17.8–33.4	31.9	24.4	26.5
Aperture Length (AL)	19.3	3.5	14.1–25.7	25.3	20.1	20.7
Shell Width (SW)	18.2	3.2	13.5–22.8	23.6	18.6	16.9
Operculum Length (OL)	5.9	1.5	4.5–9.4	6.4	—	—
BWL/SL	0.83	0.02	0.79–0.86	0.86	0.85	0.87
AL/SL	0.65	0.04	0.58–0.70	0.68	0.70	0.69
SW/SL	0.61	0.06	0.54–0.71	0.64	0.65	0.56
OL/AL	0.30	0.04	0.25–0.37	0.27	—	—
No. spiral cords on:						
Penultimate whorl	10.1	2.2	7–14	11	7	7
Body whorl	25.0	6.2	15–35	26	21	21

spaced (2.4–3 per mm), 21 on penultimate whorl, 57 on body whorl. Axial sculpture limited to growth lines. Aperture broadly ovate, deflected from shell axis by 15°. Outer lip very thin, evenly rounded, slightly reflected. Columella <½ AL, weakly concave, with strong siphonal fold. Callus consisting of a thin glaze overlying parietal region and siphonal fasciole. Siphonal notch broad, slightly dorsally recurved, with straight columellar, rounded apertural margins that mark borders of fasciole without forming raised ridge margins. Shell color white, aperture weakly glazed. Periostracum thin, light yellowish-brown, hirsute. Operculum small (0.3 AL), irregularly ovate. Radula is similar to that *C.* (*C.*) *densesculpta* except rachidian cusps are closer together, more broadly triangular, with the central cusp broader and longer than flanking cusps (Dell 1951:fig. L73).

Type locality.—1 mile east of Bouvet Island, in 40–45 m (R/V Discovery II, Sta. 456).

Type material.—Holotype (live collected) BMNH 1961500 (Fig. 8), and paratype (empty shell).

Material examined.—The type material.

Distribution.—Known only from Bouvet Island.

Remarks.—This species is thus far known only from the type material. *Chlanidota pilosa* is similar to low-spired, rotund specimens of *C. densesculpta* (e.g., Fig. 4E), but differs in having fewer and more pronounced spiral riblets on the penultimate and body whorls, and by having a fasciole that lacks a ridge along its margin. These two species are also widely separated in their distribution. *Chlanidota pilosa* differs from *C. vestita* in having a lower spire, as well as more numerous and finer spiral threads.

Chlanidota (*Chlanidota*) *signeyana* Powell, 1951
Figs. 9–11; Table 5

Chlanidota signeyana Powell, 1951:141, fig. F, 194, fig L74, 196, fig. N129, pl. 8, figs. 34–35; Carcelles, 1953:191, pl. 3, fig. 59; Powell, 1960:150; Kaicher, 1990: 5801; Dell, 1990:177, fig. 307.

Cominella (*Chlanidota*) *vestita* var. *elongata* Lamy, 1910:319; Lamy, 1911:6, pl. 1 fig. 6.

Chlanidota elongata Powell, 1951:140, 194, fig. L76; Carcelles, 1953:191, pl. 3, fig. 56; Powell, 1960:150; Cernohorsky, 1977:110; Horikoshi et al., 1979: 22, fig.

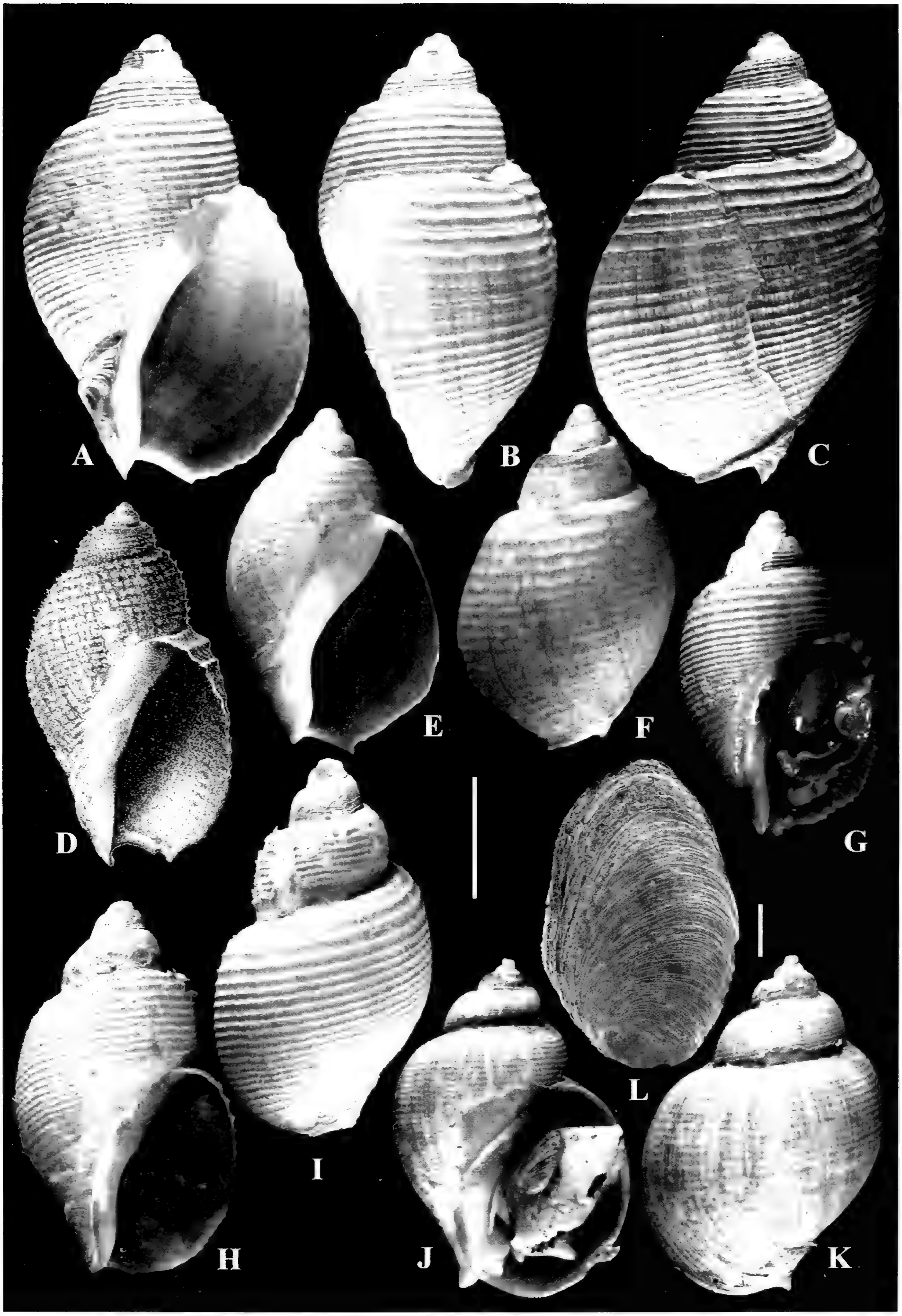

Fig. 9. *Chlanidota* (*Chlanidota*) *signeyana* Powell, 1951. A–C. Holotype, *Chlanidota signeyana*, BMNH 1961512, R/V *Discovery II*, Sta. 167, Off Signy Island, South Orkney Islands, 60°50′30″S, 46°15′00″W, in 244–344 m. D. Holotype, *Cominella* (*Chlanidota*) *vestita* var. *elongata* Lamy, 1910 (from Lamy, 1911), King George Island, South Shetland Islands, in 420 m. E, F. Holotype, *Chlanidota pyriformis* Dell, 1990, USNM 613075,

8; Hain, 1989:71, Taf. V/4, Taf. XXIII/1; Numanami, 1996: 160–162, figs. 106–107.

Chlanidota lamyi Dell, 1990:182, fig. 310, new name for *Cominella* (*Chlanidota*) *elongata* Lamy, 1910, not *Cominella elongata* Dunker, 1857.

Chlanidota pyriformis Dell, 1990:182, fig. 309.

Chlanidota cf. *lamyi* Dell, 1990:182, fig. 315.

Description.—Shell (Fig. 9) large for genus (to 42.6 mm), thin, fragile, elongate to ovate in outline, with medium to high, rounded to turreted spire. Protoconch unknown, early whorls heavily eroded. Teleoconch of up to 5+ evenly-rounded convex whorls, deeply eroded where periostracum damaged or missing. Suture deeply impressed, sharply abutting. Spiral sculpture typically of distinct, sharp, narrow cords (7–14 on penultimate whorl, 15–35 on body whorl) equal or subequal in prominence, that may be reduced or nearly absent in some specimens (Fig. 9F, K). In specimens with pronounced cords (Fig. 9H–I), including the holotype (Fig. 9A–C), 4–5 adapical cords on body and penultimate whorls usually more widely spaced, giving the illusion that they are more pronounced. Spaces between cords equal to cord width on early whorls, at least twice cord width on body whorl. Axial sculpture limited to fine, weakly recurved, prosocline growth lines. Aperture elongate to broadly ovate, deflected from shell axis by 14–17°. Outer lip thin, evenly rounded, fragile. Columella 1/3–1/2 AL, weakly convex, with strong siphonal fold. Callus of thin, silver-edged or thick, brownish glaze overlying parietal region, siphonal fasciole. Siphonal notch broad, dorsally recurved, with straight columellar and rounded apertural margins that form borders of fasciole. Ridge margin of fasciole extends from apertural margin of siphonal notch. Shell color chalky-white to brownish or orange-tan. Aperture weakly glazed. Periostracum (Fig. 10E) thin to moderately thick, orange-tan to greenish-tan, smooth in weakly sculptured specimens, forming low, axial lamellae with short, hairlike projections on intersections with spiral cords of strongly sculptured specimens. Operculum (Fig. 9L) small (0.25–0.37 AL), broadly ovate, weakly coiled, with terminal nucleus rotated nearly perpendicular to long axis. Operculum may be thin, yellowish, translucent, but usually opaque, brownish to dark brown. Attachment area oval, spanning about ⅘ of inner surface, posterior and left margins thickened, abraded.

Ultrastructure.—(Fig. 10F) Outermost layer prismatic (≈38 μm), middle layer comarginal crossed-lamellar (≈60 μm), inner layer radial crossed-lamellar (≈20 μm).

Anatomy.—Gross anatomical features of *C. signeyana* very similar to those of *C. densesculpta*, but left and right salivary glands of *C. signeyana* separate, not fused. Radular ribbon long, 9.6–12.2 mm (0.48–0.55 AL), 790–910 μm wide (0.04 AL), triserial (Fig. 10A–D), consisting of 65–75 rows of teeth, posteriormost 5–6 rows nascent. Rachidian teeth with arched base, straight lateral sides, 3 large, robust cusps of equal length. Lateral teeth with 3 cusps, outer cusp longest, intermediate cusp shortest, situated close to inner cusp.

Type locality.—[*Chlanidota signeyana*] Off Signy Island, South Orkneys, 60°50′30″S, 46°15′00″W, in 244–344 m

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R/V *Westwind*, Sta. W-10, off South Shetland Islands, 63°00′S, 60°32′W, in 159 m. G. R/V *Eltanin*, Sta. 997, Gibbs Island, Bransfield Strait, South Shetland Islands, in 769 m, USNM 881971. H–I. R/V *Eltanin*, Sta. 426, Bransfield Strait, South Shetland Islands, in 809–1116 m, USNM 886204. J–K. R/V *Islas Orcadas*, Sta. 55, Saunders Island, South Sandwich Islands, in 64–88 m, USNM 901664. L. Operculum of specimen in figs. J, K. Scale bar = 1 cm for A–K, 1 mm for L.

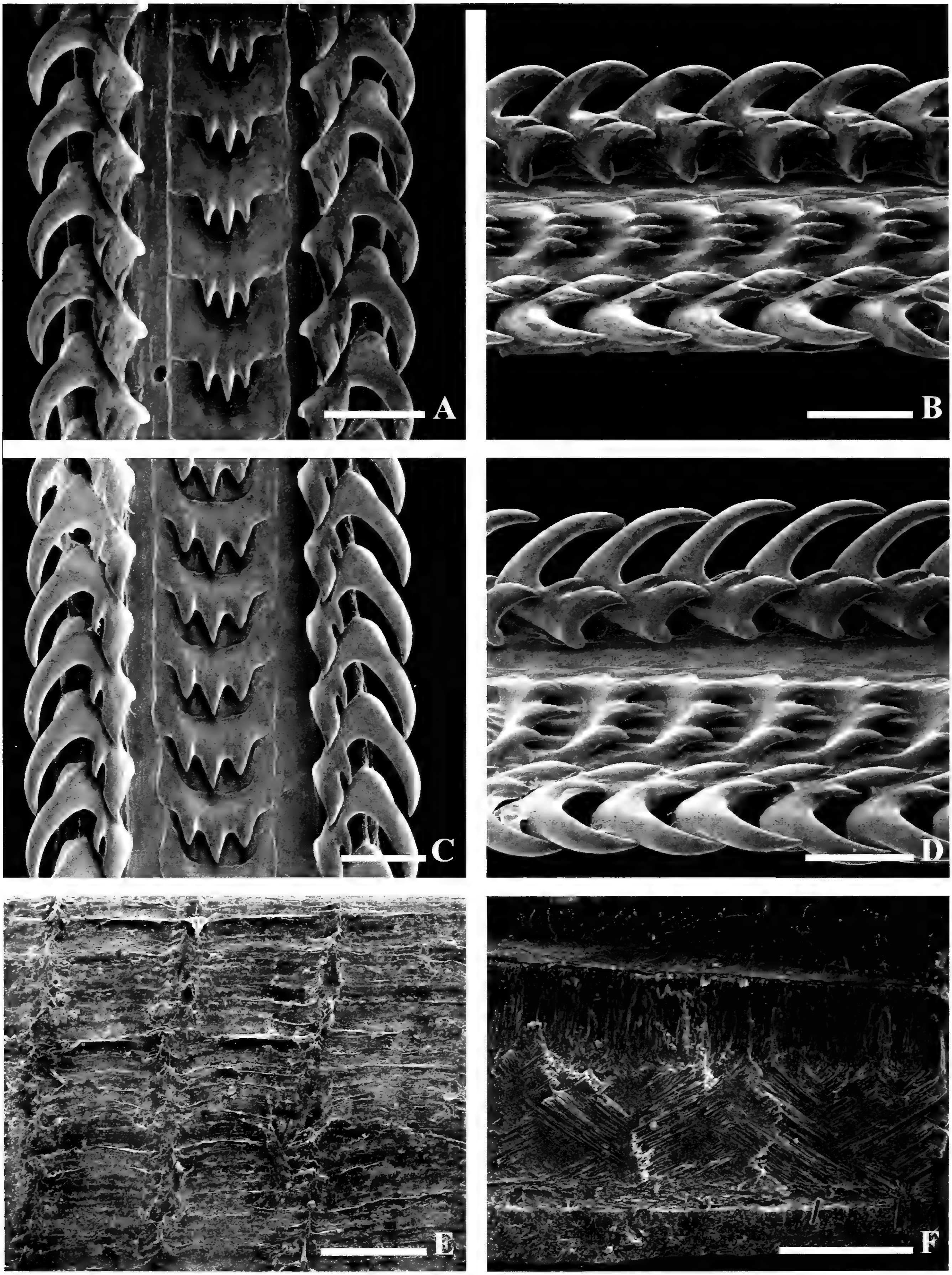

Fig. 10. *Chlanidota* (*Chlanidota*) *signeyana* Powell, 1951. A. Dorsal and B. left lateral (45°) views of the central portion of the radular ribbon taken from the animal in Fig. 9J, K. C. Dorsal and D. left lateral (45°) views of the central portion of the radular ribbon taken from the animal in fig. 9H, I. E. Periostracum and F. shell ultrastructure of the same specimen. Scale bars = 200 μm for A–D, 500 μm for E, 50 μm for F.

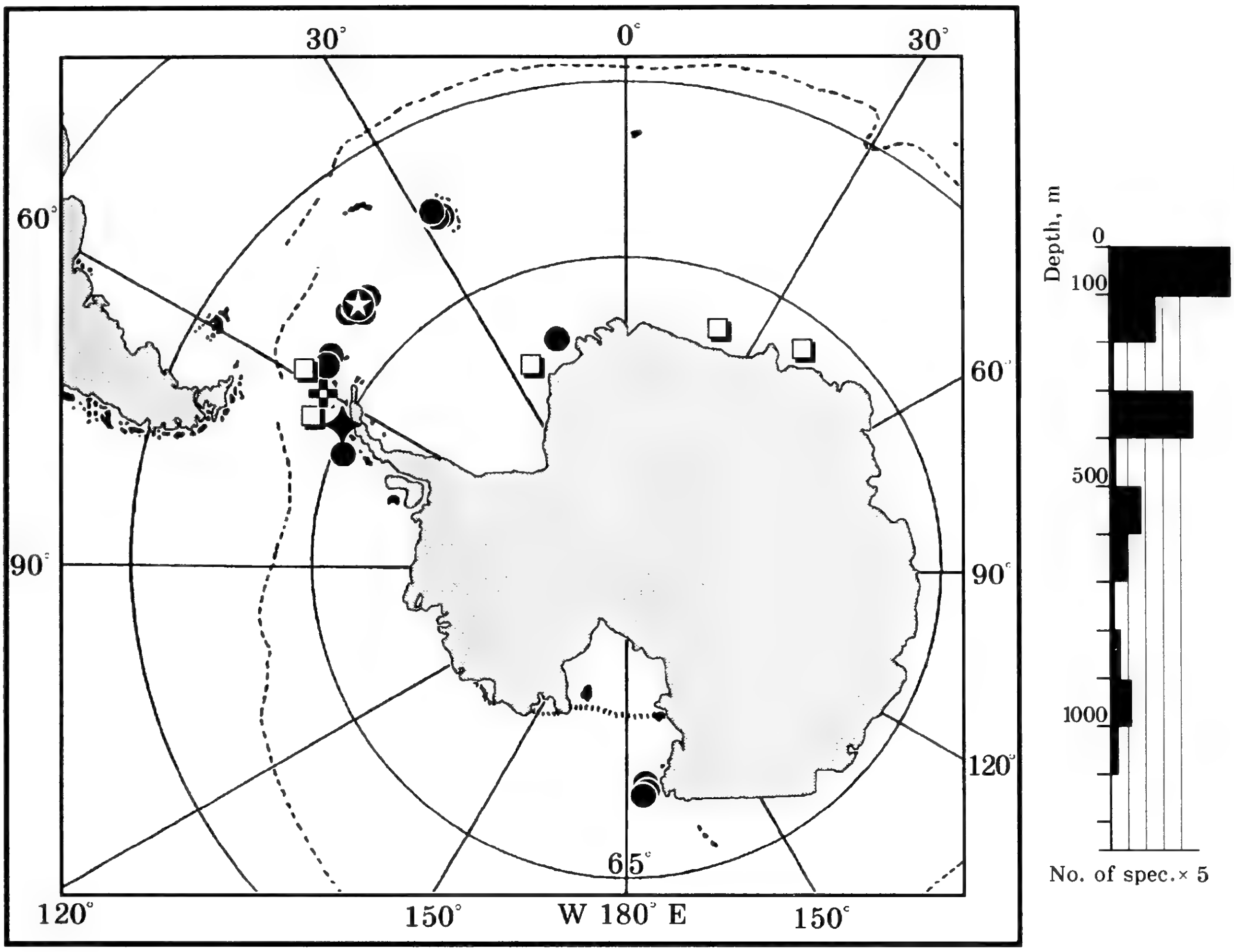

Fig. 11. Geographic distribution and bathymetric range of *Chlanidota* (*Chlanidota*) *signeyana* Powell, 1951. ✪ = type locality, *Chlanidota signeyana*; + = type locality, *Chlanidota lamyi*; ♦ = type locality, *Chlanidota pyriformis*. ● = examined material; □ = published records.

(R/V *Discovery II*, Sta. 167); [*Cominella* (*Chlanidota*) *vestita* var. *elongata* Lamy, 1910] King George Island, South Shetlands, in 420 m; [*Chlanidota pyriformis* Dell, 1990] Off South Shetland Islands, 63°00′S, 60°32′W, in 26 m (R/V *Westwind*: Sta. W.10).

Type material.—[*Chlanidota signeyana*] Holotype, BMNH 1961512 (fig. 9A–C), and 2 paratypes; [*Cominella* (*Chlanidota*) *vestita* var. *elongata* Lamy, 1910] The holotype (Fig. 9D) was not found in MNHN; [*Chlanidota pyriformis* Dell, 1990] Holotype, USNM 613075 (Fig. 9E–F) paratypes 1–6, USNM 860181, Paratype 7, MF. 47204.

Material examined.—R/V *Eltanin*: Sta. 426, South Shetland Islands, Bransfield Strait, 62°27′S, 57°58′W, in 809-1116 m, 5 Jan 1963, 3 shell fragments, USNM 870290, 7 shells or fragments, USNM 870291, 4 specimens, USNM 886204; Sta. 428, South Shetland Islands, Bransfield Strait, 62°41′S, 57°51′W, in 662–1120 m, 5 Jan 1963, 1 shell fragment, USNM 870293; Sta. 432, South Shetland Islands, 62°52′S, 59°27′W, in 884–935 m, 7 Jan 1963, fragments of 2 shells, USNM 870303; Sta. 439, Antarctic Peninsula, 63°51′S, 62°38′W, in 128–165 m, 9 Jan 1963, 1 shell, USNM 870313, 1 specimen, USNM 881919; Sta. 444, South Shetland Islands, 62°56′S, 62°02′W, in 750–732 m, 11 Jan 1963, 1 specimen, USNM 881923; Sta. 538, South Orkney Islands, Bransfield Strait, 60°30′S, 47°34′W, in 616–662 m, 6 Mar 1963, fragments of 2 shells, USNM 870330; Sta. 993, South Shetland Islands, Elephant Island, 61°25′S, 56°30′W, in 300 m, 13 Mar 1964, 1 specimen, USNM 881970; Sta. 997, South Shetland Islands, Bransfield Strait, Gibbs Island, 61°44.18′S, 55°56.06′W, in 769 m, 14 Mar 1964, 1 specimen, USNM 881971; Sta. 1079, Scotia Ridge, 61°26′S, 41°55′W, in 593–598 m, 13 Apr 1964, fragments of 3 shells, USNM 870627, 2 specimens, USNM 881983; Sta. 1084, Scotia Ridge, 60°22′S, 46°50′W, in 298–403 m, 15 Apr 1964, 3 shells, USNM 870641, 7 shells and fragments, USNM 870642, 1 specimen, USNM 881988; Sta. 1997, Ross Sea, 72°00′S, 172°28′E, in 530–549 m, 2 shells, USNM 898205; Sta. 2124, Ross Sea, 71°38′S, 172°00′E, in 606–622 m, 1 shell, USNM 898202; Sta. 2127, Ross Sea, 71°23′S, 171°36′E, in 515–521 m, 1 shell, USNM 898040.

R/V *Eastwind*: Sta. EW66-009, Palmer Peninsula 62°43.1′S, 62°17.5′W, in 561 m, 31 Jan 1966, 1 specimen, USNM 678473; EW66-012, Palmer Peninsula 63°23′S, 60°51′W, in 405 m, 3 Feb 1966, 2 specimens, USNM 678475; EW66-021, off South Orkney Islands, 60°21′S, 45°55′W, in 102 m, 9 Feb 1966, 1 specimen, USNM 678396; EW66-022, off South Orkney Islands, 60°26.5′S, 45°53.3′W, in 168 m, 9 Feb 1966, 1 specimen, USNM 678476; EW66-029, off South Orkney Islands, 61°06′S, 44°57′W, in 290 m, 15 Feb 1966, 1 specimen, USNM 678398; EW66-036, off Elephant Island, 61°16′S, 54°45′W, in 300 m, 17 Feb 1966, 2 shells, USNM 678480; off beach wrack, Collins Pt., Deception Island, 4 Jan 1966, 4 specimens, USNM 678378.

R/V *Hero*: Cruise 691, Sta. 23, off Antarctic Peninsula, Palmer Archipelago, Brabant Island, 64°12.06′S, 62°39.36′W, in 93–95 m, 9 Feb 1969, 1 specimen, USNM 896260; Cruise 691, Sta. 31, South Shetland Islands, Deception Island, 62°58.25′S, 60°45.40′W, in 37–51 m, 13 Feb 1969, 7 specimens, USNM 897557; Cruise 721, Sta. 751, off Antarctic Peninsula, 64°46′28″S, 64°04′20″W, in 33 m, 31 Dec 1971, 1 shell, USNM 901659; Cruise 721, Sta. 765, off Antarctic Peninsula, 64°47.3′S 64°07.4′W, in 55 m, 3 Jan 1972, 1 shell, USNM 901671; Cruise 721, Sta. 1058, off Antartic Peninsula, 62°19.0′S, 59°11.4′W, in 44 m, 19 Dec 1971, 1 shell, USNM 901657; Cruise 731, Sta. 1806, 64°46′31″S, 64°04′52″W, in 47–75 m, 18 Feb 1973, 1 specimen, USNM 901686; Cruise 824, Sta. 32-1, Antarctic Peninsula, Anversa Island, 64°37′S, 62°50.48′W, in 640–670 m, 23 Mar 1982, 1 shell, USNM 881583; Cruise 824, Sta. 7-1, Antarctic Peninsula, Adelaide Island, 66°40.40′S, 67°31.23′W, in 510–730 m, 17 Mar 1982, 1 specimen, USNM 896309; Sta. 32-1, Antarctic Peninsula, 64°37′S, 62°50.80′W, in 640–670 m, 25 Mar 1982, 1 shell, USNM 901658.

R/V *Islas Orcadas*: Sta. 39, South Sandwich Islands, 57°01.2′S, 26°44.3′W, in 97–100 m, 23 May 1975, 1 shell, USNM 901663; Sta. 40, South Sandwich Islands, Kadlemas Island, 57°06.8′S, 26°43.36′W, in 15–33 m, 23 May 1975, 1 specimen, USNM 901660; Sta. 42, South Sandwich Islands, Kadlemas Island, 57°06.8′S, 26°43.6′W, in 22–44 m, 24 May 1975, 12 specimens, USNM 901669; Sta. 46, South Sandwich Islands, Kadlemas Island, 57°06.2′S, 26°44.5′W, in 26–60 m, 25 May 1975, 2 specimens, USNM 901665; Sta. 48, South Sandwich Islands, Kadlemas Island, 57°06.3′S, 26°44.2′W, in 27–62 m, 23 May 1975, 4 specimens, USNM 901670; Sta. 55, South Sandwich Islands, Saunders Island, 57°47.12′S, 26°22.30′W, in 64–88 m, 27 May 1975, 1 specimen, USNM 901664; Sta. 57, South Sandwich Islands, 27 May 1975, 5 specimens, USNM 901656; Sta. 80, South Sandwich Islands, Zavodovski Island, 56°20.0′S, 27°38.8′W, in 351–393 m, 4 Jun 1975, 13 specimens, USNM 901667; Sta. 110, Inaccessible Island, 60°28.1′S, 46°27.2′W, in 115–132 m, 16 Feb 1976, 2 specimens, USNM 901666; Sta. 115, Inaccessible Island, 60°32.4′S, 47°22.7′W, in 567–671 m, 17 Feb 1976, 2 shells, USNM 901655; Sta. 118, off South Orkney Islands, 62°01.5′S, 43°06.2′W, in 759–857 m, 20 Feb 1976, 1 specimen, USNM 901661; Sta. 121, off South Orkney Islands, 61°47.00′S, 43°40.00′W, in 616–642 m, 21 Feb 1976, 1 specimen, USNM 901662.

R/V *Westwind*: Sta. W-10, off South Shetland Islands, 63°00′S, 60°32′W, in 159 m, 26 Jan 1958, 6 shells, paratypes of *C. pyriformis* Dell, 1991. USNM 860181, 4 shells, USNM 890897.

R/V *Polar Duke*: off Palmer Peninsula, 65°36′S, 67°21′W, in 200 m, 6 Sep 1985, 1 shell, USNM 846179.

R/V *Deepfreeze IV*: Sta. TD2-ED 14, off Cape Norwegia, Weddel Sea, 71°50′S, 15°50′W, 1028–1122 m, 18 Jan 1959, 1 shell and fragments, USNM 638862.

Published records.–R/V *Discovery II*, Sta. 162, Off Signy Island, South Orkneys 60°48′00″S, 46°08′00″W, in 320 m; Sta. 170, off Cape Bowles, Clarence Is., 61°25′30″S, 60°28′00″W, in 342 m; Sta. 175, Bransfield Strait, South Shetlands, 63°17′20″S, 59°48′15″W, in 200 m; Sta. 1952, between Penguin Island and Lion's Rump, King George I, South Shetlands, in 367–383 m; Sta. 1957, off south side of Clarence Island, South Shetlands, in 785–810 m (Powell, 1951). R/V *Eltanin*: Sta. 426, off South Shetland Islands, 62°27′S, 57°58′W, in 1116–809 m; Sta. 439, west of Antarctic Peninsula, 63°51′S, 62°38′W, in 128–165 m; Sta. 1084, north of South Orkney Islands, 60°22′S, 46°50′W, in 298–403 m, R/V *Hero*: Sta. 23, Antarctic Peninsula, 64°12.1′S, 62°39.6′W, in 93–95 m; Arthur Harbor, Anvers Island, Antarctic Peninsula, 30 m (Dell, 1990:180). PS ANT III/3: Sta. 345, Weddel Sea, 73°27′S, 21°37′W, in 617 m (Hain, 1989). Syowa Sta., Enderby Land, in 98 m (Horikoshi et al., 1979). JARE Sta. 9, Breid Bay, Queen Maud Land, 70°13.7′S, 24°25.7′E, in 276–289 m, Sta. 10, 25 (Numanami, 1996); NZOI: Sta. A463, 72°20′S, 174°50′E, in 460 m; Sta. A464, 72°20′S, 174°00′E, in 376 m (Dell, 1990, as *C.* cf. *lamyi*).

Distribution.—South Orkneys, South Shetlands, Antarctic Peninsula, and Queen Maud Land, and the eastern margins of the Ross Sea. Living specimens were taken in 30–1116 m (Fig. 11).

We include records for this species reported from the area of Queen Maud Land (as *C. elongata*). Figured specimens from this region (Numanami, 1996:fig. 106A–B, E–F). appear to have weaker, more numerous spiral cords. One specimen from Syowa station has rachidian teeth with narrower cusps and additional serrations, features that had not previously been observed in specimens of *C. signeyana*. Powell (1951:142, fig. L78) reported and illustrated similar additional serrations in a specimen of *Chlanidota* (*Pfefferia*) *elata*.

We have examined and also include records from the eastern margin of the Ross Sea, which had been listed as *Chlanidota* cf. *lamyi* by Dell (1990:310). Dell (1990) noted that these broken and worn specimens closely resemble *C. signeyana* (as *C. lamyi*) from the South Shetland Islands, but differed only in having more numerous spiral cords on their body whorl.

Remarks.—Lamy (1910) was the first to recognize this species, proposing the taxon *Cominella* (*Chlanidota*) *vestita* var. *elongata*, without realizing that the name was preoccupied by *Cominella elongata* Dunker, 1857. Powell (1951:141) considered *Chlanidota elongata* to be restricted to the South Shetland Islands and erected the taxon *C. signeyana* based on material from the South Orkney Islands. He recognized that *C. signeyana* was closely related to *C. elongata*, but distinguished it as being "constantly broader and of ovate rather than cylindrical outline." Cernohorsky (1977:110) noted that *Cominella* (*Chlanidota*) *vestita* var. *elongata* Lamy, 1910 was preoccupied, but questioned whether this taxon was distinct from *C. vestita*. After examining a broader range of specimens than were available to Powell, Dell (1990:180) noted that both ovate and cylindrical phenotypes co-occurred in South Shetland and South Orkney samples, but that specimens could be sorted into one or the other phenotype on the basis of the ratio of shell width (SW) to shell height (SH). He regarded *Chlanidota signeyana* to be limited to the ovate

Table 6.—*Chlanidota (Chlanidota) paucispiralis* Powell, 1951. Measurements of shell characters. Linear measurements in mm (n = 10, holotype not included).

Character	Mean	σ	Range	Holotype
Shell Length (SL)	29.8	3.0	21.9–31.7	21.9
Body Whorl Length (BWL)	25.2	2.4	19.2–27.2	19.2
Aperture Length (AL)	19.9	1.8	15.8–21.9	15.8
Shell Width (SW)	19.5	2.1	14.4–21.7	14.4
Operculum length (OL)	4.5	0.7	4.0–5.0	4.0
BWL/SL	0.85	0.01	0.84–0.88	0.88
AL/SL	0.67	0.03	0.63–0.72	0.72
SW/SL	0.65	0.02	0.62–0.68	0.66
OL/AL	0.27	0.02	0.25–0.28	0.25
No. spiral cords on:				
Penultimate whorl	4.4	0.5	4–5	4
Body whorl	10.6	1.6	8–13	10

phenotype with SW/SH ratios ranging from 0.60 to 0.66 and proposed the new name *Chlanidota lamyi* (for *Cominella elongata* Lamy, 1910, non Dunker, 1857) for the elongate phenotype, with SW/SH ratios between 0.55 and 0.60. He did, however, recognize the possibility that "these two forms are but extremes of the same species."

Dell (1990) also described *C. pyriformis* based on a single lot (11 specimens) collected off the South Shetland Islands, which he regarded to be a morphologically consistent shallow-water form allied to both *C. signeyana* and *C. lamyi*, but distinguished by its tapering, conical spire.

We examined and measured a large series of specimens from throughout the ranges of the three nominal species, but were unable to differentiate between them in any reproducible manner. Larger samples from several stations (e.g., USNM 901669, USNM 897557, USNM 860181) revealed that each population spans the range of morphologies of at least two, and sometimes all three of these nominal species. *Chlanidota signeyana* is highly variable in shell outline and spiral sculpture, and encompasses the phenotypes of *Chlanidota lamyi* and *C. pyriformis*.

There does appear to be a clinal gradient in shell shape, with northern specimens tending to be more inflated, while populations from the southern portion of the species' range, including the Antarctic mainland, have a higher proportion of narrower and more cylindrical shells. Numanami (1996:146) recognized a similar gradient in shell morphology in the taxon *Neobuccinum eatoni*, noting that specimens from the Kerguelen and South Shetland Islands tended to be more elongated, while the samples from Enderby Land tended to be more inflated and shorter spired. However, his large sample (n = 98) from Enderby Land showed a wide variability in shell form, and included examples from the entire range of variation for the species.

Chlanidota signeyana is most similar to *C. (C.) paucispiralis* Powell, 1951, but differs in having more numerous and weaker spiral cords. Moreover, *C. (C.) signeyana* has not been recorded off South Georgia, while *C. (C.) paucispiralis* is endemic to South Georgia Island.

Chlanidota (Chlanidota) paucispiralis Powell, 1951

Figs. 12, 13, 14, 15; Table 6

Chlanidota paucispiralis Powell, 1951:141, 194, fig. L77, pl. 8, figs. 36–37; Carcelles, 1953:191, pl. 3, fig. 57; Powell, 1960:150; Kaicher, 1990:5806; Dell, 1990:183–4, fig. 308.

Description—Shell (Fig. 12) large for genus (to 40.3 mm), thin, strong, ovate to elongate-ovate in outline, with moderately high, conical spire. Protoconch unknown, early whorls heavily eroded. Teleoconch of up to 5½ evenly-rounded convex whorls. Suture strongly impressed, forming very narrow channel between adapical spiral cord and previous whorl. Spiral sculpture of narrow, sharp, widely spaced cords, 4–5 on penultimate whorl, 8–13 on body whorl. Space between cords wide, evenly concave, with 0–8 very fine spiral threads. Two adapical cords form narrowly tabulate shoulder. Axial sculpture of fine, closely spaced growth lines. Aperture ovate, deflected from shell axis by 9–15°. Outer lip thin, evenly rounded, with serrated edge formed by spiral cords. Columella <½ AL, weakly concave, with pronounced siphonal fold. Parietal callus narrow, thick, overlying spiral cords. Siphonal notch dorsally recurved, with straight columellar, rounded apertural margins that define limits of fasciole. Apertural margin of siphonal notch dorsally deflected, giving rise to low, sharp keel that forms "ridge margin" of fasciole. Shell color chalky white, aperture thinly glazed, occasionally with margins of glaze discolored to gray or golden tan. Periostracum (Fig. 13C, D) thin, smooth, yellowish-tan, sometimes consisting of closely adjacent, blade-like lamellae, which overlay spiral sculpture without giving rise to hair-like projections. Operculum (Fig. 12J) small (0.25–0.28 × AL), broadly ovate, weakly coiled, with laterally terminal nucleus (usually abraded) rotated nearly perpendicular to long axis. Attachment area nearly circular, spanning ⅔ of inner surface, posterior and left margins thickened, glazed.

Ultrastructure.—(Fig. 13D) Outermost layer prismatic (≈90 μm), middle layer comarginal crossed-lamellar (≈235 μm), inner layer radial crossed-lamellar (≈55 μm).

Anatomical features of *C.* (*C.*) *paucispiralis* are very similar to those of *C.* (*C.*) *densesculpta*. Only a single female specimen (SL = 27.7 mm) was available for dissection.

External anatomy.—Soft tissues comprise ≈3½ whorls. Mantle cavity just over ½ whorl, kidney ¼ whorl, digestive gland 2¼ whorls. Columellar muscle short, broad, attaching to shell at rear of mantle cavity. Foot small, rectangular (L/W ≈ 1.4), with long (0.2 × foot length) medial, ventral pedal gland. Base color yellowish tan, mottled with patches of grayish black on dorsal surfaces of siphon, tentacles, foot. Head small, with thin cylindrical tentacles, large black eyes. Siphon long, free, muscular.

Alimentary system.—Radular ribbon ≈ 9.0 mm long (0.51 AL), 830 μm wide (0.05 AL), triserial (Fig. 13A–B), of ≈70 rows of teeth, of which 5–7 are nascent. Rachidian teeth with arched base, straight lateral sides, 3 large, robust cusps, central cusp slightly longer that lateral cusps. Lateral teeth with 3 cusps, outer cusp longest and, intermediate cusp shortest, adjacent to inner cusp. Anterior foregut very similar to that of its congeners. Stomach (Fig. 14) differs in having very short caecum, which may be homologous to caecum (posterior mixing area) of Buccinidae.

Type locality.—South Georgia, 53°52′30″S, 36°08′00″W, in 160 m (R/V *Discovery II*, Sta. 159).

Type material.—Holotype, BMNH 1961513 (fig. 12A–C), and 2 paratypes, BMNH 1961513.

Material examined.—Holotype. R/V *Islas Orcadas*: Sta. 8, off South Georgia Island, 53°35′48″S, 37°35′12″W, in 254–366 m, 11 May 1975, 1 shell, USNM 881743; Sta. 10, off South Georgia Island, 53°47′48″S, 37°26′42″W, in 165–234 m, 12 May 1975, 1 shell, USNM 881745; Sta. 12, off South Georgia Island, 53°38′12″S, 37°54′42″W, in 130–137 m, 13 May 1975, 4 shells, USNM 881708; Sta. 13, off South Georgia Island, 53°44′12″S, 37°59′30″W, in 128–137 m, 13 May 1975, 5 shells + fragments, USNM 901672; Sta. 14, off South Georgia Island, 53°41′48″S, 37°57′12″W, in 144–150 m, 14 May 1975, 1 shell, USNM

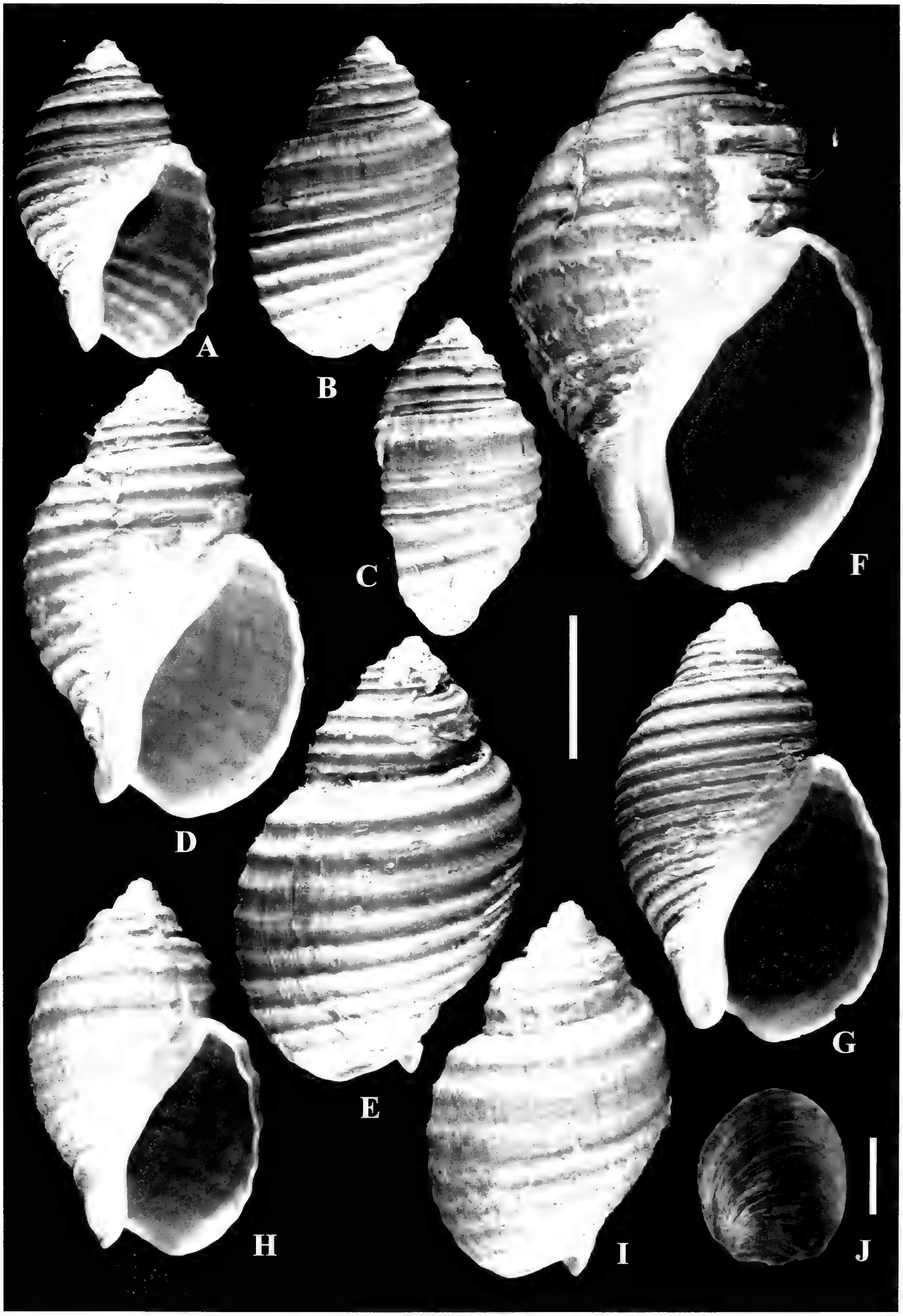

Fig. 12. *Chlanidota* (*Chlanidota*) *paucispiralis* Powell, 1951. A–C. Holotype, BMNH 1961513, R/V *Discovery II*, Sta. 159, South Georgia, 53°52′30″S, 36°08′00″W, in 160 m. D, E. R/V *Prof. Siedlacki*, Sta. 105, South Georgia, 53°40′S, 36°48′W, in 161–192 m, USNM 897515. F. R/V *Prof. Siedlacki*, Sta. 20, 53°58′S, 38°42′W, in 189–200 m, USNM 897583. G. R/V *Prof. Siedlacki*, Sta. 16, Off South Georgia Island, 53°44′S,

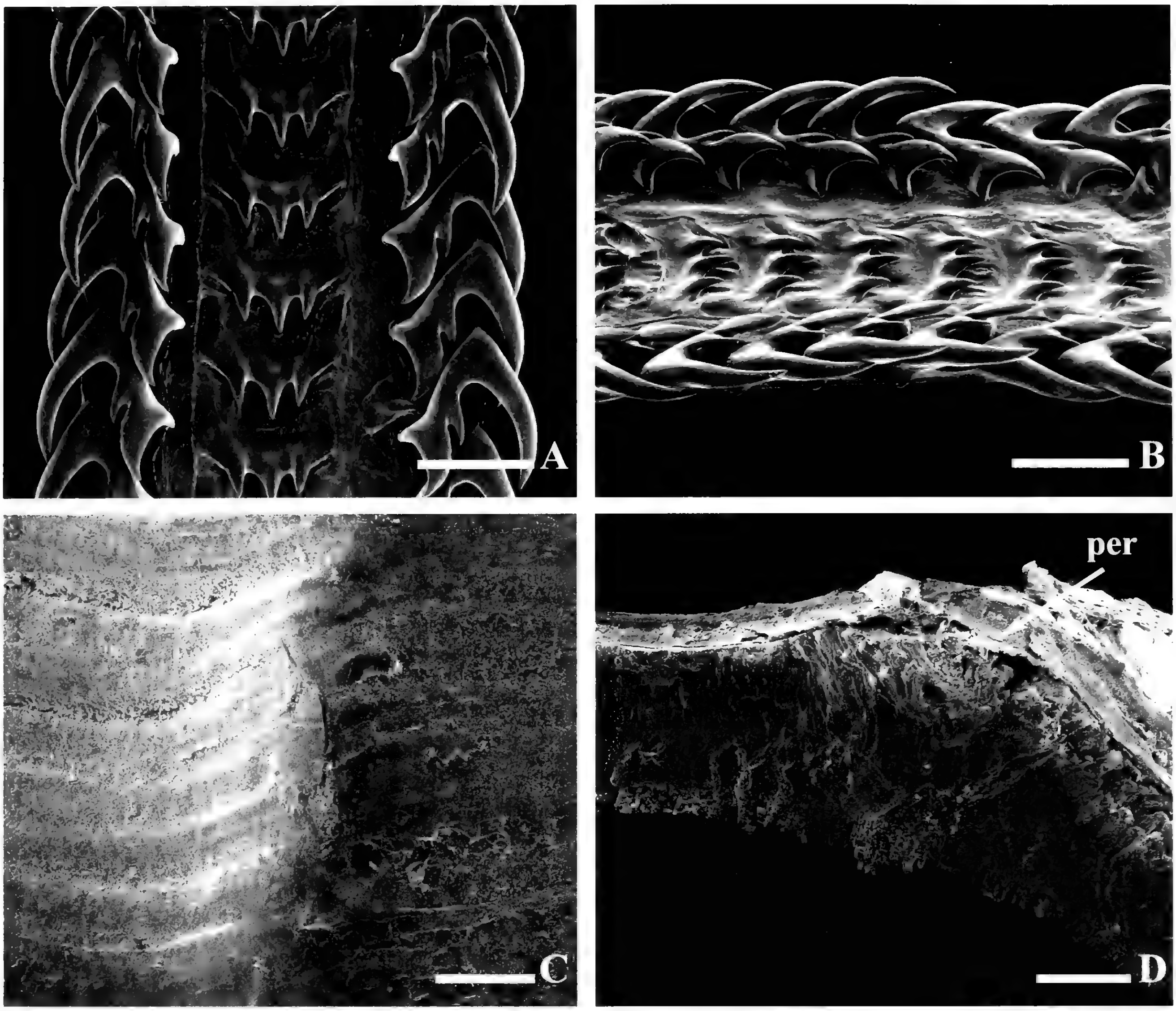

Fig. 13. *Chlanidota* (*Chlanidota*) *paucispiralis* Powell, 1951. A. Dorsal and B. left lateral (45°) views of the central portion of the radular ribbon taken from animal in fig. 12H, I. C. Periostracum and D. shell ultrastructure. R/V *Prof. Siedlacki*, Sta. 24, 54°05′S, 38°25′W, in 197–207 m, USNM 897531. Scale bars = 200 μm.

881716; Sta. 15, off South Georgia Island, 53°37′42″S, 38°04′00″W, in 128–137 m, 14 May 1975, 1 shell, USNM 901673; Sta. 16, off South Georgia Island, 53°38′12″S, 38°01′06″W, in 130–134 m, 14 May 1975, 1 shell, USNM 901675; Sta. 17, off South Georgia Island, 53°36′00″S, 38°03′00″W, in 122–124 m, 14 May 1975, 1 specimen + 2 shells, USNM 901674 (anatomy studied); Sta. 30, off South Georgia Island, 53°50′36″S, 36°18′36″W, in 185–205 m, 19 May 1975, 2 shells, USNM 887839.

R/V *Prof. Siedlecki*: off South Georgia Island, Sta. 16, 53°44′S, 39°22′W, in 304–342 m, 02 Dec 1986, 4 shells, USNM 897553; Sta. 20, 53°58′S, 38°42′W, in 189–200 m, 02 Dec 1986, 2 shells, USNM 897583; Sta. 24, 54°05′S, 38°25′W, in 197–207 m, 03 Dec 1986, 2 shells, USNM 897531; Sta. 28, 54°30′S, 38°56′W, in 220–

←

39°22′W, in 304–342 m, USNM 897553. H, I. R/V *Islas Orcadas*, Sta. 17, Off South Georgia Island, 53°36′00″S, 38°03′00″W, in 122–124 m, USNM 901674, (anatomical data based on this E specimen). J. operculum of specimen in figs. H, I. Scale bar = 1 cm for A–I, 2 mm for J.

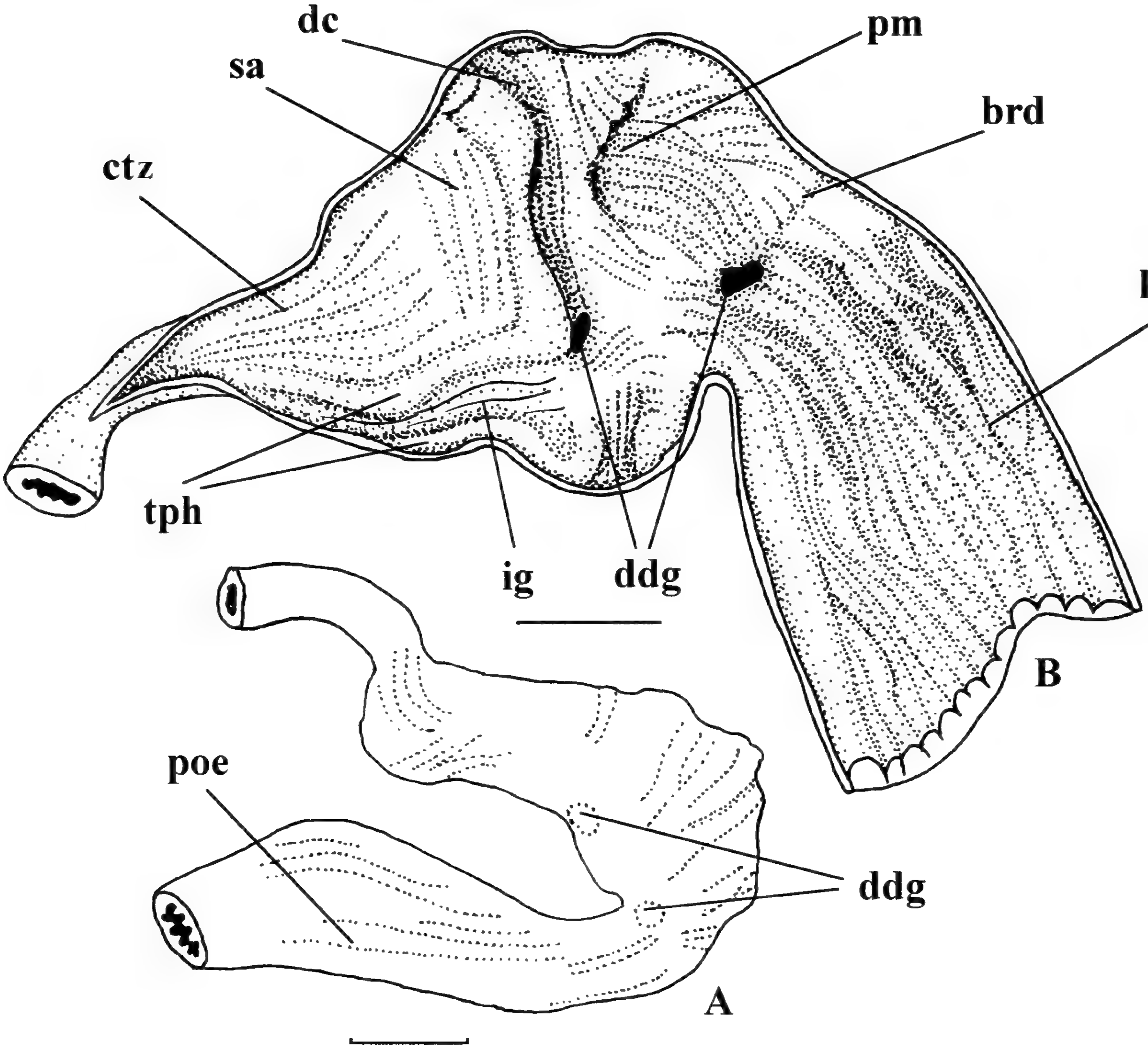

Fig. 14. *Chlanidota* (*Chlanidota*) *paucispiralis* Powell, 1951. Stomach of specimen in fig. 12H I. A. Dorsal view of the stomach. B. Stomach opened mid-ventrally. Scale bars = 2 mm. Abbreviations: ctz, compacting zone of the stomach; dc, duct pouch; ddg, duct of the digestive gland; ig, intestinal groove; pm, posterior mixing area, or caecum; poe, posterior oesophagus; sa, sorting area; tph, typhlosoles.

232 m, 03 Dec 1986, 1 shell, USNM 897484; Sta. 87, 54°18′S, 35°37′W, in 238–247 m, 11 Dec 1986, 2 shells, USNM 897537; Sta. 101, 53°47′S, 36°34′W, in 263–277 m, 1 shell, USNM 897457; Sta. 105, 53°40′S, 36°48′W, in 161–192 m, 14 Dec 1986, 1 shell, USNM 897515; Sta. 116, 53°43′S, 38°36′W, in 260–306 m, 16 Dec 1986, 1 shell, USNM 896993; Sta. 121, 53°57′S, 38°10′W, in 90–100 m, 16 Dec 1986, 1 shell, USNM 896991.

R/V *Eltanin*: Sta. 671, off South Georgia Island, 54°41′S, 38°38′W, in 220–320 m, 23 Aug 1963, 1 shell, USNM 870378; Sta. 678, off South Georgia Island, 54°49′S, 38°01′W, in 732–814 m, 24 Aug 1963, 1 juvenile specimen, USNM 881942; Sta. 1535, off South Georgia Island, 53°51′S, 37°38′W, in 97–101 m, 7 Feb 1966, 10 shells + fragments, USNM 898666.

Distribution.—South Georgia Island, in 97–814 m (Fig. 15). Live specimens were collected in 122–814 m.

Remarks.—Unlike most of its congeners, this geographically restricted species displays remarkably little variation in shell morphology. It is readily distinguished from all other *Chlanidota* sensu stricto by its prominent, broadly spaced, spiral cords. It most closely resembles *Chlanidota* (*Pfefferia*) *chordata* (Strebel, 1908), from which it is readily distinguished by its small, smooth

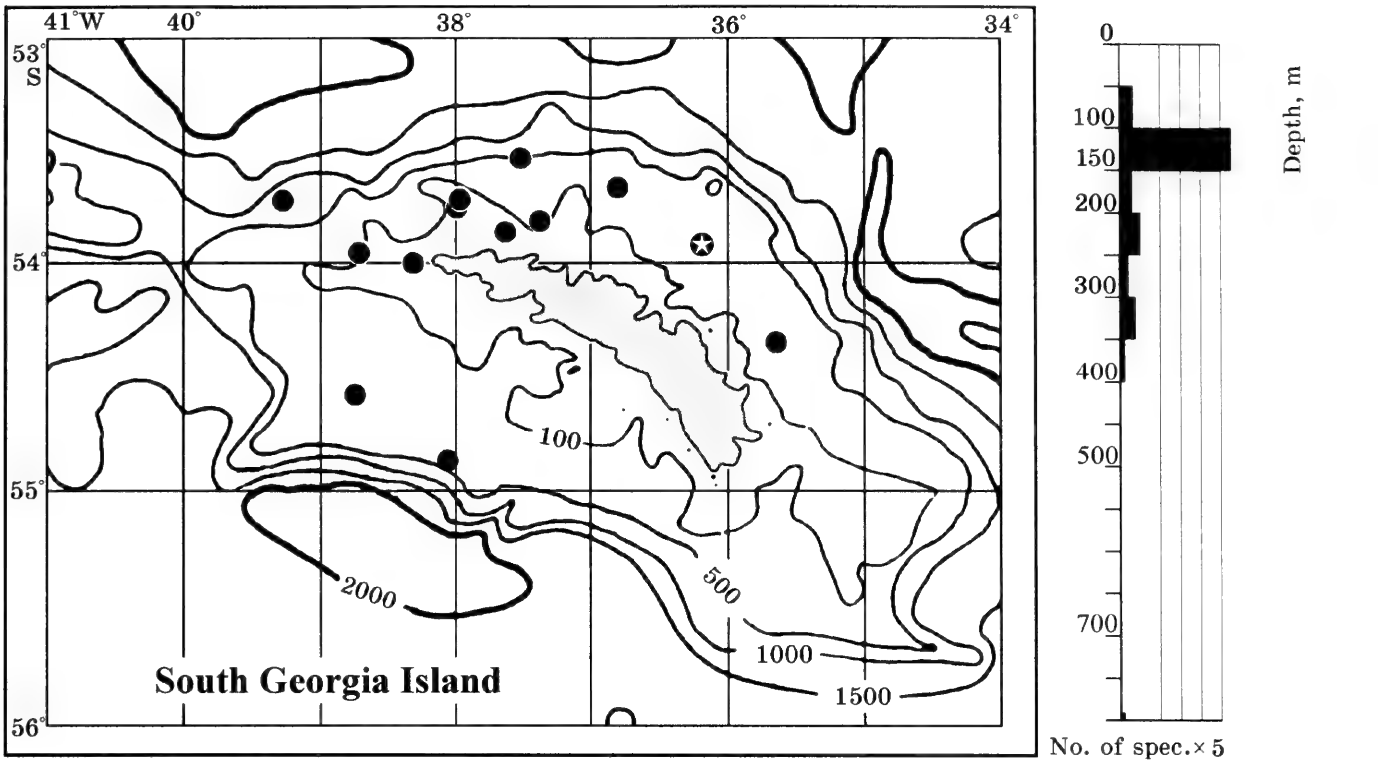

Fig. 15. Geographic distribution and bathymetric range of *Chlanidota* (*Chlanidota*) *paucispiralis* Powell, 1951. ✪ = type locality; ● = examined material.

operculum. *Chlanidota* (*Pfefferia*) *chordata* (Strebel, 1908) has a thicker shell and a thicker, hirsute periostracum.

Subgenus *Chlanidota* (*Pfefferia*) Strebel, 1908

Pfefferia Strebel, 1908:33–4; Powell, 1951: 142.
Chlanidota (*Pfefferia*) Thiele, 1929:315.

Type species.—*Pfefferia palliata* Strebel, 1908, by subsequent designation, Powell, 1951:142.

Description.—Shell medium sized for family, maximum adult size 34.5 to 38.3 mm, depending on species. Shell usually moderately thick, ovate to elongate in outline, with short spire. Shell covered with thick periostracum, either smooth or with fine axial lamellae. Spiral sculpture of thin threads or prominent cords. Aperture high, oval. Operculum (Fig. 16) large (0.48–0.83 AL), leaf-shaped, tapered above, below, with terminal nucleus rotated nearly perpendicular to long axis of operculum. Posterior edge of operculum with tall ridge of feathered lamellae, broadest just above midlength. Siphonal notch broad, dorsally recurved, siphonal fasciole with ridged margins. Shell ultrastructure and gross anatomy of mantle cavity, alimentary and male reproductive systems as in *Chlanidota* sensu stricto.

Remarks.—The subgenus *Chlanidota* (*Pfefferia*) is endemic to South Georgia Island. In his description of *Pfefferia*, Strebel (1908) noted many similarities with *Chlanidota*, especially in the morphology and sculpture of the shell and periostracum. He distinguished the two as genera on the basis of their opercula, that of *Chlanidota* being small, triangular, with rounded corners, and with its apex and nucleus along the posterior margin. The operculum of *Pfefferia* is much larger, elongated, tapering above and below, and has a characteristic, "feathered" posterior edge. Strebel further commented that low and high-spired forms (without intermediates) were encountered at each of the two stations from which *Pfefferia* had been collected. Each station also contained strongly and weakly sculpture forms. While

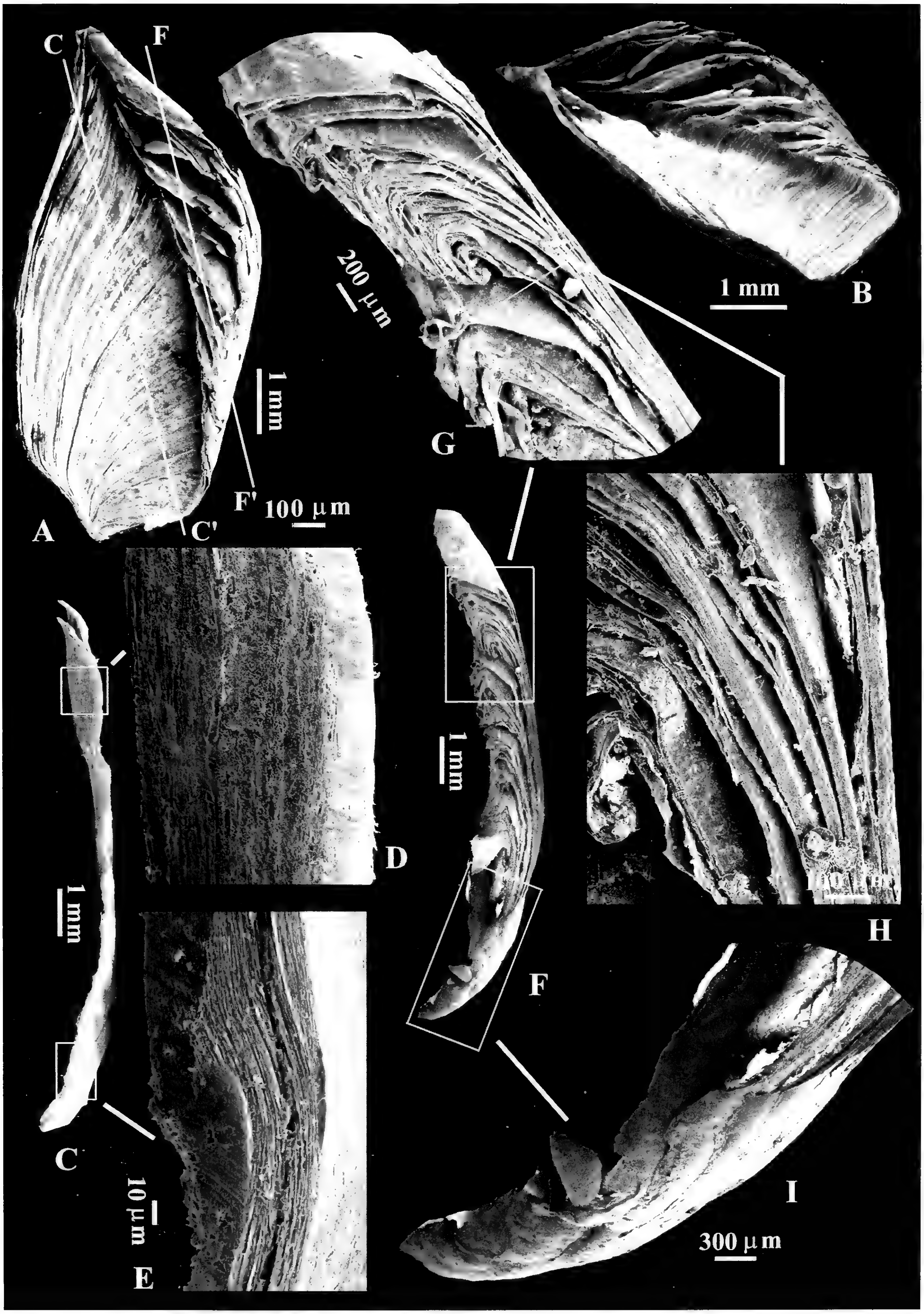

Fig. 16. *Chlanidota* (*Pfefferia*) *palliata* (Strebel, 1908). A. Operculum showing terminal nucleus rotated nearly perpendicular to long axis of operculum. Lines C-C′ and F-F′ correspond to the sections shown by Figs. C and F. B. Left lateral (45°) view of operculum. C. Section trough flat, central portion of operculum (along the line C-C′ on Fig. A), nucleus at the bottom. D, E. Successive layers are closely appressed, adherent in this

expressing uncertainty as to whether these differences warranted specific status, Strebel nevertheless described four species, commenting that additional material would allow these questions to be better answered.

Examination and dissection of additional material of three species of *Chlanidota* (*Pfefferia*) revealed that *Chlanidota* (*Pfefferia*) cannot be distinguished from *Chlanidota* sensu stricto on the basis of gross anatomy. Of special interest is the variable operculum of the newly described *C.* (*P.*) *invenusta*, which ranges from the typical *Chlanidota* (*Pfefferia*) operculum to one very similar to, but larger than, that of *Chlanidota* (*Chlanidota*), and includes intermediate morphologies. Due to the paucity of distinguishing features, we consider *Chlanidota* (*Pfefferia*) to warrant only subgeneric distinction from *Chlanidota* sensu stricto.

Chlanidota (*Pfefferia*) *palliata*
(Strebel, 1908)
Figs. 17, 18, 19, 20; Table 7

Pfefferia palliata Strebel, 1908:34–5, pl. 3, fig. 39a–f; Thiele, 1912:pl. 16, fig. 20 (radula); Powell, 1951:143; Carcelles, 1953: 193.

Pfefferia elata Strebel, 1908:35, pl. 3, fig. 40; Powell, 1951:142, 194, fig. L78 (radula), 196, fig. N 128 (operculum).

Pfefferia cingulata Strebel, 1908:36, pl. 3, fig. 42a–c; Powell, 1951:142–3, 194, fig. L79 (radula); Carcelles, 1953: 193.

Description.—Shell (Fig. 18) large for genus (to 34.5 mm, Powell, 1951:142), thick, solid, ovate-rounded. Protoconch, early teleoconch whorls eroded in all specimens. Teleoconch with up to 4 evenly inflated whorls. Shoulder not pronounced. Suture deep, adpressed, narrowly channeled. Spiral sculpture of alternating broad, low cords (10–17 on body whorl, 3–5 on penultimate whorl) and fine threads (20–24 per 5 mm), spanning entire shell surface. Cords more clearly visible on young specimens with thinner periostracum. Axial sculpture limited to indistinct growth lines. Aperture tall, ovate, deflected from the shell axis by 16–18°. Siphonal canal is not pronounced. Outer lip evenly rounded, thick, weakly reflected in adults, very thin in juvenile and some adult specimens. Columella <½ AL, weakly concave, with fine pustules. Siphonal fold strong. Callus thick, clearly demarcated, narrowly overlying parietal region, siphonal fasciole in mature specimens. Siphonal notch broad, dorsally reflected, columellar margin straight, apertural margin rounded, reflected, forming pronounced ridge margin along adapical edge of fasciole. Shell color grayish white, translucent. Periostracum very thick, tightly adherent to shell surface, with evenly spaced, axially reflected lamellae with fringed edges evident on early whorls and juvenile specimens (Fig. 19C). Operculum (Fig. 16A, D) large, leaf-shaped, with apical nucleus, massive, raised, lamellose border along posterior margin, 0.67–0.83 AL. Attachment area spans nearly entire inner surface, posterior, left margins thickened, glazed.

Ultrastructure.—(fig. 19E) Outermost layer prismatic (≈50 μm), middle layer comarginal crossed-lamellar (≈175 μm), inner layer radial crossed-lamellar (≈95 μm). Inner surface of the outer aperture lip with numerous, fine spherules (Fig. 17D).

External anatomy.—Body of 2½ whorls (Fig. 18A, B), mantle cavity spanning ≈½ whorl, kidney ⅕ whorl, digestive 1¾ whorl. Foot of preserved specimens short (L/W ≈1), with rounded posterior edge. Head

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region of the operculum. F. Section through "feathered" portion of operculum (along the line F-F′ on Fig. A), nucleus at the bottom. G, H. Successive layers are unattached along apical portion of posterior edge of operculum. I. new lamellae are deposited along the entire length of the operculum.

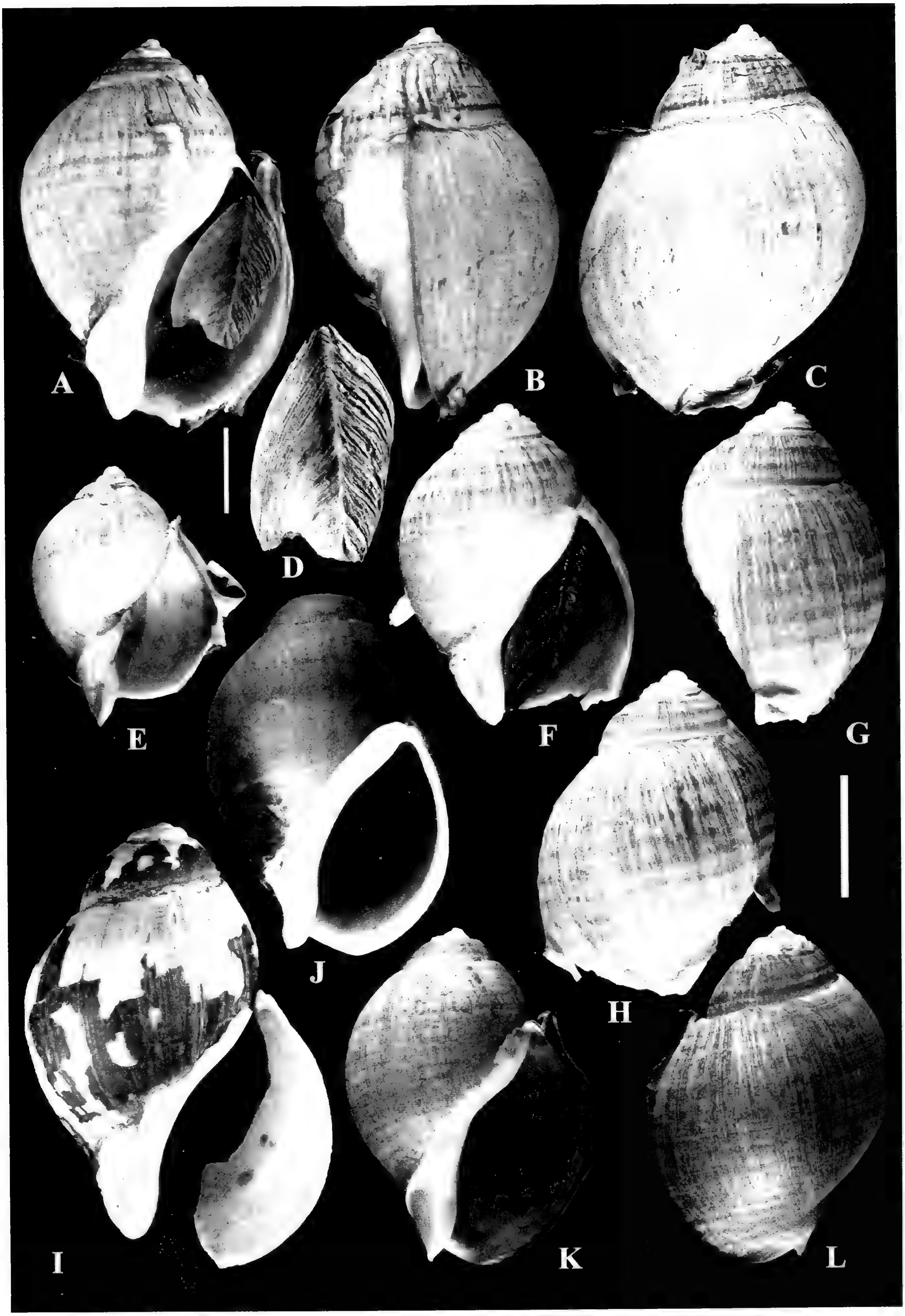

Fig. 17. *Chlanidota* (*Pfeffeira*) *palliata* (Strebel, 1908). A–C. Lectotype, SMNH (here designated), Sveska Südpolarexp., Sta. 22, South Georgia, 54°17′S, 36°28′W, in 75 m. D. Operculum of lectotype, enlarged.

Table 7.—*Chlanidota* (*Pfefferia*) *palliata* (Strebel, 1908). Measurements of shell characters. Linear measurements in mm ($n = 10$, type material not included).

Character	Mean	σ	Range	Lectotype of *C. palliata*	Lectotype of *C. cingulata*	Holotype of *C. elata* (broken)
Shell Length (SL)	27.1	3.6	18.1–30.0	32.8	25.9	~37
Body Whorl Length (BWL)	24.6	3.4	16.4–27.1	29.2	23.7	~32
Aperture Length (AL)	19.3	2.0	14.4–20.4	23.5	19.8	~23
Shell Width (SW)	19.4	2.3	14.0–21.2	23.4	19.4	~22
Operculum Length (OL)	14.1	2.0	9.6–16.7	—	15.4	—
BWL/SL	0.91	0.02	0.86–0.95	0.89	0.92	~0.86
AL/SL	0.72	0.04	0.67–0.80	0.72	0.76	~0.62
SW/SL	0.72	0.03	0.68–0.78	0.71	0.75	~0.60
OL/AL	0.73	0.06	0.67–0.83	—	0.78	—

narrow, with stout, conical tentacles, eyes on small lobes. Body lacks pigmentation.

Mantle cavity.—Mantle edge smooth. Siphon medium to long, muscular, extending substantially beyond mantle edge (≈⅓ AL). Osphradium dark greenish-brown, bipectinate, spans ≈½ mantle length. Hypobranchial gland of few, distinct, widely spaced folds. Ctenidium large, wide, spans ≈¾ mantle length, lamellae tallest in posterior ¼ of ctenidium, becoming shorter anteriorly.

Alimentary system.—Proboscis (Fig. 19C, D, pr) thick (L/D ≈ 3.5), of moderate length (0.9 AL). Mouth opening, triangular slit. Buccal mass muscular, large, nearly equal to retracted proboscis in length. Odontophoral cartilages paired, fused anteriorly, spanning ≈⅔ of proboscis length. Radular ribbon (Fig. 18A, B) of moderate length, 10.6 mm (0.66 AL), ≈760 μm wide (0.05 AL), triserial, consisting of 60–65 rows of teeth, posteriormost 5 nascent. Rachidian teeth with arched base, nearly straight lateral sides, 3 large, robust cusps of equal length. Central cusp longer than flanking cusps in one specimen (Fig. 18A, B). Lateral teeth with 3 cusps, outer cusp longest, intermediate cusp shortest, adjacent to inner cusp. Intermediate cusp nearly fused to inner cusp in one specimen (fig. 18A, arrow). Salivary glands small, fused (Fig. 19G), situated above nerve ring. Right salivary gland completely covering valve of Leiblein. Salivary ducts run loosely along both sides of oesophagus, entering esophageal wall near posteriormost portion of retracted proboscis. Valve of Leiblein (Fig. 18E, vL) well defined, large, without ciliated cone. Gland of Leiblein (Fig. 18C–E, gL) long, tubular, coiled anteriorly, tapering posteriorly. Oesophagus wide, muscular, expanding posteriorly to form crop (Fig. 18I, poe) lined with tall longitudinal folds. Stomach (Fig. 18H, I) U-shaped, without caecum. Ducts of digestive gland paired, closely spaced, transverse fold slightly raised. Typhlosoles present, poorly defined. Rectum terminating with well defined anal papilla.

Female reproductive system.—Typically buccinoidean. Oviduct opens into medium-sized albumen gland. Ingesting gland single. Capsule gland large, occupies ≈½ of

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E. Paralectotype, SMNH, from the type locality. F–H. Lectotype of *Pfefferia cingulata* (Strebel, 1908) (here designated), Sveska Südpolarexp., Sta. 34, Cumberland Bay, South Georgia, 54°11′S, 36°18′W, in 252–310 m. I. Holotype of *Pfefferia elata* (broken specimen), same station as types of *C.* (*P.*) *palliata*. J, K, L, both from R/V *Islas Orcadas*, Sta. 33, 54°30.7′S, 35°35.9′W, in 261–267 m, USNM 901676. Scale bar = 1 cm for A–C, E–L, 5 mm for D.

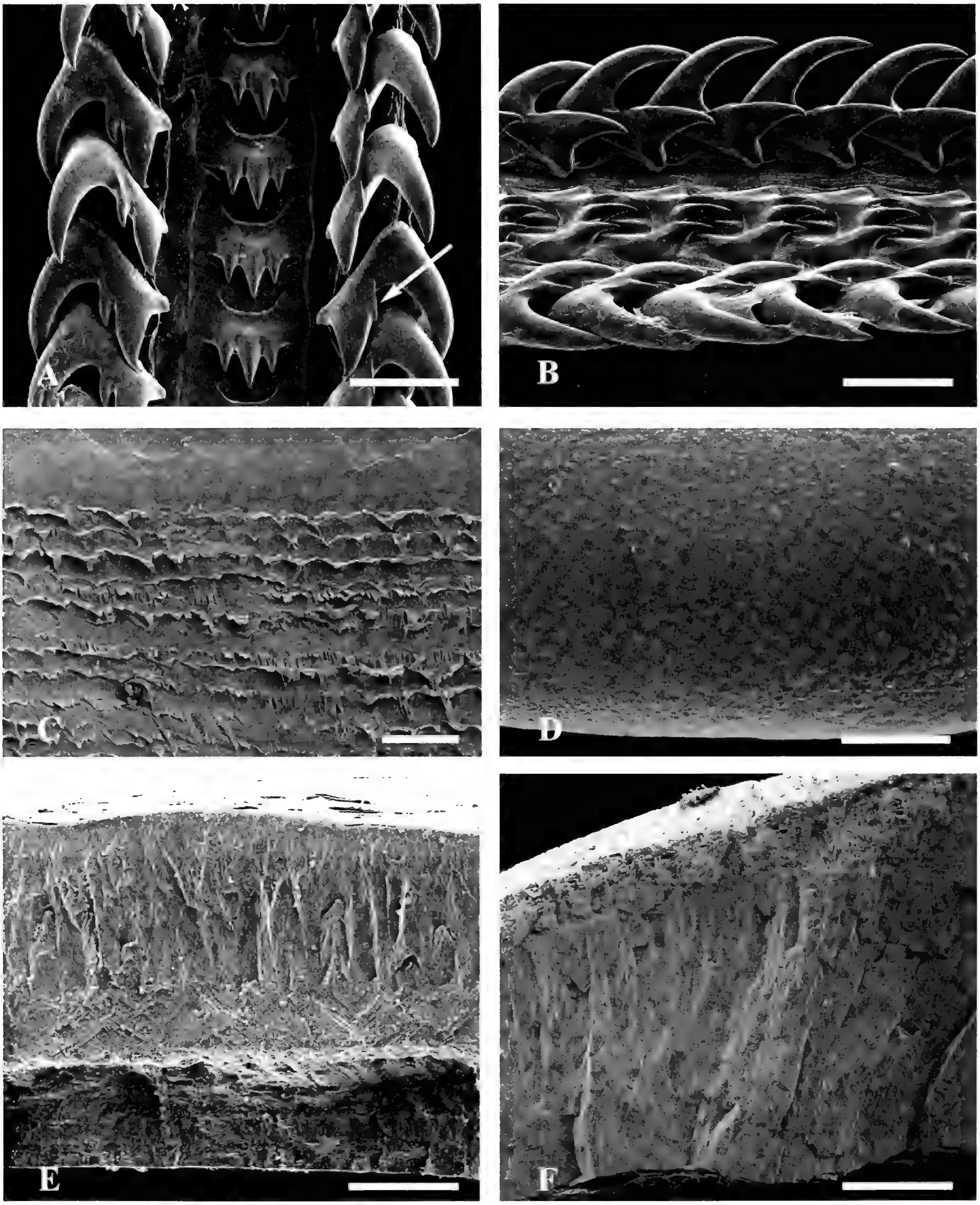

Fig. 18. *Chlanidota* (*Pfefferia*) *palliata* (Strebel, 1908). A. Dorsal, and B. left lateral (45°) views of the central portion of the radular ribbon taken from animal in Fig. 17J. C. Periostracum. D. Edge of outer lip. E, F. Shell ultrastructure. E. Fracture surface parallel to outer lip. F. Fracture surface perpendicular to outer lip. Scale bars = 200 μm for A, B, 100 μm for C–F.

mantle cavity. Bursa copulatrix present, simple, hemispherical.

Male reproductive system.—Very similar to that of *C.* (*C.*) *densesculpta*, penis has the same size, overall shape, terminal papilla.

Type locality.—[*Pfefferia palliata* & *P. elata*] South Georgia, 54°17′S, 36°28′W, in 75 m (Sveska Südpolarexp., Sta. 22); [*Pfefferia cingulata*] Cumberland Bay, South Georgia, 54°11′S, 36°18′W, in 252–310 m. (Sveska Südpolarexp., Sta. 34).

Type material.—[*Pfefferia palliata*] Lectotype (here designated) SMNH (fig. 17A–C), and 2 paralectotypes SMNH (fig. 17E); [*Pfefferia elata*] Holotype, SMNH 3661 (Fig. 17I), broken specimen; [*Pfefferia cingulata*] Lectotype (here designated) (Fig. 16F–H) and juvenile paralectotype, SMNH.

Material examined.—Type material. R/V *Islas Orcadas*: Sta. 31, 19 May 1975, 54°05.36′S, 36°30.48′W, 130–143 m, 1 shell, USNM 887863; Sta. 32, 19 May 1975, 54°21.36′S, 35°58.42′W, 141–164 m, 1 shell, USNM 887872; 9 shells, USNM 887867; Sta. 33, 19 May 1975, 54°30.7′S, 35°35.9′W, 261–267 m, 27 specimens, USNM 901676.

Published records.—R/V *Discovery II*, Sta. 30, West Cumberland Bay, South Georgia, 2.8 miles S, 24°W of Jason Light [16 Mar 1926], 251 m (Powell, 1951:142).

Distribution.—Known only from off the northeastern coast of South Georgia (Fig. 19). Live material was collected between 75 and 310 m.

Remarks.—The type specimens of *Chlanidota* (*Pfefferia*) *palliata* and *C.* (*P.*) *elata* were taken from the same dredge haul. Strebel (1908) distinguished these taxa primarily on the difference in their spire height and the strength of their spiral sculpture, but questioned whether these differences merited specific recognition. We were able to examine a larger sample than was available to Strebel (USNM 901676, *n* = 27) and found it to contain specimens spanning a morphological continuum between these two forms. The type series of *C.* (*P.*) *cingulata* was collected very near the type locality of *C.* (*P.*) *palliata*, but at slightly greater depth. The specimen selected as lectotype of *C.* (*P.*) *cingulata* is, in our opinion, conspecific with the specimen selected as lectotype of *C.* (*P.*) *palliata*, as both fall within the range of morphological variation found in a single population (USNM 901676). Since Powell (1951) designated *P. palliata* to be the type species of *Pfefferia*, we retain this name for this species, and synonymize the remaining nomina.

Powell (1951:142) noted that the only radula he examined was abnormal, with two small, "incipient" cusps flanking the normally tricuspid rachidian teeth. The radulae we examined were typical of *Chlanidota.*

Juvenile specimens are bicolored, with the periostracum being dark chestnut brown above the periphery, and a pale, olive green below the periphery. The periostracum of adult specimens is thicker and uniformly chestnut brown in color. Conchologically this species is similar to *C.* (*C.*) *densesculpta*, but may be readily distinguished on by the presence of weakly raised spiral cords, as well as by its distinctive operculum.

Chlanidota (*Pfefferia*) *chordata*
(Strebel, 1908)
Figs. 21, 22, 23; Table 8

Pfefferia chordata Strebel, 1908:36–7, pl. 3, fig. 41a–c; Powell, 1951:143; Carcelles, 1953:193.

Description.—Shell (Fig. 20) large for genus (to 35.3 mm), thick, solid, ovate-rounded, highly variable. Protoconch, early teleoconch whorls eroded in all specimens. Teleoconch with up to 4+ evenly rounded, very convex whorls. Shoulder not pronounced. Body whorl comprises 0.6–0.89 of the total shell length. Suture strongly impressed, forming narrow channel between adapical spiral cord and previous whorl. Spiral sculpture variable, spiral cords (7–26 on body whorl, 4–11 on penultimate whorl)

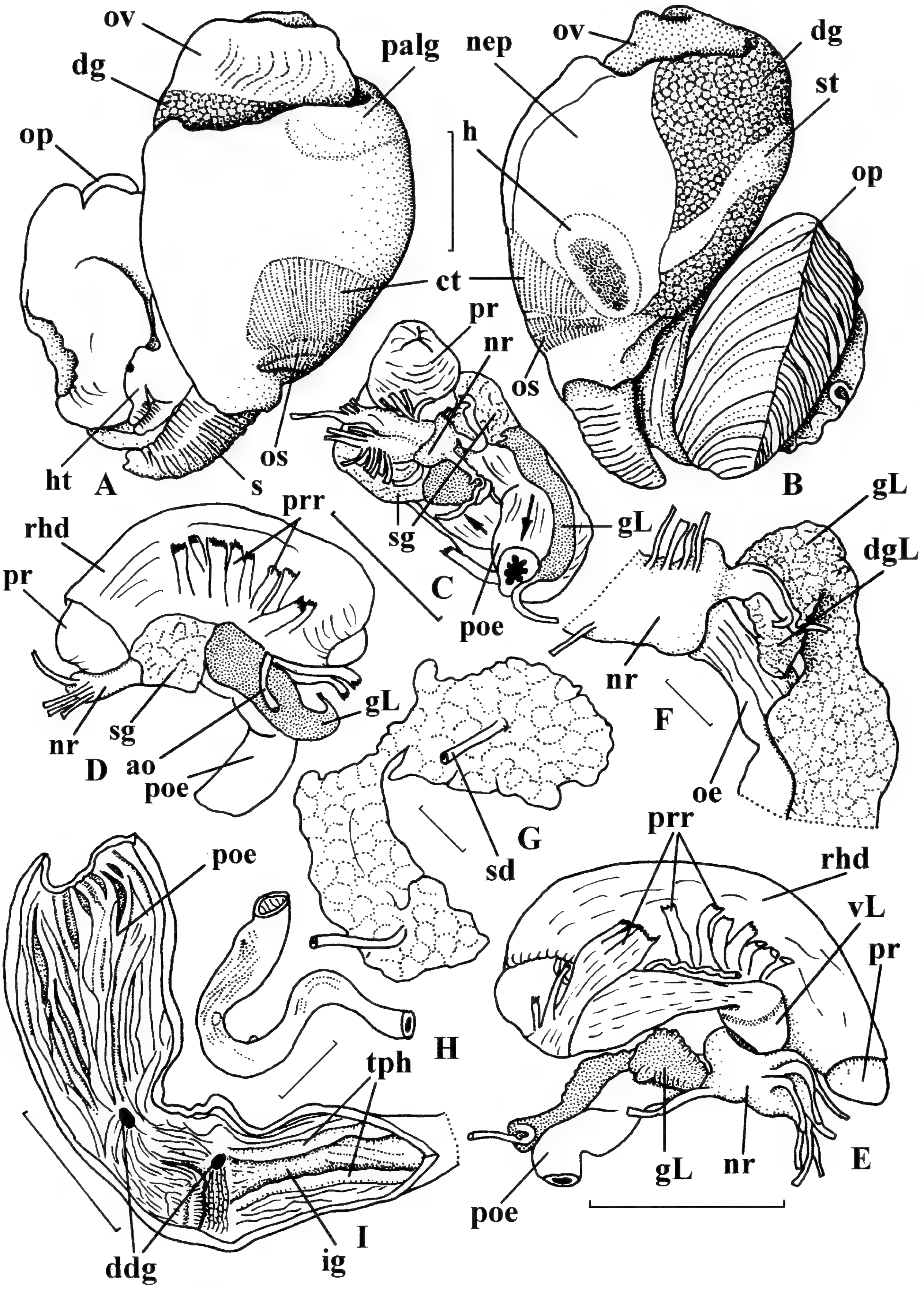

Fig. 19. Anatomy of *Chlanidota* (*Pfefferia*) *palliata* (Strebel, 1908). Specimen in fig. 17 J. A. Right and B. left lateral views of animal removed from shell (SL = 29.7 mm). C. Ventral, D. left lateral, and E. right lateral views of anterior alimentary system (salivary glands removed to show valve of Leiblein in E). F. Juncture of gland of Leiblein and esophagus. G. Ventral view of fused salivary glands. H. Dorsal view of stomach. I. Stomach, opened mid-dorsally. Scale bars = 5 mm for A–E, H–I; 2 mm for F, G. Abbreviations: ao, anterior

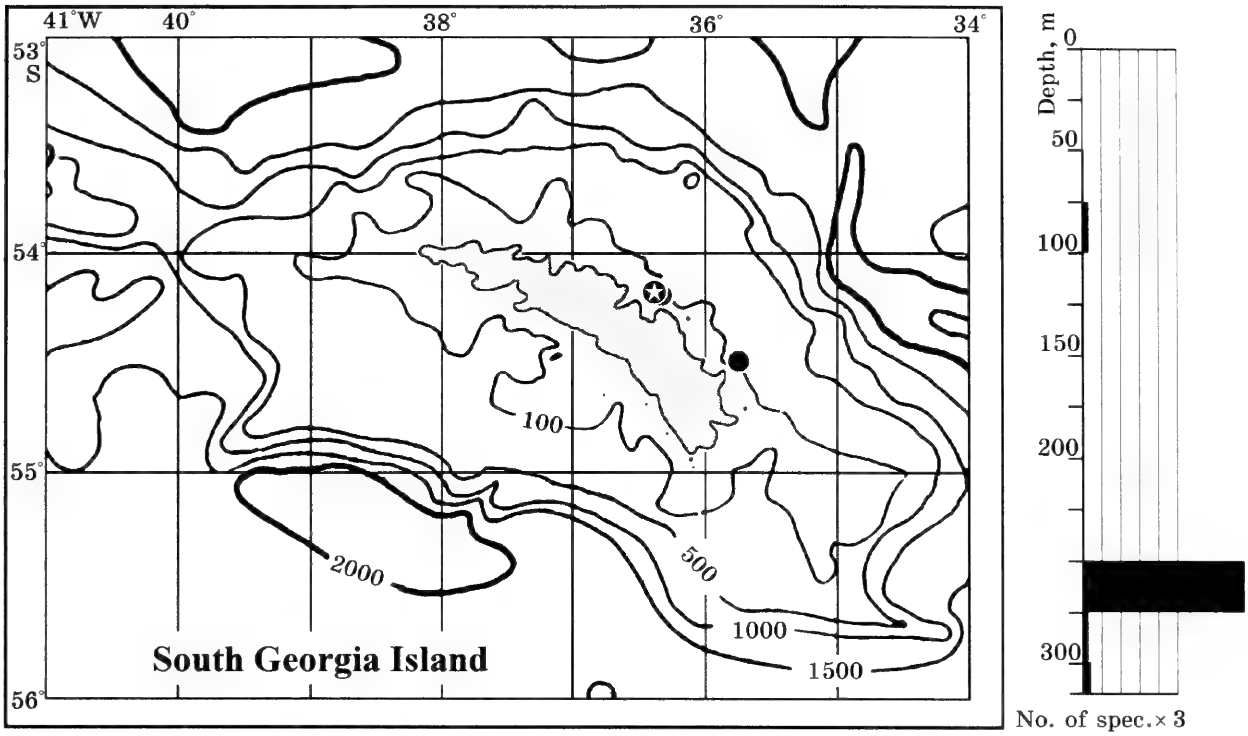

Fig. 20. Geographic distribution and bathymetric range of *Chlanidota* (*Pfefferia*) *palliata* (Strebel, 1908). ✪ = type locality; ● = examined material.

low, weak, and smooth to very tall and sharply-defined, forming corresponding spiral grooves on inner surface of outer lip. Cords of weakly sculptured specimens (Fig. 20L, M) closely spaced, as wide or wider than intervening spaces. Cords of moderately sculptured specimens (e.g., Fig. 20A–C, F–G) ½ to ⅓ width of intervening spaces. Cords of strongly sculptured specimens (Fig. 20D–E, K–J) more than ½ the width of intervening spaces. Adapical cord of strongly corded specimens may form narrowly concave subsutural rim. Fine spiral threads may be present on cords and in interspaces. Axial sculpture limited to weakly defined growth lines. Aperture tall (0.60–0.84 SL), ovate, deflected from shell axis by 16–19°. Outer lip thin to moderately thick, evenly rounded or scalloped, fragile to strong, sometimes slightly reflected. Columella less than half aperture length, weakly convex or straight, with strong siphonal fold. Callus usually thick, narrow, overlying parietal region, siphonal fasciole, grayish to brownish in color. Siphonal notch broad, dorsally recurved, with straight columellar and rounded apertural margins that form borders of fasciole. Ridge margin of fasciole pronounced, originating at apertural margin of siphonal notch, sometimes protruding through callus. Shell color chalky-white. Periostracum (Fig. 21) yellow-orange, olive to dark brown, nearly black, moderately to extremely thick, tightly adherent to the shell surface. Periostracum surface smooth or of closely adjacent, blade-like lamellae that overlay spiral sculpture without giving rise to hair-like projections, or hairy, producing one or several hairs at intersections of lamellae with

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aorta; ct, ctenidium; ddg, duct of the digestive gland; dg, digestive gland; dgL, duct of gland of Leiblein; gL, gland of Leiblein; h, heart; ht, cephalic tentacles; ig, intestinal groove; nep, nephridium; nr, circumoesophageal nerve ring; oe, oesophagus; op, operculum; os, osphradium; ov, ovary; poe, posterior oesophagus; pr, proboscis; prr, proboscis retractors; rhd, proboscis sheath; s, siphon; sd, salivary duct; sg, salivary gland; st, stomach; vL, valve of Leiblein.

Table 8.—*Chlanidota* (*Pfefferia*) *chordata* (Strebel, 1908). Measurements of shell characters. Linear measurements in mm (*n* = 10, including holotype).

Character	Mean	σ	Range	Holotype
Shell Length (SL)	27.9	3.5	23.2–34.4	34.7
Body Whorl Length (BWL)	21.9	3.7	16.7–29.7	29.0
Aperture Length (AL)	19.1	2.9	15.3–23.2	21.7
Shell Width (SW)	21.1	3.4	17.2–26.7	23.8
Operculum Length (OL)	12.0	3.3	7.7–16.2	—
BWL/SL	0.79	0.12	0.60–0.89	0.83
AL/SL	0.68	0.05	0.60–0.74	0.62
SW/SL	0.75	0.06	0.68–0.86	0.69
OL/AL	0.61	0.09	0.46–0.73	—
No. spiral cords on:				
Penultimate whorl	5.7	2.4	4–11	5
Body whorl	13	6.3	7–26	12

spiral cords. Operculum large (0.46–0.73 AL), massive, typical of genus.

Ultrastructure.—(Fig. 22C, E) Outermost prismatic layer comprising spiral cords, greatly variable in thickness, ranging from 825 μm in strongly corded specimens (Fig. C) to 58 μm in lightly corded shells (Fig. E). Middle, comarginal layer ranges from 60 to 210 μm, inner, radial layer reaches ≈60 μm in thickness.

Anatomy.—Gross anatomy of *C.* (*P.*) *chordata* very similar to that of *C.* (*P.*) *palliata.* Radular ribbon long (0.66 AL), ≈720 μm wide (0.036 AL), triserial (Fig. 22A–B), of ≈65 rows of teeth, of which 5 are nascent. Rachidian teeth with deeply arched base, nearly straight lateral sides, 3 large, robust cusps of equal-length. Lateral teeth with 3 cusps, outermost cusp largest, intermediate cusp thinnest and shortest, adjacent to inner cusp. Stomach U-shaped without obvious caecum, too poorly preserved to reveal internal details.

Type locality.—Cumberland Bay, South Georgia, 54°11′S, 36°18′W, in 252–310 m (Sveska Südpolarexp., Sta. 34).

Type material.—Holotype, SMNH 3660

Material examined.—Holotype. R/V *Islas Orcadas*: South Georgia: Sta. 9, 53°43′30″S, 37°30′06″W, 271–313 m, 12 May 1975, 2 specimens, USNM 901677; Sta. 18, 54°02′30″S, 37°39′36″W, 60–71 m, 15 May 1975, 3 specimens, USNM 901678; Sta. 19, 54°01′42″S, 37°40′00″W, 46–70 m, 15 May 1975, 3 specimens + 1 shell, USNM 901679; Sta. 20, 54°00′06″S, 37°40′36″W, 68–80 m, 15 May 1975, 4 specimens, USNM 901680; Sta. 22, 54°02′48″S, 37°23′42″W, 66–75 m, 16 May 1975, 3 specimens + 6 shells, USNM 881724; Sta. 25, 53°51′02″S, 36°49′03″W, 199–247 m, 17 May 1975, 1 shell, USNM 901681; Sta. 26, 53°43′06″S, 36°49′18″W, 183–192 m, 17 May 1975, 3 specimens + 3 shells, USNM 881756; Sta. 88, 54°31′45″S, 36°48′42″W, 150–154 m, 7 Jun 1975, 2 specimens + 1 shell, USNM 896287; Sta. 89, 54°44′12″S, 37°11′12″W, 225–265 m, 7 Jun 1975, 6 specimens + 7 shells, USNM 881760; Sta. 90, 54°50′48″S, 37°23′48″W, 223–227 m, 7 Jun 1975, 8 shells, USNM 881762; Sta. 101, 54°14′10″S, 37°54′20″W, 164–183 m, 10 Jun 1975, 1 shell, USNM 901682. R/V *Prof. Siedlecki*: South Georgia: Sta. 20, 53°58′S, 38°42′W, 189–200 m, 2 Dec 1986, 1 shell, USNM 901683; Sta. 37, 54°18′S, 37°54′W, 158–194 m, 5 Dec 1986, 1 shell, USNM 897573; Sta. 83, 54°39′S, 35°49′W, 98–127 m, 11 Dec 1986, 2 specimens + 4 shells, USNM 897534; Sta. 84, 54°28′S, 35°39′W, 231–249 m, 11 Dec 1986, 1 specimen, USNM 897536; Sta. 88, 54°15′S, 35°51′W, 232–254 m, 11 Dec 1986, 2 shells, USNM 897506; Sta. 90, 54°10′S, 35°15′W, 242–262 m, 12 Dec 1986, 1 shell, USNM 896998; Sta. 91, 54°09′S, 35°55′W, 218–227 m, 12 Dec 1986, 3 specimens, USNM 897450; Sta. 101, 53°47′S, 36°34′W, 263–277 m, 2 shells, USNM 897457; Sta. 105, 53°40′S, 36°48′W, 161–192 m, 14 Dec 1986, 2 specimens + 6 shells, USNM 897515; Sta. 106, 53°44′S, 36°51′W, 178–201 m, 14 Dec 1986, 5 shells, USNM 896985.

Distribution.—Off Southern Georgia (Fig. 22). Living specimens collected at depths from 46 to 313 m.

Remarks.—*Chlanidota* (*Pfefferia*) *chordata* is highly variable in shell morphology, with the extremities of the morphological range appearing very different (compare, e.g., Fig. 21K, J to L, M). Incrementally transitional forms ranging from nearly smooth to highly corded individuals were present in our samples (e.g., Fig. 21M↔L↔F↔A↔D↔H↔J). Specimens from depths (<100 m) (e.g., Fig. 21L, M) tend to have smaller shells with more numerous and more densely spaced spiral cords than specimens from deeper water (>150 m) (e.g., Fig. 21D, H, J). Intermediate specimens between these extremes occur within single dredge hauls at both shallow and deep stations. Specimens with intermediate shell morphology might be confused with *Chlanidota* (*Pfefferia*) *palliata* (compare Fig. 21F–G with Fig. 17F–G).

Chlanidota (*Pfefferia*) *invenusta*,
new species
Figs. 24–26; Table 9

Chlanidota densesculpta (partim)—Dell, 1990:183, fig. 306.

Description.—Shell (Fig. 23) thick, solid, ovate-rounded. Protoconch, 1½ upper teleoconch whorls eroded. Teleoconch with ≈4 strongly convex whorls. Shoulder rounded. Suture adpressed, deep, wide, nearly channeled. Subsutural rim well pronounced, slightly convex. Spiral sculpture of weak cords (25–40 on body whorl, 5–14 on penultimate whorl) constant in width adapically, of variable width and prominence below shoulder. Axial sculpture limited to fine, often indistinct growth lines. Aperture of moderate height (0.60–0.72 SL), elongate-ovate, deflected from the shell axis by 17–21°. Outer lip thin to thick, evenly rounded, weakly reflected in thick-lipped adults. Outer lip thin and evenly rounded, slightly deflected. Columella short (<½ AL), straight, with strong, long siphonal fold, siphonal region slightly elongated, inflected in some specimens. Callus narrow, thin to thick overlying parietal region, siphonal fasciole, white when thin, greenish-gray at margins when thick. Siphonal notch broad, dorsally recurved, with straight columellar, rounded apertural margins forming borders of fasciole. Apertural margin of siphonal notch gives rise to weak ridge margin. Shell color grayish white. Periostracum (Fig. 24D) light-olive, moderately thick, tightly adherent to shell surface, forming very low, densely spaced lamellae along the growth lines. Operculum (Fig. 23D, H, J, L) large (0.47–0.62 AL), oval, light to dark brown, apical end rounded to weakly tapering, nucleus, terminal, rotated nearly perpendicular to long axis of operculum, posterior edge smooth (Fig. 23d, J), or with weakly (Fig. 23H) to strongly (Fig. 23L) feathered lamellae.

Ultrastructure.—(Fig. 25C) Outer prismatic layer comprises spiral cords, variable in thickness, ranging from ≈80 μm to ≈140 μm, depending on strength of cord. Middle layer comarginal (≈120 μm). Inner layer radial, reaching ≈50 μm in thickness, is the last layer to be deposited, may not be evident in immature specimens (Fig. 25C).

Anatomy.—The gross anatomy of paratype 1 was examined, and found to be similar in all details to that of *C.* (*P.*) *palliata* with the exception that the animal lacked eyes. Radular ribbon (Fig. 24A–B) long, 13.6 mm (0.54 AL), ≈760 μm wide (0.030 AL), triserial, consisting of ≈80 rows, 6 of which are nascent. Rachidian teeth with arched base, straight lateral sides, 3 large, robust cusps, central cusp slightly larger that flanking cusps. Small intermediate ser-

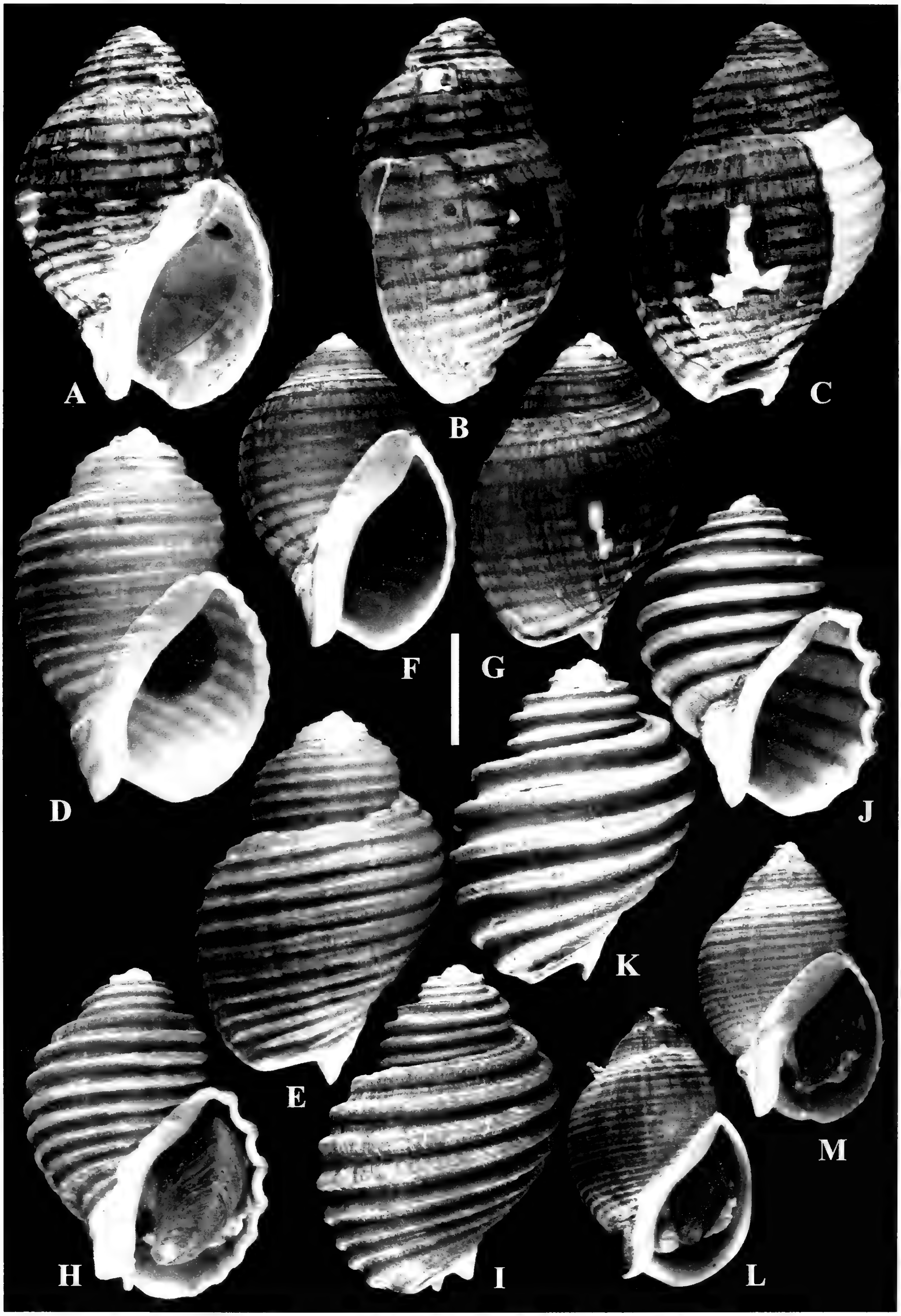

Fig. 21. *Chlanidota* (*Pfefferia*) *chordata* (Strebel, 1908). A–C. Holotype, SMNH 3660, Sveska Südpolarexp., Sta. 34, Cumberland Bay, South Georgia, 54°11′S, 36°18′W, in 252–310 m. D, E. R/V *Islas Orcadas*, Sta. 89, South Georgia, 54°44′12″S, 37°11′12″W, in 225–265 m, USNM 881760. F, G. R/V *Islas Orcadas*, Sta. 9, South Georgia, 53°43′30″S, 37°30′06″W, in 271–313 m, USNM 901677. H, I. R/V *Prof. Siedlecki*, Sta. 105, South

ration present between central cusp and right flanking cusp of one specimen. Lateral teeth with 3 cusps, as in genus.

Type locality.—South Georgia Island, 53°31′12″S, 37°50′54″W, in 1267–1599 m (R/V *Islas Orcadas*, Sta. 7).

Type material.—Holotype, USNM 881782, paratypes 1–9, USNM 880280, all from the type locality.

Material examined.—South Georgia: R/V *Islas Orcadas*, Sta. 7, 53°31′12″S, 37°50′54″W, 1267–1599 m, 11 May 1975, Holotype, USNM 881782, paratypes 1–9, USNM 880280, 17 shells, USNM 901684; STa. 27, 53°34.9′S, 36°47.8′W, 448–872 m, 17 May 1975, 1 specimen, USNM 901685; R/V *Eltanin*: Sta. 731, 53°35′S, 36°28′W, 796–824 m, 11 May 1975, 13 specimens, USNM 896048; Sta. 734, 53°23′S, 37°11′W, 1299–1400 m, 11 May 1975, 4 shells, USNM 870389, 8 specimens, USNM 896049.

Distribution.—Known only from the northwestern coast of South Georgia (Fig. 25). Living material was collected at depths ranging from 448 to 1599 m.

Etymology.—*invenustus* (Lat.)—unattractive.

Remarks.—*Chlanidota* (*Pfefferia*) *invenusta* may be distinguished from the other species in the subgenus *Pfefferia* by its more inflated shell, with a stepped rather than conical spire, more numerous and finer spiral cords, a broader, more rounded aperture, and an operculum in which the feathering along the posterior edge is much narrower to entirely absent. Some specimens superficially resemble *Chlanidota densesculpta*, but may be distinguished on the basis of their larger operculum, thicker shell, more rounded and stepped spires, and proportionally smaller, more rounded, and more deflected apertures.

The nine paratypes collected with the holotype exhibit some variation in shell outline and the number of spiral cords. Smaller specimens tend to have more rounded shells, while the number of spiral cords does not correlate with shell size. Opercula of the smallest specimens are yellow and translucent, and clearly show that the terminal nucleus is coiled, as in *Neobuccinum*.

Species excluded from *Chlanidota* sensu lato

Chlanidota smithi Powell, 1958
Fig. 27

Chlanidota smithi Powell, 1958:192, pl. 3, fig. 3; Dell, 1990:177.

Type locality.—Off Enderby Land, 65°50′S, 54°23′E, in 220 m (BANZARE, Sta. 42).

Material examined.—Holotype, SAM D15471 (Fig. 27).

Published records.—BANZARE, Sta. 41, Off Enderby Land, 65°48′S, 53°16′E, 193 m (Powell, 1958:192).

Remarks.—Powell (1958) placed this species in a group with *Chlanidota densesculpta*, *C. vestita*, and *C. pilosa*, but distinguished it from these taxa on the basis of its "disproportionally large," bulbous protoconch and the almost smooth surface on all whorls. Powell (1958) conjectured that Smith's (1902) record of *C. vestita* from Cape Adare, 24–26 fm [45–48 m] might represent *C. smithi*. However, Dell (1990: fig. 311) illustrated the Cape Adare specimen and showed it to represent *C. vestita*. Thus, records of *C. smithi* are restricted to Enderby Land. This species differs from typical *Chlanidota* in number of characters, most notably its very large size (SL = 51.5 mm) and very large protoconch. Compari-

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←

Georgia, 53°40′S, 36°48′W, in 161–192 m, USNM 897515. J, K. R/V *Islas Orcadas*, Sta. 26, South Georgia, 53°43′06″S, 36°49′18″W, in 183–192 m, USNM 881756. L, M. Both from R/V *Islas Orcadas*, Sta. 19, Off South Georgia Island, 54°01′42″S, 37°40′00″W, in 46–70 m, USNM 901679. Scale bar = 1 cm.

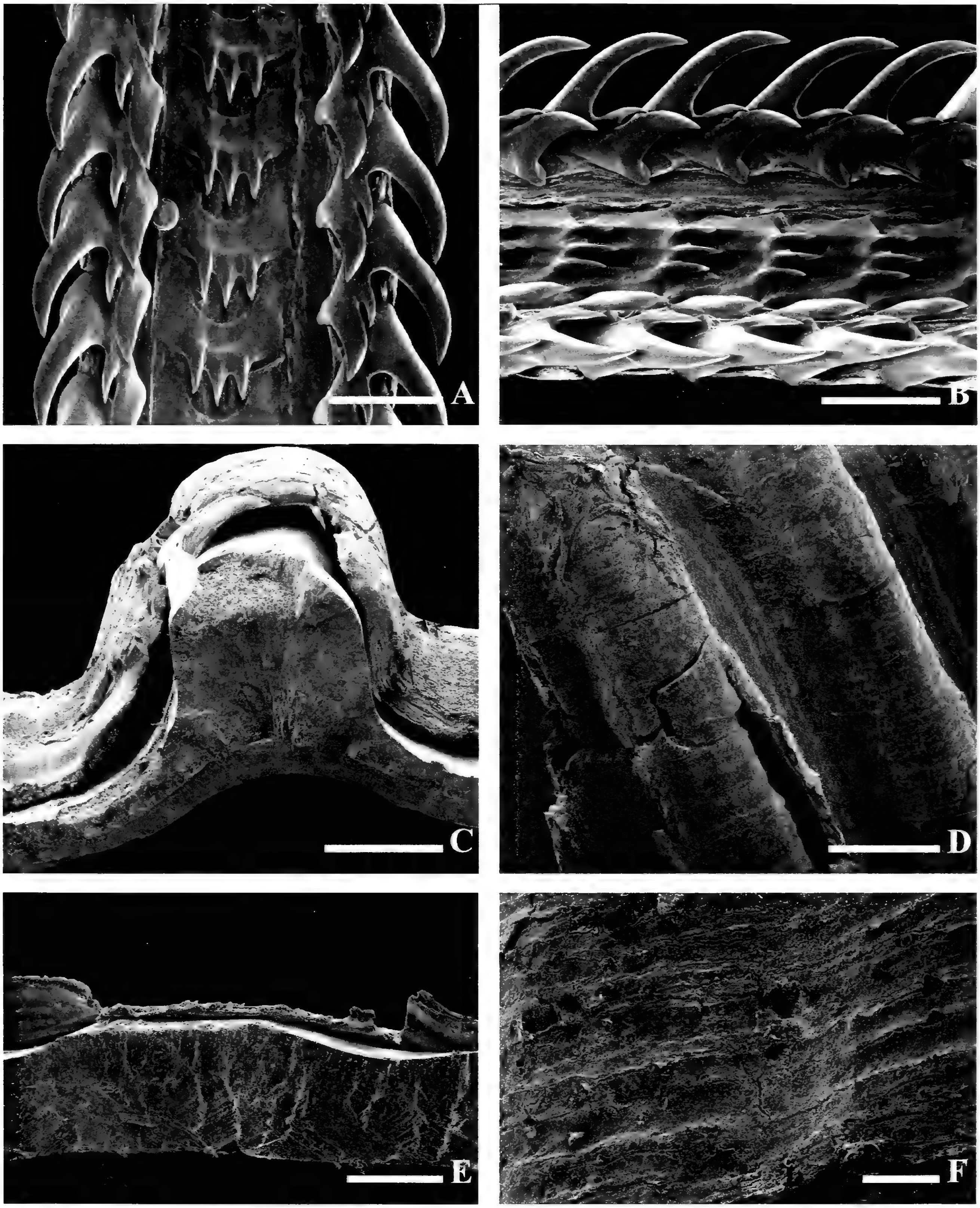

Fig. 22. *Chlanidota* (*Pfefferia*) *chordata* (Strebel, 1908). A. Dorsal and B. left lateral (45°) views of the central portion of the radular ribbon taken from specimen in fig. 21F–G. C. Shell ultrastructure and D. periostracum of the strongly corded shell. R/V *Prof. Siedlecki*, Sta. 83, South Georgia, 54°39′S, 35°49′W, in 98–127 m, USNM 897534. E. Shell ultrastructure and F. periostracum of the weakly corded shell (fig. 20M). Scale bars = 200 μm for A, B, E, F, 500 μm for C, 1000 μm for D.

Table 9.—Measurements of shell characters of the type series of *Chlanidota (Pfefferia) invenusta*, new species.

Character	Holotype	Paratype 1	Paratype 2	Paratype 3	Paratype 4	Paratype 5	Paratype 6	Paratype 7	Paratype 8	Paratype 9	Mean	σ
Shell Length (SL)	38.3	39.6	32.6	38.6	31.8	31.0	36.0	26.5	22.2	19.0	31.6	7.1
Body Whorl Length (BWL)	31.6	31.9	27.3	30.7	25.8	26.3	30.3	22.2	18.7	16.3	26.1	5.5
Shell Width (SW)	26.4	27.2	23.4	25.6	22.9	22.0	25.6	17.4	16.0	14.4	22.1	4.6
Aperture Length (AL)	24.6	25.0	21.9	23.2	19.0	20.1	22.0	18.2	15.6	13.7	20.3	3.7
Operculum Length (OL)	12.4	12.2	10.2	—	11.7	11.7	10.5	8.8	8.0	7.2	10.3	2.0
BWL/SL	0.82	0.81	0.84	0.80	0.81	0.85	0.84	0.84	0.84	0.86	0.83	0.02
AL/SL	0.64	0.63	0.67	0.60	0.60	0.65	0.61	0.69	0.70	0.72	0.64	0.04
SW/SL	0.70	0.69	0.72	0.66	0.72	0.71	0.71	0.67	0.72	0.76	0.70	0.03
OL/AL	0.50	0.49	0.47	—	0.62	0.58	—	0.48	0.51	0.53	0.53	0.06
Number of spiral cords												
Penultimate whorl	15	14	16	19	12	11	?	8	8	5	12	4.5
Body whorl	32	26	25	40	24	29	29+	29	38	27	29.9	5.3
No. whorls	3+	3++	3+	3++	3+	3+	3+	2++	2++	2+		

son of the holotype of *C. smithi* (Fig. 27) with the specimens of *Neobuccinum eatoni* Smith, 1875, clearly reveal a striking conchological similarity between these species. Numanami (1996:146) noted that the majority of specimens of *N. eatoni* taken off Syowa Station (Enderby Land) are obese, with a large, well inflated body whorl. Comparison of Numanami's (1996:fig. 94A, B, D–G) illustrations of *Neobuccinum eatoni* with the holotype of *Chlanidota smithi* leave no doubt that these two taxa are conspecific.

Chlanidota gaini (Lamy, 1910)

Sipho gaini Lamy, 1910:319; Lamy, 1911: 7, pl. 1, figs. 7–8.
Prosipho? gaini Thiele, 1912:262.
?Chlanidota gaini Powell, 1951:142.
Chlanidota gaini Carcelles, 1953:191; Dell, 1990:177.

Type locality.—Off King George Island, South Shetlands, in 420 m.

Material examined.—Holotype, NMNH.

Remarks.—"*Sipho*" *gaini* was provisionally attributed to *Chlanidota* by Powell (1951) and by Carcelles (1953). Dell (1990) considered *Chlanidota gaini* to be a species of uncertain affinity, known only from its holotype.

Examination of the holotype, which had not been illustrated since its description, clearly indicates that this species is referable to the family Conidae (sensu Taylor et al., 1993), and is, in fact, the senior synonym of *Belaturricula antarctica* (Dell, 1990). The composition and relationships of the genus *Belaturricula* are the subject of a separate report (Kantor & Harasewych 1999). Hedley (1916) was the first to surmise the conoidean affinities of *Sipho gaini*, suggesting that it was closely related to *Pontiothauma ergata* Hedley, 1916.

Chlanidota eltanini Dell, 1990

Chlanidota eltanini Dell, 1990:184–5, figs. 290, 292, 297, 314.

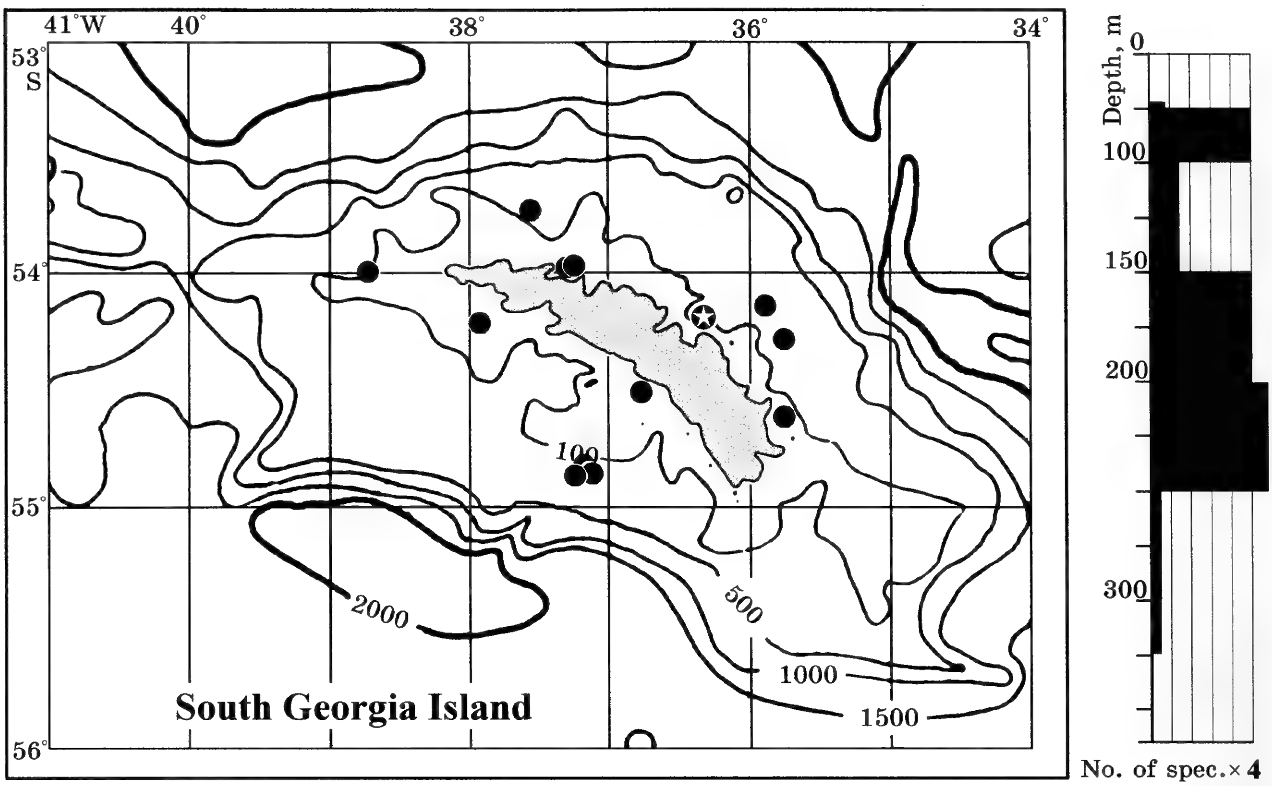

Fig. 23. Geographic distribution and bathymetric range of *Chlanidota* (*Pfefferia*) *chordata* (Strebel, 1908). ✪ = type locality; ● = examined material.

Type locality.—East of Falklands Islands (Islas Malvinas), 51°58′S, 56°38′W, depth 845–646 m (R/V *Eltanin*, Sta. 558).

Type material.—Holotype, USNM 860124, 2 paratypes USNM 860125, 1 paratype NMNZ MF.56613, from the type locality. R/V *Eltanin*: Sta. 557, East of Falkland Islands, 51°56′S, 56°39′W, 855–866 m, 2 paratypes USNM 860126; Sta. 1521, South Atlantic Ocean, 54°09′S, 52°08′W, 419–483 m, 2 paratypes USNM 860127, 1 paratype NMNZ MF.56614.

Remarks.—Dell (1990) described *Chlanidota eltanini*, *C. bisculpta* and *C. polyspeira* from the Magellanic Province. While these three species are likely congeneric, they differ significantly from species assigned to the subgenera *Chlanidota* and *Pfefferia*. Conchologically, these species are readily distinguished by their small (15–16 mm), slender, thick shell, very thin, smooth periostracum, and large (0.6 AL), coiled operculum. We were able to examine the anatomy of *Chlanidota bisculpta*, as well as of a closely related but as yet undescribed species, and found differences in radular morphology, stomach shape, size of gland of Leiblein, and penis morphology. We provisionally consider these species to be more closely related to *Neobuccinum*, and exclude them from *Chlanidota*.

A revision of this group will be published separately.

Chlanidota bisculpta Dell, 1990

Chlanidota bisculpta Dell, 1990:185, figs. 291, 294, 295, 312.

Type locality.—Burdwood Bank, 53°08′S, 59°23′W, in 578–567 m (R/V *Eltanin*, Sta. 340).

Type material.—Holotype, USNM 860128; R/V *Eltanin*: Sta. 557, East of Falkland Islands (Islas Malvinas), 51°56′S, 56°39′W, 855–866 m, 6 paratypes USNM 860129, 1 paratype NMNZ MF.56615; Sta. 740, off Cape Horn, 56°06′S, 66°19′W, 384–494 m, 2 paratypes USNM 860130, 1 paratype NMNZ MF.56616.

Remarks.—See remarks under *Chlanidota eltanini* Dell, 1990.

Fig. 24. *Chlanidota* (*Pfefferia*) *invenusta* new species. A–C. holotype, USNM 881782, R/V *Islas Orcadas*, Sta. 7, South Georgia, 53°31′12″S, 37°50′54″W, in 1267–1599 m. D. Operculum of holotype, enlarged. E. Paratype 1, (anatomy studied), and F. paratype 5, USNM 880280, both from type locality. G, H. Specimen with narrowly rimmed operculum. I, J, M. Specimens with smooth operculum. K, L. Specimen with broadly rimmed operculum, all from R/V *Eltanin*, Sta. 734, South Georgia, 53°23′S, 37°11′W, in 1299–1400 m, USNM 896049. Scale bar = 1 cm for shells, 5 mm for opercula.

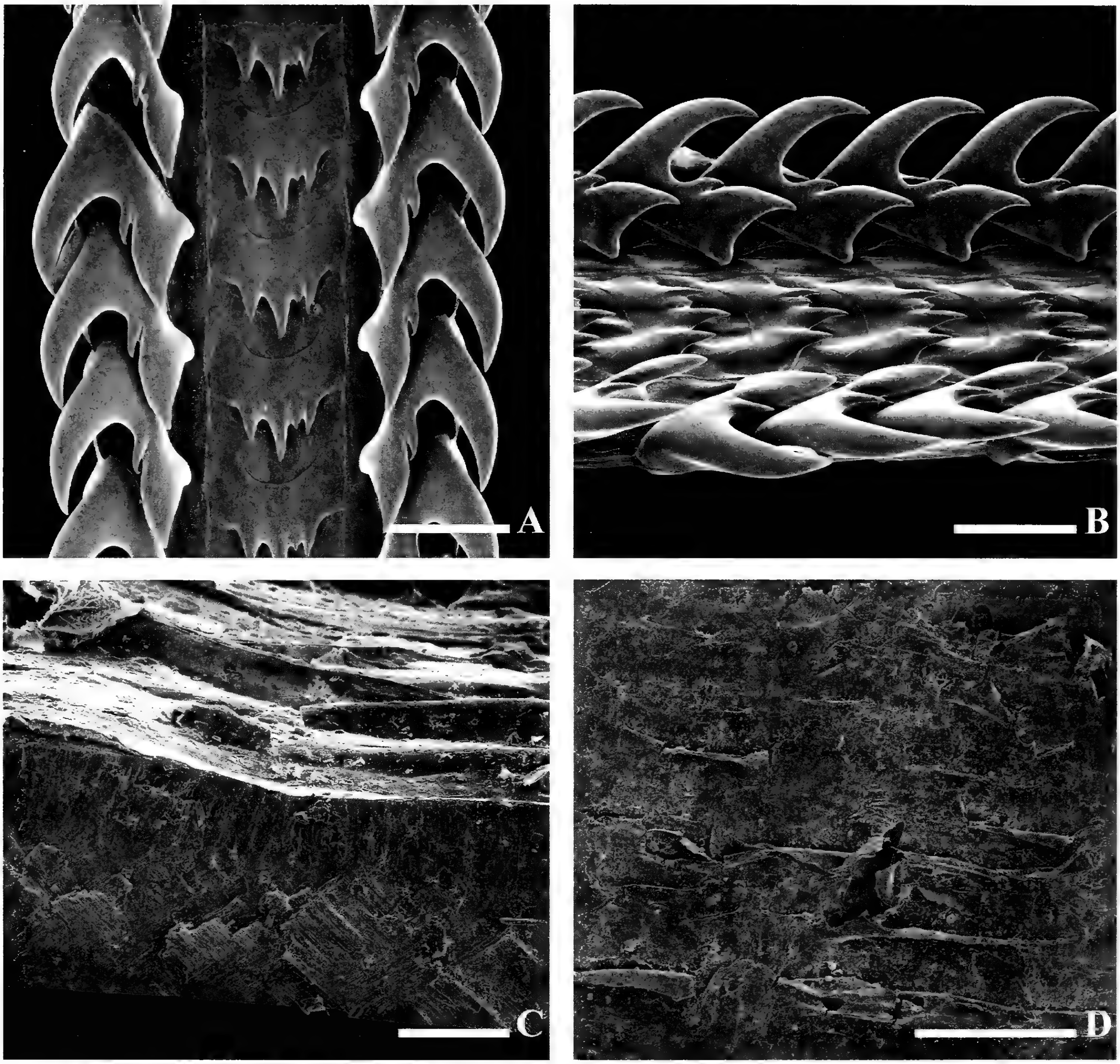

Fig. 25. *Chlanidota* (*Pfefferia*) *invenusta*, new species. A. Dorsal and B. left lateral (45°) views of the central portion of the radular ribbon of paratype 1 (Fig. 24E). C. Shell ultrastructure, and D. periostracum of the paratype 5 (Fig. 24F). Scale bar = 200 μm for A, B, 100 μm for C, 500 μm for D.

Chlanidota polyspeira Dell, 1990

Chlanidota polyspeira Dell, 1990:186, figs. 292, 293, 313.

Type locality.—Patagonian Shelf, 54°04′S, 63°35′W, depth 247–293 m (R/V *Eltanin* Sta. 369).

Type material.—Holotype, USNM 860131, 3 paratypes, USNM 860132, 1 paratype NMNZ MF.56617, all from the type locality.

Remarks.—See remarks to *Chlanidota eltanini* Dell, 1990.

Discussion

Buccinoidean classification has traditionally been based on a combination of shell, opercular, and radular characters, and these structures are well documented for the majority of Antarctic genera (e.g., Thiele 1904, Powell 1951, Hain 1989, Dell 1990, Numanami 1996). Ponder (1974) reported that most organ systems were weakly differentiated among buccinoidean higher taxa, and that it was difficult to identify anatomical features that could be used to seg-

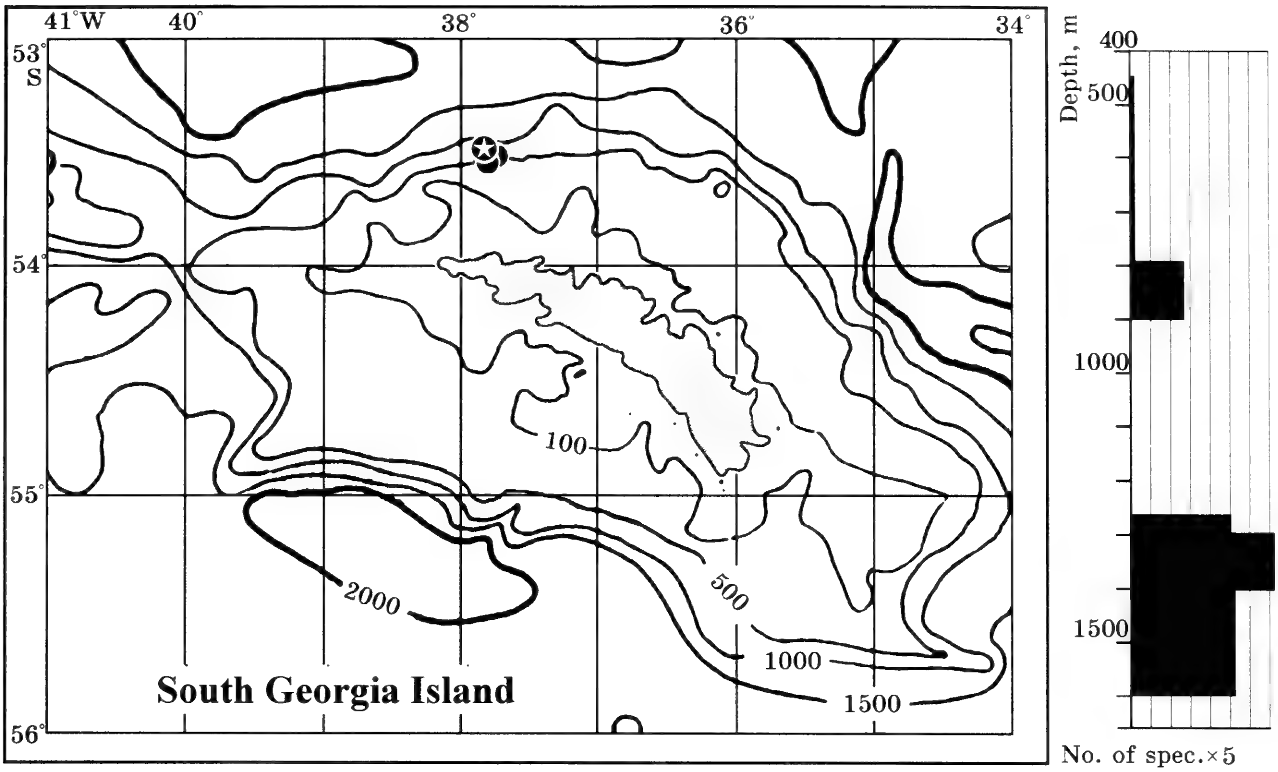

Fig. 26. Geographic distribution and bathymetric range of *Chlanidota* (*Pfefferia*) *invenusta*, new species. ✪ = type locality, ● = examined material.

regate them reliably. More recently, Harasewych (1990) identified several characters, including the morphology of the gland of Leiblein and the presence of an ingesting gland, that vary among buccinoideans and may be phylogenetically informative. While there have been a substantial number of anatomical investigations of boreal (e.g., Da-

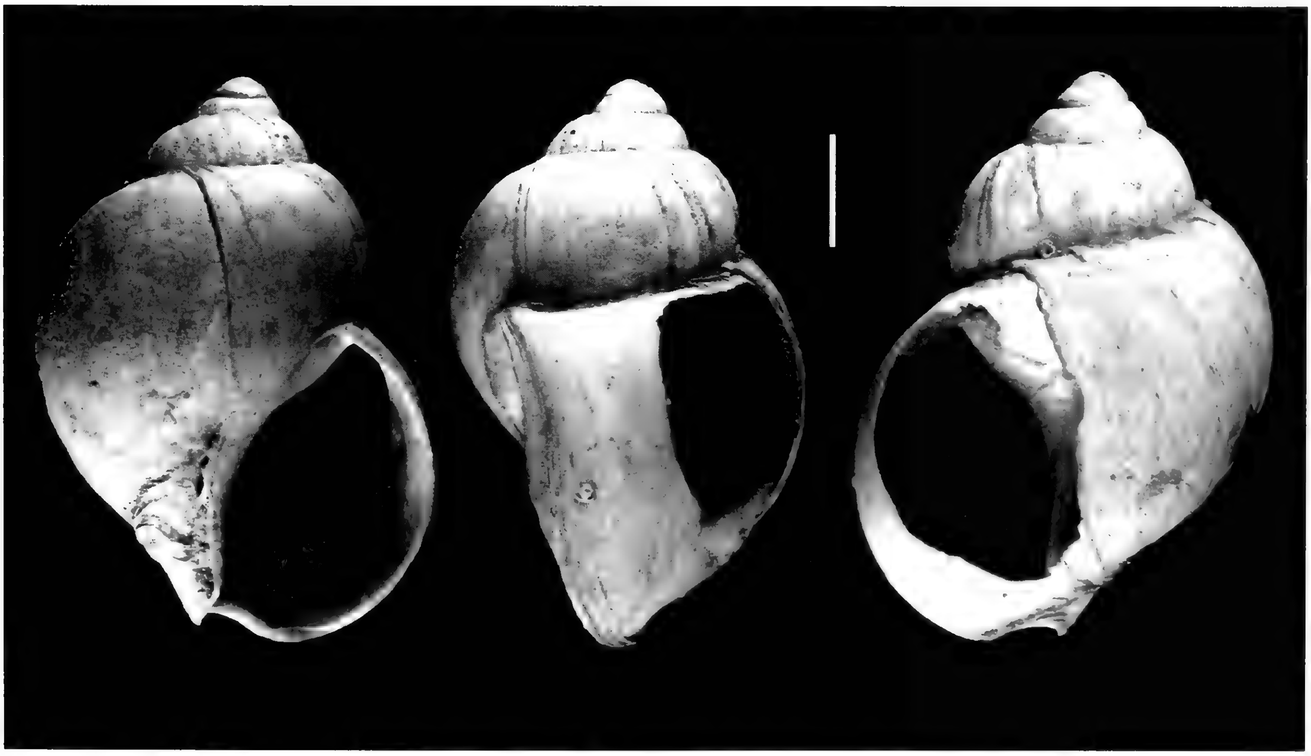

Fig. 27. *Chlanidota smithi* Powell, 1958. Holotype, SAM D15471, BANZARE Sta. 42, Off Enderby Land, 65°50′S, 54°23′E, in 220 m. Scale bar = 1 cm.

kin 1912; Lus 1978, 1981, 1989; Kantor 1988, 1990), tropical (e.g., Marcus & Marcus 1962, 1964) and deep-sea (e.g., Ponder 1968, Harasewych 1990) buccinoidean taxa, the anatomy of Antarctic representatives has not previously been studied in any detail.

It is not surprising that *Chlanidota* shares many anatomical features with the boreal family Buccinidae, among them similar arrangements of the mantle cavity organs, reproductive system, and many characters of the digestive system. Characters such as a long, thick proboscis and fused salivary glands occur in *Chlanidota* as well as in the buccinid taxa *Habevolutopsius* (Kantor 1990) and Ancistrolepidinae (Kantor 1988). The stomach of *Chlanidota*, however, differs from that of most Buccinidae in being broadly U-shaped and in lacking a caecum. The caecum, or posterior mixing area, is usually well developed in boreal Buccinidae, and is sometimes very large (e.g., in *Volutopsius*, subfamily Volutopsiinae), making the stomach appear sac-like. The stomach of Southern Hemisphere taxa, such as *Penion adustus* (Philippi, 1845) (Ponder 1973) and *Ratifusus mestayerae* (Iredale 1915) (Ponder 1968), which had been assigned to Buccinulidae by Powell (1961), also lack a caecum.

The northern Atlantic buccinid *Colus gracilis* (da Costa 1778) is unusual in lacking a gastric caecum (Smith 1967). However, its stomach differs from the stomach of *Chlanidota* in having a cuticularized shield and a distinct sphincter between the oesophagus and stomach. The stomach epithelium of *Colus gracilis* is glandular and darker than the esophageal epithelium, while in *Chlanidota* the epithelial lining of the esophagus is dark and that of the stomach is lighter.

Unlike all other *Chlanidota* and *Pfefferia*, the stomach of *Chlanidota* (*Chlanidota*) *paucispiralis* has a small enlargement (Fig. 14, pm) corresponding in position to the caecum of *Neptunea* (Smith 1967), *Buccinum* (Medinskaya 1993) and other boreal buccinids. It is still not clear, whether the presence of a gastric caecum is an advanced or plesiomorphic character, as the structure occurs in many neogastropod families (e.g., Buccinidae, Volutomitridae, Muricidae, Mitridae) but is absent in others (e.g., Columbellidae, Volutidae, Cancellariidae and all Conoidea).

The posterior oesophagus of *Chlanidota* is greatly enlarged, thick-walled, and lined with tall epithelial folds (e.g. Fig. 5H), which are darker than the rest of esophageal epithelium. The transition between the posterior oesophagus and the stomach is clearly evident on dissection, as it is marked by a color change of the epithelium near the posterior duct of the digestive gland.

The morphology of the radula and major organ systems is remarkably invariant in all of the species of *Chlanidota* and *Pfefferia* that we examined. The only exceptions were the presence of a small caecum in *C.* (*C.*) *paucispiralis* and of separate rather than fused salivary glands in *C.* (*C.*) *signeyana*. Preliminary dissections of other Antarctic buccinulids generally regarded as being closely related to *Chlanidota* (e.g., *Neobuccinum eatoni*, "*Chlanidota*" *bisculpta*, see above) revealed significant differences in their alimentary and male reproductive systems, providing support for reducing *Pfefferia* to a subgenus of *Chlanidota*.

The morphology of the operculum of *Chlanidota* (*Pfefferia*) is both striking and unique within Neogastropoda. The mechanism by which the characteristic "feathered" margin is formed along the posterior edge of the operculum is readily inferred. Newly secreted layers of conchiolin are broader adapically than abapically, and are attached to the posterior edge of the operculum only along their proximal margins. While operculum morphology is constant in *C.* (*P.*) *palliata* and *C.* (*P.*) *chordata*, it varies considerably in the newly described *C.* (*P.*) *invenusta*. Juveniles of *C.* (*P.*) *invenusta* have an operculum with a "feathered" margin. The width of this margin decreases with increasing shell size, the margin disappearing entirely in large specimens (see Fig. 24L→H→J→D). The size of the operculum of *C.* (*P.*) *invenusta* (0.47–0.62 AL) is larger than in any species of *Chlanidota* (*Chlanidota*) (0.18–0.37 AL), comparable to that of *C.* (*P.*) *chordata* (0.46–0.73 AL), but smaller than that of *C.* (*P.*) *elata* (0.68–0.78 AL). The large operculum of *Chlanidota* (*Pfefferia*) allows it to seal the aperture tightly when the animal withdraws into its shell (e.g., Figs. 17F, 21H), while its "feathered" posterior margin provides a flexible, tight seal against the outer lip. In contrast, the small size of the operculum in *Chlanidota* s.s. precludes its utility for sealing the aperture. The decrease in relative size and "degree of feathering" of the operculum in *C.* (*P.*) *invenusta* with increasing shell size, suggests that the ability to seal the aperture tightly diminishes in importance as the animal grows.

While the anatomy and radular morphology are largely invariant in *Chlanidota* and *Pfefferia*, shell shape and the strength and number of spiral cords and threads vary considerably. The limited number of specimens available to previous workers has, in a few instances, led to the description of species based on differences that now appear to fall within a broad continuum of morphological variability revealed by larger sample sizes spanning wider geographical areas.

As restricted in this paper, the genus *Chlanidota* is confined to the Antarctic region, with only the type species ranging slightly beyond the Antarctic Convergence. The present revision reduces the number of recognized species within *Chlanidota*. Nevertheless, it remains the second most diverse buccinoidean genus (following *Prosipho*) in Antarctic waters.

Of the eight recognized species in the genus *Chlanidota*, only *C.* (*C.*) *signeyana* has a broad circum-Antarctic distribution (although records from the poorly sampled Ross Quadrant are lacking). Except for a single record of *C.* (*C.*) *vestita* from Cape Adare, all remaining species of *Chlanidota* are restricted to subAntarctic islands, with two species of *Chlanidota* sensu stricto, and all three species of *Pfefferia* endemic to South Georgia. Of the species inhabiting subAntarctic islands, most are sublittoral, and only *Chlanidota* (*Pfefferia*) *invenusta* is restricted to bathyal depths. In contrast, the circum-Antarctic *C. signeyana* has a broad bathymetric range (30–1116 m).

The protoconchs of all specimens of *Chlanidota* were severely eroded, hampering inference of developmental mode. However, most polar species, including buccinoideans, develop directly without a pelagic larval stage (Thorson 1946). Thus, it seems likely that the island populations of *Chlanidota* are vicariant isolates from a more broadly ranging species.

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Hydroid and medusa stages of the new species *Ectopleura obypa* (Cnidaria: Hydrozoa: Tubulariidae) from Brazil

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Abstract.—*Ectopleura obypa*, a new species referable to the family Tubulariidae, is described from the southeastern coast of Brazil. Specimens were collected on experimental panels and other artificial substrates at depths from about 1 to 15 m. The hydroid stage is a remarkable green color when blastostyles are developed. A free medusa, with 2 opposed capitate marginal tentacles and 8 meridional tracks of nematocysts on the exumbrella, is present in the life cycle.

During a study of hydroid recruitment on experimental plates in waters of southeastern Brazil we discovered a species of *Ectopleura*, not yet described, remarkable for its bright green color. Several other specimens of the species were found at various times later on other artificial substrates including nylon ropes, buoys, and iron pipes. Specimens kept in the laboratory and cultured under controlled conditions liberated free medusae.

The genus *Ectopleura* L. Agassiz, 1862, a basal clade of the family Tubulariidae, has 20 valid species divided in two phylogenetic groups distinguishable basically by their cnidomes and stolon growth pattern (Petersen 1990:160). There is much confusion between the genera *Tubularia* and *Ectopleura*, the first having sessile gonophores and the latter traditionally considered as having free medusae (e.g., Millard 1975: 31–32; Bouillon 1985:112). However, Petersen (1979:120; 1990:160) redefined the tubulariid genera based on features of the hydroid stage. His classification of tubulariid polyps included: the solitary *Zyzzyzus*, with a thin perisarc and tuber-like attachment of hydrocaulus; the solitary *Tubularia* with firm perisarc and producing either eumedusoid or cryptomedusoid gonophores of the symmetrical type; the solitary *Hybocodon*, producing fixed asymmetrical gonophores; the colonial or solitary *Ectopleura* with firm perisarc and producing either free medusae or fixed gonophores; the solitary or colonial *Ralpharia* with firm perisarc and producing reduced medusae with an internal raised collar around bell opening; and the solitary *Bouillonia* with barrel-shaped hydranth, firm perisarc and reduced medusae.

Material and Methods

Hydroids of *Ectopleura obypa*, new species, were collected on a number of substrates (experimental plates, ropes, buoys, iron pipes) on the coast of São Sebastião, São Paulo State, Brazil. Type material, studied here, was collected by skin and SCUBA diving from a light buoy in the São Sebastião Channel. Part of the material was anesthetized in a 1:1 solution of 7.5% $MgCl_2$ solution and seawater, and preserved in 4% formaldehyde solution in seawater; part was kept alive in the laboratory. Live hydranths were examined under a stereomicroscope, and newly liberated medusae were transferred to finger bowls and kept in constant temperature chambers at 19, 24 and 26°C with a 12 h light/12 h dark photoperiod. Water in the bowls was changed daily, shortly after medusae were measured and fed with *Artemia* nauplii.

Stems for scanning electron microscopy (SEM) were post-fixed in 1% OsO_4, dehydrated in a graded series of ethanol, dried in a critical-point drier, and sputter-coated with gold. Nematocyst types and their distributions were determined using a light microscope with interference-contrast. Nematocyst nomenclature used here is that of Mariscal (1974) and Millard (1975). Only capsules of undischarged nematocysts were measured. Abbreviations are: AM (collection of A. Migotto); MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo); USNM (United States National Museum, Smithsonian Institution, Washington D.C.).

Results and Discussion

Genus *Ectopleura* L. Agassiz, 1862

Ectopleura obypa, new species

Figs. 1–3; Tables 1–2

Material.—Holotype, 1 hydroid colony, 2.0 cm high, São Sebastião Channel, São Sebastião, São Paulo State, Brazil (23°49.86′S, 045°25.28′W), 4 Jan 1996, 5 m, colony with gonophores and several hydranths growing epibiotically on barnacles and mussels, on light buoy, collected by hand, coll. A. E. Migotto (MZUSP-12.813); paratypes (all from same locality as holotype), medusae liberated in the laboratory 6 Jan 1996 from hydroid colony collected 4 Jan 1996, 6 medusae ca. 2 h old (AM1325); 2 medusae, 6 d old (MZUSP-12.814); 4 medusae, 7 d old (AM1327); 26 medusae, 34 d old (AM1328); one hydroid colony 35 mm high, on mussels and ascidian, with gonophores, 16 Jan 1996, 2 m, coll. A. C. Morandini (AM1323); one hydroid colony 25 mm high, on mussel, with gonophores, 17 Jun 1996, 2–3 m, coll. A. E. Migotto (AM1324; USNM 99449); 84 medusae ca. 3 h old, liberated in the laboratory on the same day of collection, from colony collected 17 Jun 1996 (AM1329).

Description.—colony up to 35 mm high, arising from branched stolons. Hydrocaulus unbranched, increasing in width from base to distal end, covered with a smooth light brown perisarc without annuli. Neck region long (Figs. 1C, 3A), flexible and contractile, covered by a filmy perisarc; extended neck up to 3.5 times longer than contracted; in live specimens, neck entirely white or light pink, with white pigments concentrated in 2 narrow longitudinal bands. Hydranth vasiform, pink-white and transparent, with one whorl of 16–30 aboral tentacles and one whorl of 14–29 oral tentacles (Figs. 1A, 2A, 3A). Aboral tentacles long, filiform, laterally flattened (Fig. 1A), with nematocysts concentrated along adoral surface, and on tip. Oral tentacles short, circular in cross section, basal part adnate to hypostome (Fig. 1D), with nematocysts concentrated in a terminal capitulum and 1–3 irregular swellings on the adoral surface of the tentacle (Fig. 1B, D); free part of oral tentacles slightly fused at base (Fig. 1B). Medusa buds on 4–14 (usually 7–10) blastostyles arising above aboral tentacles; older medusa buds at ends of blastostyles (Fig. 3B). Blastostyles yellow-green, composed of a main stem on which medusae arise either directly or from irregular branches; main stem may bifurcate. In large specimens the developed blastostyles hang between aboral tentacles.

Newly-liberated medusa with thin umbrella, dome-shaped and without a distinct apical projection but with a small apical canal, with 8 slightly raised exumbrellar, meridional nematocyst tracks; with 4 marginal bulbs, 2 of which with opposed tentacles; marginal tentacles with a terminal knob and 1–3 abaxial nematocyst clusters (Fig. 2B); abaxial nematocyst cluster grows and involves the tentacle (Figs. 2D, 3C). Manubrium tubular, without lips, with nematocysts around mouth, and about ⅔ the length of bell cavity. Apical

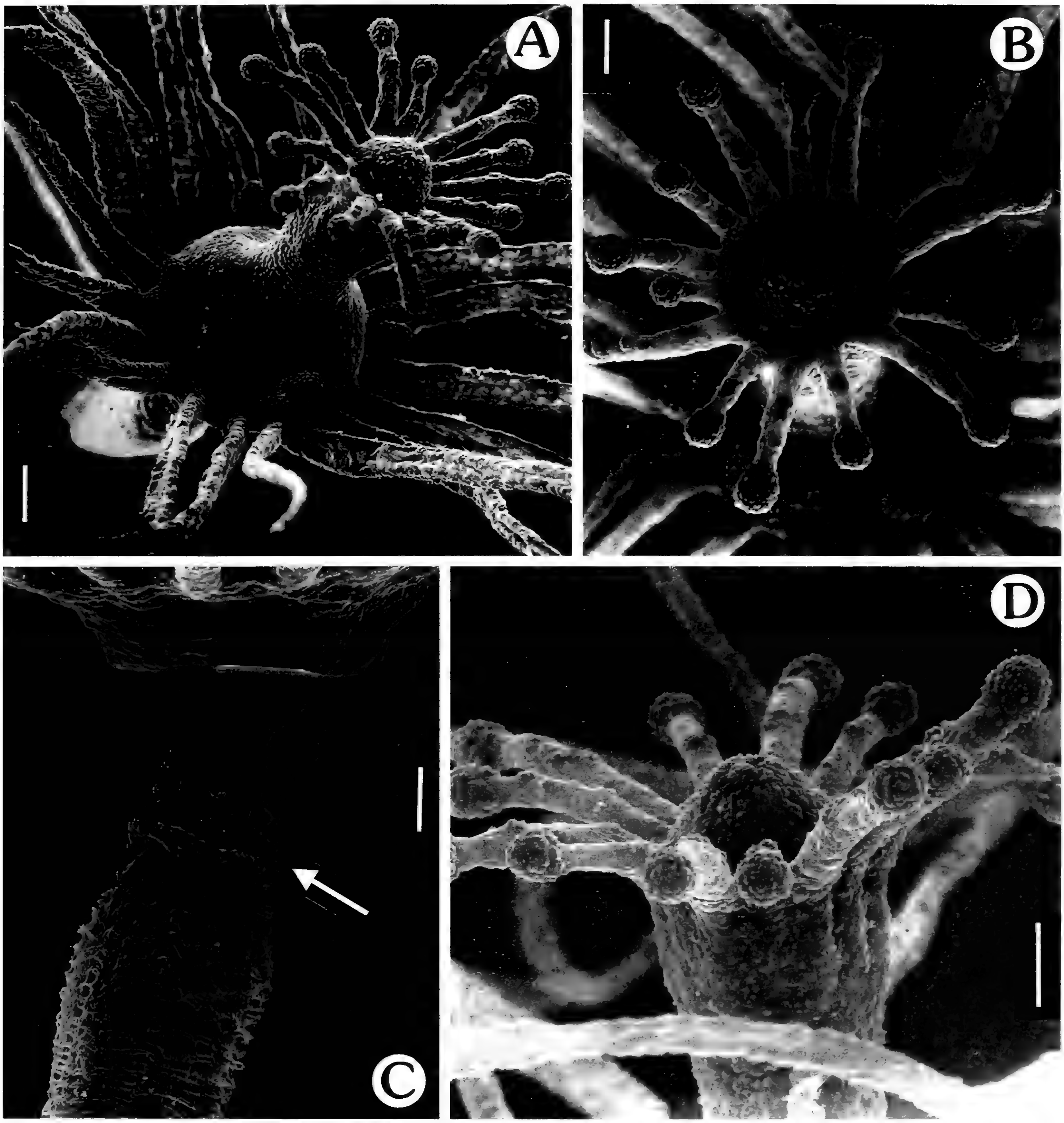

Fig. 1. Scanning electron micrographs of *Ectopleura obypa*, new species. A, fronto-lateral view of hydranth, note incipient blastostyles just above aboral tentacles; B, oral view of hydranth; C, neck region; the arrow points to the groove where filmy perisarc is secreted; D, lateral view of hypostome and oral tentacles. Scale bar, A, B = 100 μm; C, D = 50 μm.

canal short. Color: umbrella transparent; subumbrella green when illuminated sideways; manubrium pink-white; marginal bulbs milky-white with small red dots.

The types and measurements of nematocysts of hydranth and medusa are listed below. Morphological character variation of many colonies and newly released medusae are in Tables 1 and 2, respectively.

Nematocysts.—(in μm) (Fig. 3D)
Hydranth
Oral tentacle:
- Stenotele − 13.5 − 14.0 × 12.0 − 13.0 (abundant)
- Stenotele − 6.0 − 8.5 × 6.0 − 7.5 (abundant)
- Microbasic eurytele − 9.0 − 10.0 × 4.0 − 4.5

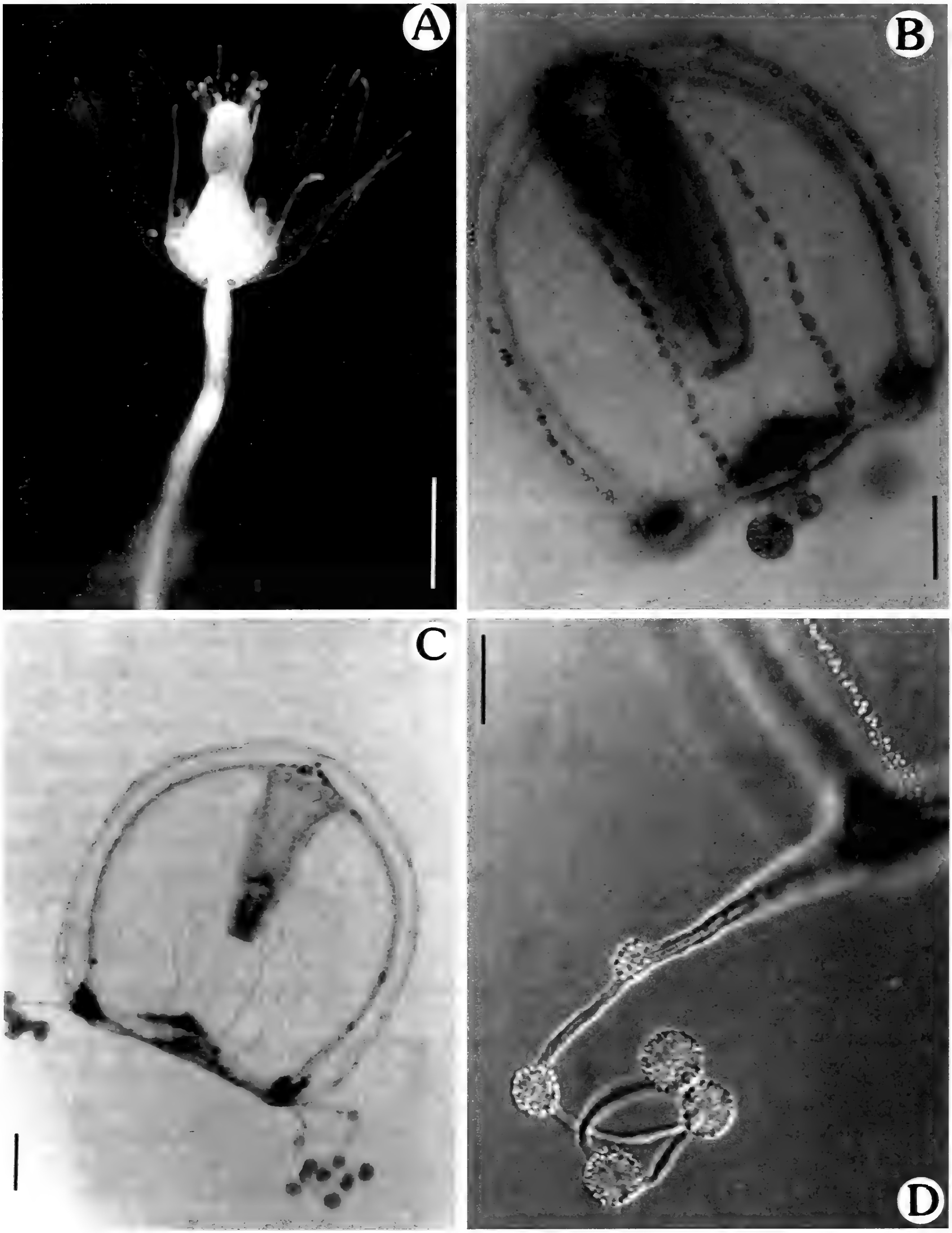

Fig. 2. Photographs of live specimens of *Ectopleura obypa*, new species. A, lateral view of a hydranth with incipient blastostyles; B, lateral view of a newly-liberated medusa; C, lateral view of a 6-day-old medusa; D, detail of a tentacle of a 7-day-old medusa. Scale bar, A = 1.0 mm; B, D = 100 μm; C = 200 μm.

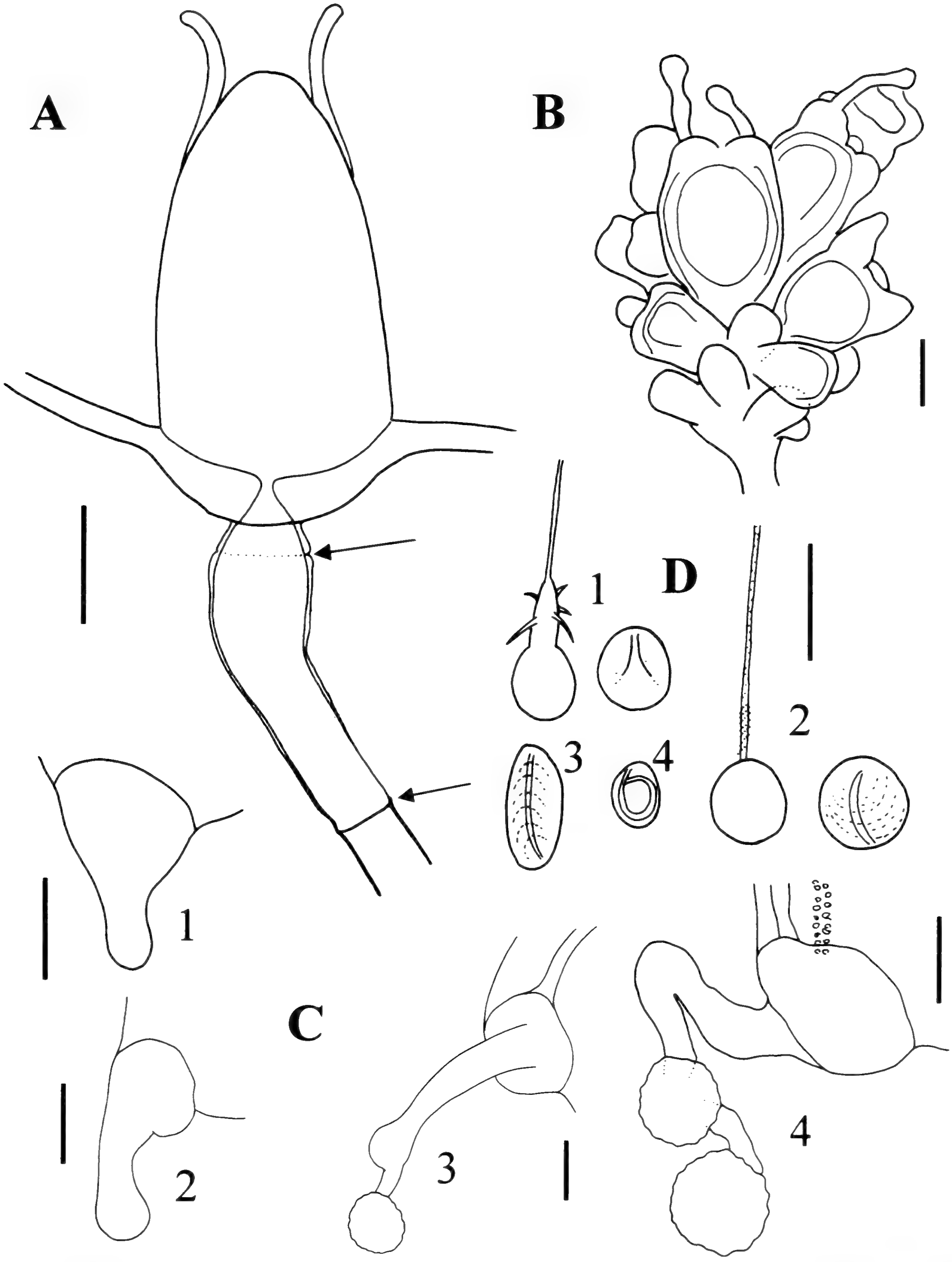

Fig. 3. *Ectopleura obypa*, new species. A, outline diagram of hydranth, traced from a whole mount preparation; the upper arrow points to the region where the film perisarc is secreted; the lower arrow indicates the beginning of the firm perisarc; B, lateral view of a blastostyle with several well developed medusa buds; C. sequence in the development of a medusa tentacle; C4 is the oldest stage, just before liberation from blastostyle; D. nematocysts; D1, stenotele; D2, basitrichous isorhiza; D3, microbasic mastigophore; D4, desmonome. Scale bar, A = 0.5 mm; B = 100 μm; C = 50 μm; D = 10 μm.

Table 1.—Morphological character variation of hydroids of *Ectopleura obypa,* new species.

	Measurements [average ± SD (range)]
Hydrocauli	
Length (mm)	18.5 ± 6.9 (0.87–30.3)
Distal diameter (mm)	0.20 ± 0.03 (0.13–0.26)
Proximal diameter (mm)	0.34 ± 0.07 (0.22–0.60)
Hydranth	
Total length (mm)	1.85 ± 0.55 (1.18–3.30)
Length from the base of aboral tentacles to the apex of hypostome (mm)	1.41 ± 0.42 (0.88–2.70)
Diameter at the level of aboral tentacles (mm)	1.09 ± 0.30 (0.62–1.80)
Tentacles	
Aboral	
Number	23.8 ± 2.9 (16–30)
Length (mm)	2.50 ± 0.59 (0.91–3.90)
Oral	
Number	20.8 ± 3.25 (14–29)
Length (mm)	0.79 ± 0.16 (0.42–1.20)
Gonosome	
Number	8.55 ± 2.10 (4–14)
Length (mm)	0.91 ± 0.55 (0.15–2.10)

Aboral tentacle:
- Stenotele − 13.5 − 14.0 × 12.0 − 13.0 (rare)
- Stenotele − 6.0 − 8.5 × 6.0 − 7.5 (abundant)
- Microbasic eurytele − 9.0 − 10.0 × 4.0 − 4.5 (abundant; more at tip)
- Desmoneme − 4.0 − 5.0 × 3.5 − 4.0 (abundant)

Newly released medusa
- Basitrichous isorhiza − 8.0 − 10.5 × 8.0 − 9.0
- Stenotele − 8.0 − 8.5 × 7.0 − 8.0
- Microbasic eurytele − 9.0 − 10.5 × 4.0 − 4.5
- Desmoneme − 6.0 × 4.0

Etymology.—The species name is derived from the word "obypa", in the language of the Brazilian Tupi natives, meaning green, the color of the blastostyles. It is pronounced "õ-bi-på".

Development of medusa.—Medusae kept in the laboratory, despite several different combinations of temperature, salinity, type of food and volume of culturing water, grew slowly and did not change significantly in morphology. Medusae usually did not capture food by themselves. Ingestion occurred only when the offered nauplius was touched to the manubrium; we never saw the transfer process of the prey from the tentacles to the mouth of the medusa. From the several cultures started only one batch had medusae with gonads, although even these were not completely developed (medusae 25 days old, from colony collected 17 Jun 1996, kept at 19°C). We are aware that these unsuccessful efforts probably indicate the cultivated medusae do not represent the species under natural conditions, but we decided to include our observations on growth rate and morphology. Developing gonads were first observed in 7 to 9 d old medusae. These medusae were 1380–1440 μm high, 1050–1150 μm in maximum diameter and had tentacles with 6 knobs, attaining ca. 800 μm in length (Fig. 2C, D). They lived 16 more days, maintaining approximately the same size and general features except for a slight growth of the gonads, which bulged a little around the middle of the manubrium. Tentacles developed up to 7 nem-

Table 2.—Morphological character variation of newly-released medusae of *Ectopleura obypa,* new species, from three different colonies.

	[average ± SD (range)]
Height (μm)	594.5 ± 101.9 (460–780)
Maximum diameter (μm)	516.0 ± 82.1 (396–660)
Diameter at base (μm)	344.5 ± 69.6 (240–440)
Diameter of aperture (μm)	~120
Length of manubrium (μm)	510.2 ± 141.7 (276–780)

atocyst knobs. The number of tentacles did not change in any specimens during growth; nor was there any indication that the two other perradial bulbs would give rise to tentacles.

Remarks.—This description of *Ectopleura obypa,* new species, especially color, size and general shape, is based mainly on live material. Colors in fixed material disappeared. Some anesthetized and fixed hydranths, although well preserved, did not keep their natural shape: hydranths from AM1324 are inflated and most have the upper part of the neck dilated. Fixed medusae usually have longer manubria than live specimens, and perradial and interradial grooves appear in the umbrella (as also observed for *E. sacculifera,* see Brinckmann-Voss 1970:28).

The long, flexible and contractile neck enables the hydranth to bend in any direction. In still water under laboratory conditions, the hydranths performed regular circular movements interspersed with strong contractions of the neck. We could not ascertain the number of ridges in the endoderm of hydrocaulus, but we suppose the two bands of white pigments present along the neck indicate the existence of two of these ridges in *E. obypa.* The blastostyles were so vivid a green, even early in development, that when fully developed the whole hydranth appeared green to the naked eye. The medusa started pulsating hours before liberation, already capable of catching and ingesting food, and the manubrium moved peristaltically and vermicularly.

Besides *E. obypa,* new species, two other species of *Ectopleura* were recorded from the region of São Sebastião: *Ectopleura dumortieri* (Van Beneden, 1844) and *Ectopleura warreni* (Ewer, 1953) (see Migotto & Silveira 1987:100–103, Migotto 1996: 24–25). The polyp of *Ectopleura dumortieri* is solitary, and has free medusae with 4 marginal tentacles; *E. warreni* has fixed gonophores.

Ectopleura obypa is referred to a large group of species diagnosed by the presence of free medusae with 8 meridional nematocyst tracks in the umbrella, issuing in pairs from tentacle bulbs (Schuchert 1996: 107). Complementary characters are: evenly rounded umbrella; four radial canals and tentacle bulbs; manubrium short, not extending beyond bell margin; medusa tentacles moniliform or with abaxial nematocyst clusters (Schuchert 1996:107). The cnidome of species having free medusae is characterized by microbasic euryteles (besides other types such as stenoteles and desmonemes), a type of nematocyst not present in the species of *Ectopleura* with fixed gonophores (see Petersen 1990:160; note that the author interchanged the distribution of anisorhiza and microbasic euryteles in figure 19, characters 2 and 6).

Among species of *Ectopleura* with free medusae, two subgroups are clearly recognized on the basis of the number of marginal tentacles in the medusa: 2 tentacles and 4 tentacles.

Species described as having 4 perradial tentacles are *E. americana* Petersen, 1990, *E. dumortieri* (Van Beneden, 1844), *E. be-*

Table 3.—Comparisons of morphology of species of *Ectopleura* having two-tentacled medusae. Information from Brinckmann-Voss (1970), Calder (1988), Kramp (1957), Mayer (1900), Petersen (1990) and Thornely (1900).

	E. wrighti	*E. pacifica*	*E. mayeri*	*E. xiamenensis*[a,b]	*E. sacculifera*[a]	*E. minerva*[a]	*E. obypa* new species
Hydrocaulus	equal in width throughout, with 2 endodermal ridges	with 2 endodermal ridges	increasing in width from base to distal end, with 2 endodermal ridges	—	—	—	increasing in width from base to distal end, with 2 endodermal ridges
Length of hydrocaulus	10–20 mm	10–20 mm	up to 25 mm	—	—	—	up to 30 mm
Aboral tentacles	11–20; circular in cross section	15–20; circular in cross section	17–22; circular in cross section	—	—	—	16–30; laterally flattened
Oral tentacles	5–10; not adnate to hypostome, moniliform	12–18; slightly adnate to hypostome; nematocysts concentrated in a swollen tip	15-20; not adnate to hypostome, filiform, with evenly distributed nematocysts	—	—	—	14–19; slightly adnate to hypostome nematocysts concentrated in a distal capitulum and on 1–3 adoral swellings
Number of blastostyles	5–8, short, dichotomously branched	6–8, short, dichotomously branched	8, short, dichotomously branched	—	—	—	4–14, long; occasionally bifurcated
Sexual condition of attached medusa	without gonads	without gonads	without gonads	—	—	—	without gonads
Manubrium	as long as bell cavity	?	⅔ length of bell cavity	as long as bell cavity	½ length of bell cavity	⅔ length of subumbrellar cavity	½ length of bell cavity
Umbrella	liberated medusa 1 mm high, nearly hemispherical; thin; without apical projection and canal (?)	mature medusa not known	2.8 mm high before liberation, dome-shaped; with apical projection; thin	0.7 mm high, dome-shaped, without apical canal; thin	3 mm high, slightly conical; thick; without apical canal	2.5 mm high; pear-shaped; with apical projection and apical canal	up to 1.5 mm high; dome-shaped; with apical projection

[a] Hydroid stage not known.

[b] Data obtained from Petersen (1990).

thae (Warren 1908) and *E. indica* Petersen, 1990.

Besides *E. obypa* there are six species of *Ectopleura* having medusae with 2 opposed tentacles: *Ectopleura wrighti* Petersen, 1979, *E. pacifica* Thornely, 1900, *E. mayeri* Petersen, 1990, *E. minerva* Mayer, 1900, *E. sacculifera* Kramp, 1957, and *E. xiamenesis* Zhang & Lin, 1984 (see Table 3). The last three of these are known only from the medusa stage. *Ectopleura sacculifera* and *E. xiamenensis* do not have an apical canal, contrasting in this with *E. minerva* and *E. obypa*. Moreover, *Ectopleura sacculifera* is clearly distinct from the rest by having a thick umbrella and pendent gonads on the manubrium wall (Kramp 1957:7, plate 3, figs. 1–3). Neither an apical canal nor an apical projection were mentioned by Brinckmann-Voss (1970:25–27) in the description of young and adult medusae of *E. wrighti* (as *E. larynx*), and we suppose they are not present in this species. Nematocyst clusters of the marginal tentacles in medusae of *E. obypa* are clearly diffrent from those of *E. minerva* Mayer, 1900 (Mayer 1900, fig. 125) and *E. sacculifera* (cf. Brinckmann-Voss 1970:28, fig. 29.1), which are exclusively abaxial and do not involve the tentacle as in *E. obypa* (exclusively abaxial clusters of nematocysts are also present in an unidentified species of *Ectopleura* with a two-tentacled medusa described by Schuchert 1996:112, fig. 67).

It is difficult to link the species known only by the medusoid stage with polypoid stages already described in the literature, due to the lack of life cycle studies. Except for *E. wrighti* (see Brinckmann-Voss 1970: 25, as *E. larynx*) and *E. obypa*, data on medusa stages are few and based on immature specimens still attached to blastostyles. *Ectopleura wrighti* is the only species in which medusae obtained from hydroid colonies were raised through maturity (Brinckmann-Voss 1970:25). Petersen (1990:166) described *Ectopleura mayeri* (=*E. pacifica* of Calder 1988:53–55) as a "new species", even though he acknowledged the possibility of its being the hydroid stage of *E. minerva* Mayer, 1900, because the medusa of the first "has not been reared to a stage where it can be identified with certainty".

Hydroid stages of other species with two-tentacled medusae have many similar features: general size, number of oral and aboral tentacles, and number of blastostyles. They all have 2 endodermal ridges in the hydrocaulus, but this character is shared with other species having different numbers of tentacles. The aboral tentacles of *E. obypa* and *E. pacifica* are slightly adnate to the hypostome, in which they differ from *E. wrighti* and *E. mayeri*. *Ectopleura obypa* differs from *E. pacifica* in the morphology of its oral tentacles (see Table 3), and is unique in having flattened aboral tentacles.

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Striatodoma dorothea (Cheilostomatida: Tessaradomidae), a new genus and species of bryozoan from deep water off California

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Abstract—*Striatodoma dorothea*, a new genus and species of cheilostomate bryozoan, is described from material found attached to hexactinellid sponges and pogonophoran tubes at an abyssal station (4100 m depth) off central California. Members of this new genus can be distinguished from other members of the family Tessaradomidae by the presence of biserial, rather than quadriserial branches, and a peristomial sinus, rather than an enclosed spiramen. Two other Pacific species, *Diplonotos striatum* Canu & Bassler, 1930, and *Tessaradoma bifax* Cheetham, 1972, are transferred to *Striatodoma*.

Although bryozoans have been identified from deep-sea stations down to 8300 m, reviews by Schopf (1969) and Hayward (1981) have shown that only a tiny portion of the deep ocean floor has been sampled for the group. Nothing is known of the deep-sea bryozoan fauna of the eastern Pacific with the exception of three species found at two stations in the eastern Pacific between Acapulco and Panama during the *Galathea* Expedition (Hayward 1981). Recently, as part of a study by Beaulieu (1998) of hard substrate epifauna at abyssal depths off California, an attempt was made to identify all taxa attached to biogenic structures that protruded from the soft sediment of the sea floor. Individual stalks of the hexactinellid sponge *Hyalonema* sp. and individual tubes of the pogonophoran *Unibrachium* sp. were sampled in tube cores using the submersible *Alvin* at 4100 m depth. Two of the approximately 140 species found attached to the sponge stalks and pogonophoran tubes were bryozoans. One is a ctenostome, *Arachnidium hippothooides* Hincks, 1862. The other is an undescribed genus and species of deep-sea cheilostome which we name and describe below.

Tessaradomidae Jullien, 1903

Striatodoma, new genus

Diagnosis.—Tessaradomidae characterized by subcylindrical, proximally thickened branches with two series of zooids, longitudinally striated calcification, a spiramen in close association with zooid peristome, rows of marginal pores, some of them replaced by oval avicularia, and a subglobular imperforate ovicell. *Striatodoma* differs from *Tessaradoma* in possessing branches made up of two, rather than four series of zooids, and in confluence of the spiramen with a peristomial sinus.

Type species.—*Striatodoma dorothea*, new species, by present designation.

Additional species of Striatodoma.—*Tessaradoma bifax* Cheetham, 1972 and *Diplonotos striatum* Canu & Bassler, 1930.

Etymology.—The first part of the genus name is from the Latin, *striatus* = furrowed, channeled, descriptive of the striated appearance of colony walls. The second part, *doma*, is derived from the Greek δωμα, δωματοζ, house, roof, to parallel the other genus name in the family, *Tessaradoma*. Gender neuter.

Remarks.—During the last hundred years seven living and fossil species of deep water cheilostomes have been described and placed in the family Tessaradomidae Jullien, 1903, and genus *Tessaradoma* Norman 1869, type species *Onchopora borealis* Busk, 1860. Jullien defined the family as having erect or encrusting colonies and zooids, a tubular peristome with a tubuliform spiramen opening into its base, and with a small, spherical, imperforate ovicell, also opening into the peristome above the zooidal operculum. The genus *Tessaradoma* has a colony form consisting of erect, unjointed cylindrical branches arising from an encrusting base, zooids with a projecting peristome and prominent spiramen, imperforate ovicells obscured by increasing calcification, and adventitious avicularia (Hayward & Ryland 1979). The type species, *Tessaradoma boreale*, has a Recent distribution in both the North and South Atlantic and is also known from Neogene fossil localities in western Europe and the Mediterranean (Cheetham 1972, Lagaaij & Cook 1973). Its colonies are erect, rigid, and spreading, with quadriserial branches consisting of elongate oval zooids, arranged back to back in alternating pairs. The zooid primary orifice is concealed by a tubular peristome with a spiramen tube near its base, its opening projecting from the zooid frontal surface about one third of the way down the frontal wall. Wall calcification is granular, becoming striated around the conspicuous marginal pores. Oval adventitious avicularia are also developed in the margins, particularly lateral to the spiramen, The ovicell is small, smooth, imperforate, subspherical (slightly broader than long), and though conspicuous in young zooids becomes increasingly immersed in calcification as zooids age (Hayward & Ryland 1979).

Hayward (1981) described *Tessaradoma brevissima* from the Tasman Sea, but Gordon (1989), who recorded *T. brevissima* from additional deep water localities off New Zealand, placed the species in the genus *Galeopsis* (family Celleporidae) on the basis of the following characters: paired avicularia in close association with peristome and sinus, and an ovicell with a central tabulate or fenestrate area and labellum. Two South African species, *Tessaradoma bispiramina* and *Tessaradoma circella*, described by Hayward & Cook (1979), and the Indonesian species *Tessaradoma bipatens*, described by Harmer (1957) also seem to belong in this group.

In contrast, the new Pacific species described below, as well as two other Pacific species, the Eocene *Tessaradoma bifax* from the small western Pacific Island of Tonga (Cheetham 1972), and the Recent *Tessaradoma striatum* from the Galapagos (Canu & Bassler 1930), differ from them in the furrowed appearance of frontal wall calcification, the subspherical imperforate ovicell and the association of the spiramen with the peristomial sinus. These Pacific species appear to be related to *Tessaradoma*, but their shared features indicate they should be grouped with the new species described below in a new genus, *Striatodoma*. The Eocene *Tessaradoma bifax* described by Cheetham (1972) from Tonga, is very similar in morphology to *Striatodoma dorothea*, with biserial branches, tubular peristome, and with lateral pores and avicularia making a sinuate double trail along the sides of branches. In this species, however, the sinus (at least in the fragmentary material available) does not become calcified into a tube. In addition, its ovicell is not as prominent as that of *S. dorothea*, appearing only as a slight enlargement of the peristome of the maternal zooid, and a swelling of the frontal shield of the distal zooid. The Recent *Diplonotos striatum* collected from the Galapagos at 1251 m depth (Canu & Bassler 1930) also belongs in this group. Based on his studies of syntype material, Cheetham (1972) transferred that species to

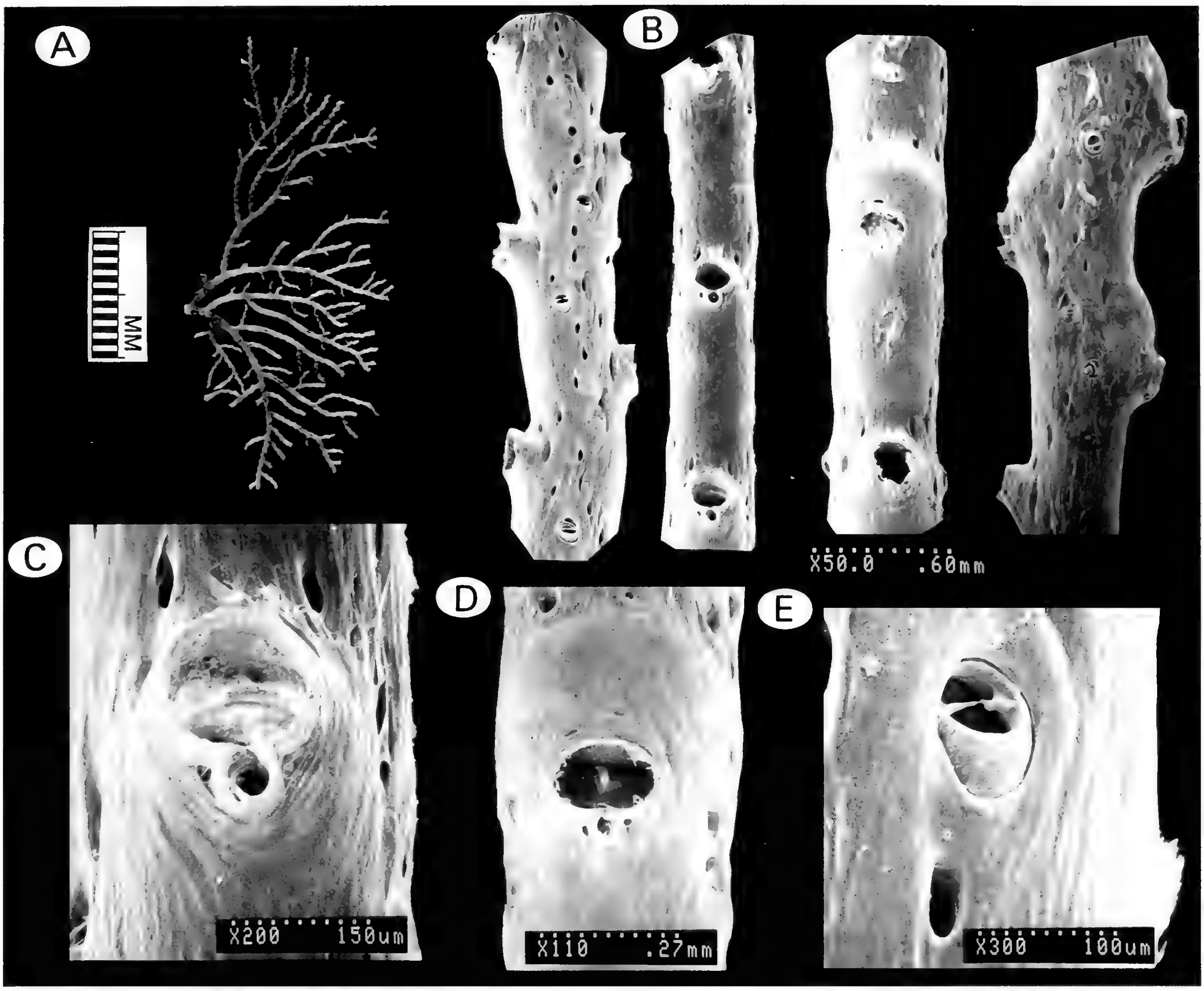

Fig. 1. *Striatodoma dorothea* new species. All illustrations from portions of holotype colony. CASIZ 113579, attached to pogonophoran tube collected 4100 m depth on *Alvin* Dive 2828 at 34°42′N, 123°00′W, off California. (A) Largest colony fragment showing colony form and branching pattern [scale = 2 cm]. (B) Zooid morphology [from left to right] autozooids in side and front view; ovicelled zooids in front and side view [scale bar = 0.6 mm]. (C) Closeup of peristome, showing spiramen sinus [scale bar = 150 μm]. (D) Closeup of mature ovicelled zooids, showing constricted peristome and completely enclosed sinus [scale bar = 0.270 mm]. (E) Closeup of lateral avicularium, showing diagonally tilted rostrum and calcified pivotal hinges [scale bar = 100 μm].

Tessaradoma on the basis of its similarity to *T. bifax*, remarking that, contrary to Canu and Bassler's original description, the primary orifice does lie at the base of a peristomial shaft, but that shaft is almost completely immersed in the thickened frontal shield. Its chief difference from the other two species lies in the extreme development of frontal wall calcification, in which striation becomes rugosity and external zooid boundaries are lost. The positions of lateral avicularia and pores may still be faintly discerned, however, and match the pattern in the other two species. Like *S. dorothea*, the sinus in *S. striatum* may become completely enclosed to form a tube.

Striatodoma dorothea new species
Fig. 1

Holotype.—California Academy of Sciences, CASIZ 113579, attached to pogonophoran tube collected as stalk no. 3 (Beaulieu 1998) at 34°42′N, 123°00′W, 4100 m depth, 17 Sep 1994.

Paratypes.—Virginia Museum of Natural History 567; from stalk 4, ~4100 m, PULSE 22 Cruise, Chief Scientist Kenneth

Table 1.—Measurements (in mm) of holotype and paratype specimens of *Striatodoma dorothea.*

Character	Range	Mean	SD	*n*
Zooid Length	0.364–0.501	0.444	0.038	12
Zooid Width	0.191–0.273	0.231	0.027	12
Orifice Length (autozooid)	0.073–0.100	0.085	0.009	12
Orifice Width (autozooid)	0.091–0.109	0.102	0.008	12
Orifice Length (ovicelled zooid)	0.073	—	—	2
Orifice Width (ovicelled zooid)	0.100	—	—	2
Ovicell Length	0.109–0.155	0.134	0.016	6
Ovicell Width	0.182–0.210	0.196	0.011	6
Avicularia Length	0.036–0.055	0.044	0.007	11
Avicularia Width	0.027–0.046	0.036	0.004	11
Branch Width (Distal end)	0.291–0.337	0.301	0.025	12
Branch Width (Basal end)	0.364–0.728	0.558	0.103	9

L. Smith, Jr., Scripps Institution of Oceanography, *Alvin* Dive 2828, 17 Sep 1994. Water temperature 1.2°C, 34°42′N, 123°00′W; CASIZ 113580, stalk 37, 34°56′N, 123°07′W, 4100 m, PULSE 24 FVGR, 16 Feb 1995; CASIZ 113581, stalk 33, 34°42′N, 123°00′W, 4100 m, PULSE 25, Dive 2920, 30 Apr 1995; CASIZ 113582, stalk 12, 34°42′N, 123°00′W, 4100 m, PULSE 22, Dive 2834, 23 Sep 1994; collector for all, Stace Beaulieu.

Etymology.—dorothea, the Latinized spelling of Dorothy, used as a noun in apposition. The species is named in honor of Dorothy F. Soule, in recognition of her elegant studies of Pacific bryozoans and of her active stewardship of California marine environments.

Diagnosis.—Characterized by subcylindrical branches made up of two series of rectangular zooids, with longitudinally striated calcification, rows of marginal pores, with occasional pores replaced by oval avicularia, short peristome with spiramen enclosed in proximal peristomial sinus, and relatively prominent ovicell.

Description.—Colony erect, rigidly calcified, unjointed, broadly branching in a planar fashion, up to several cm in size, the two biggest branch fragments of the largest specimen found (the holotype), measuring 3 cm h × 7 cm w and 5 cm h × 5 cm w, respectively (Fig. 1A). Attached to stalks of deep water glass sponges and pogonophoran tubes by an encrusting base. Zooids elongate, rectangular, growing back to back in two alternating longitudinal series (Fig. 1B). Frontal wall convex, with faint longitudinal striations, most of its surface imperforate, but with a row of small oval pores just inside zooid lateral margins. Primary orifice transversely oval, surrounded by a short peristome (Fig. 1C). No outwardly visible spiramen; instead, the peristome of young zooids has a proximal sinus, which is encircled by calcification as the zooid ages, becoming increasingly tubular and projecting. Ovicells are smoothly calcified and globular, reaching the height of the peristome opening, which becomes slightly narrowed in fertile zooids (Fig. 1D). About one pore per zooid is replaced by an oval adventitious avicularium, about 50 μm in length. In side view the sinuate double track of pores and avicularia is distinctive (Fig. 1E, B). In basal regions of the colony zooid openings are calcified over and branches become thickened. Some of the avicularia and pores are calcified over also. Branch thickness (the depth of two back to back zooids) averages 0.301 mm in zooids near the growing edge of branches and 0.558 mm in zooids near the colony base. Zooid measurements are summarized in Table 1.

Distribution and ecology.—The species was observed and/or collected at 4060–4100 m depths off California, between latitudes 34°38′ and 34°56′N and longitudes 122°59′ and 123°15′W. General area: 220 km west of Point Conception, CA. Beaulieu (1998) collected a total of 35 tube core samples at the abyssal station and found seven colonies of *S. dorothea* (one colony per substrate; Table 2). The species was attached to pogonophoran tubes, the basal spicules of *Hyalonema* sp., and to other organisms that were attached to the host substrate. The branches of *S. dorothea* also provided substrate on which other species attached (Table 2).

In order to determine the abundance of *S. dorothea* at the abyssal station, all colonies large enough to identify with certainty were enumerated in photographic transects of the sea floor (procedures described in Beaulieu 1998). We photographed approximately 9 km of the sea floor (total of seven transects) in which we encountered 55 colonies of *S. dorothea.* Of these, 53 were attached to dead *Hyalonema* spicules, one to a pogonophoran tube, and one to an unidentified structure. The encrusting bases of most of the colonies were attached at the middle of the host substrate, elevating the colonies about 10 cm above the sea floor. Density estimates (no. colonies per unit area of sea floor) were calculated using the computer program DISTANCE (Laake et al. 1994). Mean density estimates for the individual transects ranged between 3 and 8 colonies per 1000 m^2. Only about 2% of the biogenic structures enumerated in photographic transects appeared to be colonized by *S. dorothea.* However, 20% of the structures collected from the sea floor had *S. dorothea* attached; therefore, the density estimates from the photographic transects may be an order of magnitude low.

Discussion.—Tessaradomids belong to the fauna of the outer continental shelf and slope. The 4100 m depth recorded for *S. dorothea* in this study is the deepest recorded, but it is not much deeper than the 3700 m recorded for *T. boreale.* However, *T. boreale* is found in much shallower water in the Arctic (70 m depth), and Cheet-

Table 2.—Ecological information for *Striatodoma dorothea* collected in tube cores.

Colony no.	Host substrate	Attached to:	Epizoites attached to *S. dorothea*
1[a]	Pogonophoran	Pogonophoran and terebellid (*Thelepus* sp.) tubes	Agglutinated foraminifera, calcareous foraminiferan (*Cibicides lobatulus*), colonial hydroid, sabellid, serpulids (*Bathyvermilia* sp. and *Hyalopomatus mironovi*), isopod (*Arcturus* sp.)
2	Pogonophoran	Pogonophoran tube	Agglutinated foraminiferan, calcareous foraminiferan (*Cibicides lobatulus*), colonial hydroid, serpulid (*Hyalopomatus mironovi*)
3	*Hyalonema*	n.d.	Overgrown by colonial hydroid
4	*Hyalonema*	n.d.	None
5	*Hyalonema*	*Hyalonema* spicules	Overgrown by colonial hydroid
6	*Hyalonema*	Serpulid (*Bathyvermilia* sp.) tube	None
7	*Hyalonema*	*Hyalonema* spicules	None

[a] Holotype specimen.

n.d. not determined.

ham (1972) suggested that distribution of such deep-sea species may be temperature controlled, limited to water temperatures between 2° and 13° C. This paper and Beaulieu (1998) provide a glimpse of how erect bryozoans with an attached base may survive on the muddy deep sea floor. But as yet, these species are known only from a few broken fragments, collected at widely scattered localities by various expeditions. Better understanding of their ecology as well as clarification of their relationships with shallow water species must await the kinds of collections that can provide material adequate for the detailed anatomic study necessary for phylogenetic analysis.

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Two new species of *Dentatisyllis* and *Branchiosyllis* (Polychaeta: Syllidae: Syllinae) from Venezuela

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Abstract.—A new species of the genus *Dentatisyllis* Perkins, 1981 and another new species of the genus *Branchiosyllis* Ehlers, 1887 are described: *Dentatisyllis morrocoyensis* and *Branchiosyllis lorenae*. The specimens of both new species were collected during a study of the polychaetes from *Thalassia testudinum* beds in Morrocoy Park, Venezuela. One specimen of *B. lorenae* was previously collected and reported as *Branchiosyllis* sp., from Cuba by San Martín (1991), so this species could be distributed throughout the Caribbean area. *Dentatisyllis morrocoyensis* is distinguished from all other species of the genus by the high number and shape of teeth in the trepan and shape of the blades of the compound setae, unique in the genus. *Branchiosyllis lorenae* is very similar to *B. exilis* but differs by having, on the anterior and midbody parapodia, 1–2 compound setae, the bidentate blades of which are slightly curved and bear a distal tooth somewhat shorter than the proximal one. This latter characteristic is unique to the genus.

During a study on the ecology of the polychaetes inhabiting *Thalassia testudinum* beds in the Morrocoy Park, Venezuela, specimens of two undescribed species of Syllidae were collected. A series on the taxonomy and ecology of several families of polychaetes from this area and habitat has been recently begun (Bone & Viéitez 1999). This paper deals with the description of the two new species of Syllidae: *Dentatisyllis morrocoyensis* and *Branchiosyllis lorenae*. The study of the syllids from Morrocoy Park has been supported by the Agreement between the Universities Simón Bolívar (Venezuela) and Autónoma de Madrid (Spain).

Materials and Methods

All samples were collected in shallow *Thalassia testudinum* seagrass beds in less than 0.5 m depth. The samples were taken using a 38 cm^2 corer which was pushed 25 cm into the sediment. Sediment samples were preserved in 10% buffered formalin and washed through a 1 mm mesh sieve. All organisms were hand-picked under a magnifying-lens from the remaining material and separated for taxonomic identifications. Measurements are referred to the holotype or largest specimen studied; width is measured across the proventriculus and excludes cirri, parapodia, and setae. Observations, drawings, and measurements were made using a microscope with interference contrast optics. Drawings were made with the aid of a drawing tube. The SEM micrographs were taken at the SIDI (Servicio Interdepartamental de Investigación) of the University Autónoma of Madrid. Types are deposited in the Museo Nacional de Ciencias Naturales de Madrid, Spain.

Results and Discussion

Family Syllidae Grube, 1850
Subfamily Syllinae Grube, 1850
Genus *Dentatisyllis* Perkins, 1981
Dentatisyllis morrocoyensis, new species
Fig. 1

Material examined.—Morrocoy Park (Venezuela), *Thalassia testudinum* beds, Holotype.

Description.—Body small, thin, cylindrical, without color marking, incomplete, about 4.2 mm long, 0.32 mm wide, 30 setigers. Prostomium semicircular; four small eyes in open trapezoidal arrangement and two anterior eyespots. Only one lateral, broken antenna present on this specimen, with 10 articles, originating in front of anterior eyes. Palps slightly longer than prostomium, fused at bases. Tentacular segment distinct, somewhat shorter than following segments; dorsal tentacular cirri with about 13 articles; ventral tentacular cirri somewhat shorter, with about 8 articles. Dorsal cirri of first setiger long, with about 23 articles; remaining dorsal cirri alternating long and short; long dorsal cirri similar in length to body width, with about 17–18 articles, short dorsal cirri shorter than body width, with about 10 articles (Fig. 1A). Parapodia elongate, each with distal anterior lobe, somewhat shorter than distal posterior lobe; ventral cirri long, digitiform, extending past tips of parapodial lobes, distally broad (Fig. 1D). Compound setae all heterogomph falcigers, similar throughout; about 8–10 setae on each parapodium. Blades bidentate, with both teeth very close, similar in length. Marked dorso-ventral gradation in shape and length of blades; blades of dorsal-most compound setae long, about 38 μm, with short and coarse spines on margin; remaining blades provided with long, coarse, upwards dressed, 3–4 spines on bases, especially on medium size ones, and shorter and thinner spines distally; blades of ventral-most compound setae about 20 μm length (Fig. 1F). Simple dorsal and ventral setae not seen. Parapodia each with two slender aciculae, ending with fine tips (Fig. 1E). Pharynx long, everted on this specimen (Fig. 1A); anterior margin (Fig. 1A, B) surrounded by a trepan of about 50 curved, hooked teeth (Fig. 1B, C), and a crown of about 20 soft papillae; midorsal pharyngeal tooth rhomboidal, small, located subterminally to anterior margin. Proventriculus shorter than pharynx, through 4 segments, with about 27 muscle cell rows.

Remarks.—The genus *Dentatisyllis* was erected by Perkins (1981) for species having a cylindrical body, pharyngeal tooth and a trepan on the anterior margin of the pharynx; the genus has been recently revised by Ding et al. (1998) who provided a diagnosis and a key to all the known species of the genus. *Dentatisyllis morrocoyensis* n. sp., is the only species of the genus provided with a very high number of marginal teeth on the trepan; all other species have about 10, whereas *D. morrocoyensis* has about 50. The blades of the compound setae and the aciculae of *D. morrocoyensis* n. sp. are very similar to those of *Opisthosyllis longidentata* San Martín, 1991, but the pharyngeal armature is completely different (San Martín 1991).

Etymology.—The species is named after the type locality, Morrocoy Park (Venezuela).

Genus *Branchiosyllis* Ehlers, 1887
Branchiosyllis lorenae, new species
Figs. 2, 3, 4

Branchiosyllis sp. San Martín (1991):234, fig. 1O–S.

Material examined.—Morrocoy Park (Venezuela), *Thalassia testudinum* beds, Holotype and 27 paratypes. Additional material: 2 specimens used for SEM.

Description.—Body long, cylindrical (Figs. 2A, 4A), holotype incomplete specimen, 5.3 mm long, 0.4 mm wide, 54 setigers; longest complete paratype 7.2 mm long, 0.48 mm wide, 50 setigers, a few somewhat longer, incomplete paratypes. Most anterior segments without color mark-

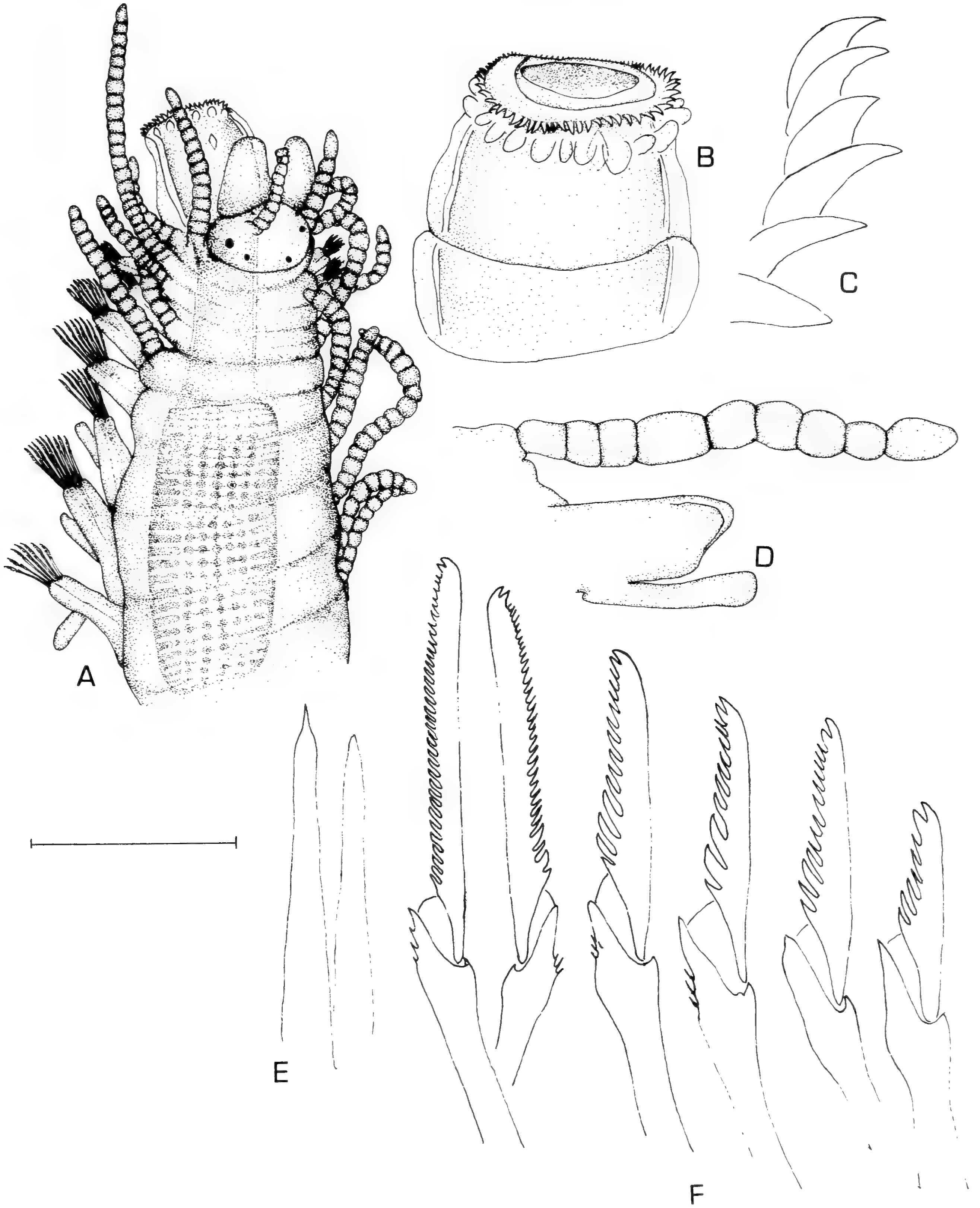

Fig. 1. *Dentatisyllis morrocoyensis*, n. sp. Holotype. A, anterior end, dorsal view; B, ventral view of the anterior end of the pharynx; C, detail of the teeth of the trepan; D, midbody parapodium, anterior view; E, aciculae, from midbody; F, compound setae, midbody. Scale.—A:0.11 mm. B, D:65 μm. C:48 μm. E, F:20 μm.

ing, anterior and midbody segments provided dorsally each with three ovate dark spots, sometimes forming nearly a row; some articles of antennae, tentacular and dorsal cirri with dark spots (Fig. 2A). Prostomium oval, wider than long; four eyes in very open trapezoidal arrangement, nearly on line, and two small anterior eyespots.

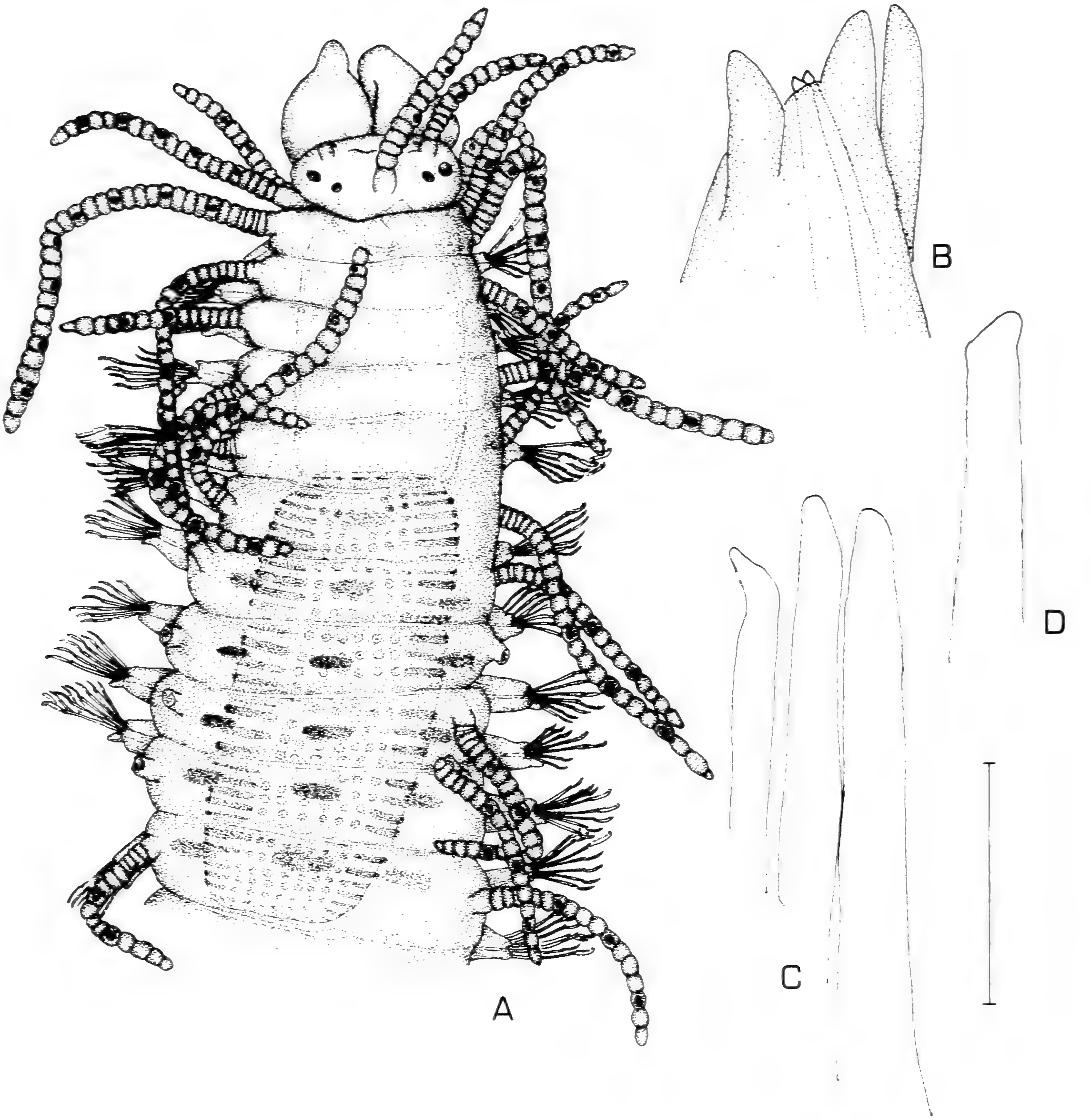

Fig. 2. *Branchiosyllis lorenae*, n. sp. Holotype. A, anterior end, dorsal view; B, parapodial lobe, dorsal view. C, aciculae, anterior parapodium; D, aciculum, posterior parapodium. Scale.—A:0.11 mm. B:48 µm. C, D:20 µm.

Median antenna originating between posterior pair of eyes, somewhat longer than prostomium and palps together, with 14 articles; lateral antennae shorter than median antenna, originating between anterior pair of eyes and eyespots, with 12–13 articles. Palps broad, longer than prostomium, fused at bases. Tentacular segment reduced, covered dorsally by prostomium and setiger 1; dorsal tentacular cirri longer than median antenna, with about 20 articles; ventral tentacular cirri similar in length to lateral antennae, with about 13 articles. Dorsal cirri of setiger 1 very long, with about 30–33 articles; remaining dorsal cirri alternating long, somewhat longer than body width, with 25–30 articles, and short cirri, shorter than body width, with about 16–18 articles. Parapodial lobes conical, provided with two distal, triangular lobes (branchiae), anterior

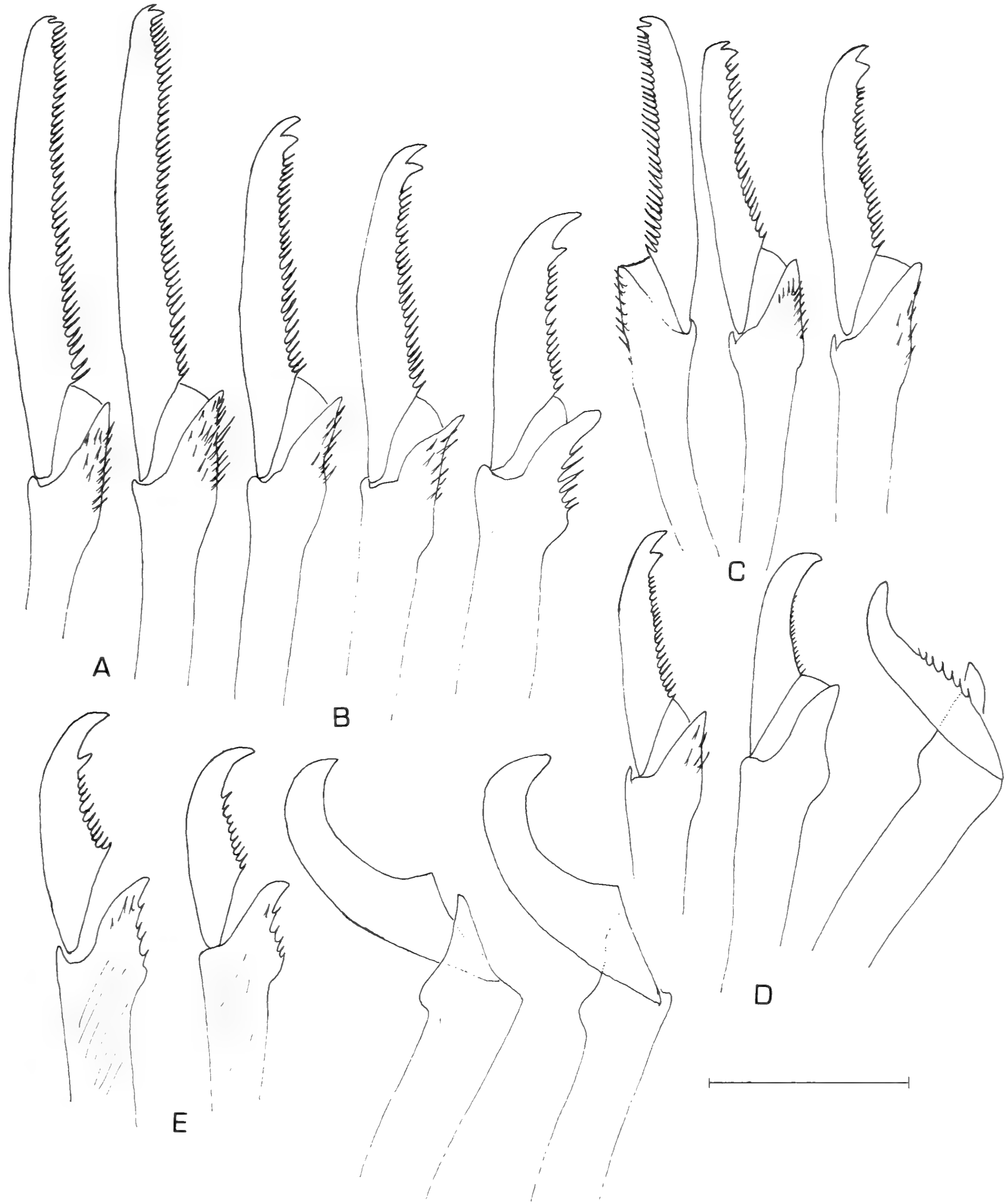

Fig. 3. *Branchiosyllis lorenae*, n. sp. Compound setae: A, dorsal from anterior parapodium; B, median and ventral from anterior parapodium. C, from anterior midbody; D, from posterior midbody; E, from posterior parapodium; F, claw-shaped setae, from posterior-most parapodia. Scale.—20 μm.

lobe somewhat shorter than posterior lobe (Figs. 2B, 4E). Ventral cirri digitiform, elongate, reaching distal level of parapodial lobes. Anterior parapodia each with 1–2, sometimes 3, dorsal, compound setae provided with long, somewhat curved, bidentate blades, 50–55 μm, distal tooth short and small proximal tooth somewhat larger, more prominent (Figs. 3A, 4C); spines on margin short, several rows of spines observed by SEM, slightly longer than those of the rest of blade, partially covering prox-

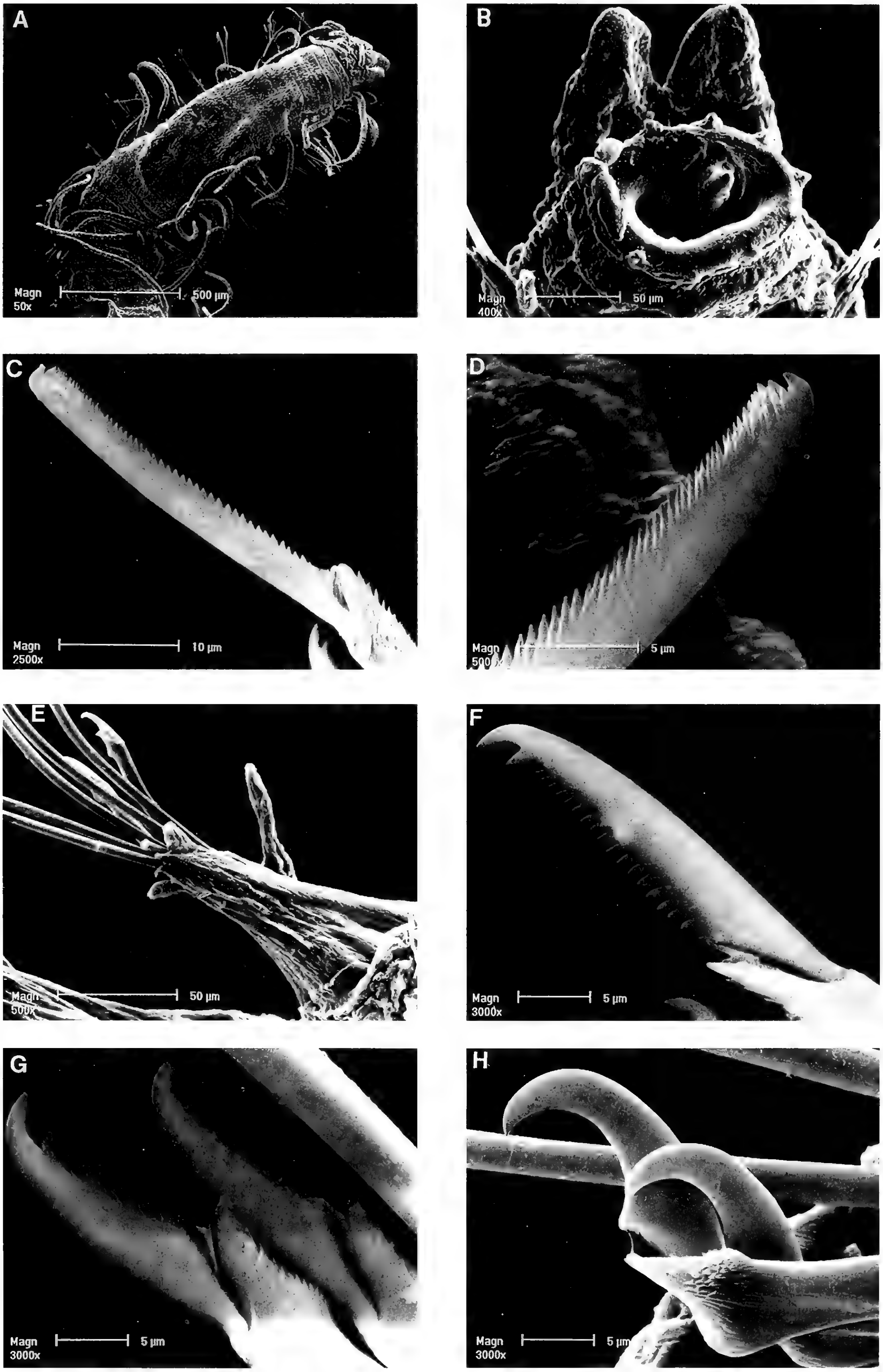

Fig. 4. *Branchiosyllis lorenae*, n. sp. SEM. A, anterior end, dorsal view; B, anterior rim of pharynx; C, long bladed, dorsal compound seta, anterior parapodium; D, detail of the same, showing several rows of spines on distal part. E, midbody posterior parapodium; F, dorsal compound seta from midbody; G, ventral compound setae from midbody; H, claw-shaped compound setae, from posterior-most parapodia.

imal tooth (Fig. 4D), 7–10 median and ventral compound setae with blades curved, bidentate, both teeth similar on longer blades, proximal tooth shorter than distal one on shorter blades; gradation in length, 32 μm above, 24 μm below (Fig. 3B). Progressively decreasing number of compound setae on each parapodium, blades shorter, lacking compound setae with long blades; midbody parapodium with a few bidentate blades and several unidentate, smooth or slightly bidentate, hooked blades (Figs. 3D, 4F, G); posterior parapodia each with a few modified compound setae with blades turned 180°, smooth, strongly hooked, claw-shaped (Fig. 4H); posterior-most parapodia only with 2–3 claw-shaped compound setae (Fig. 3F). Shafts of compound setae distally provided with spines, which are increasingly more numerous and longer in dorsal and anterior setae. Solitary dorsal and ventral simple setae absent. Anterior parapodia each with 3–4 aciculae, diminishing progressively to only 1–2 on posterior parapodia; aciculae with curved tip (Fig. 2C, D). Pharynx broad, through 5 segments; anterior margin provided with a crown of ten soft papillae and one conical middorsal tooth (Figs. 2A, 4B). Proventriculus somewhat longer than pharynx, through 6 segments, with about 30 muscle cell rows. Pygidium small, with two long, articulated anal cirri.

Remarks.—*Branchiosyllis* is a genus with only five described species: *B. oculata* Ehlers, 1887 (Ehlers 1887), distributed in the Caribbean Sea; *B. exilis* (Gravier, 1900) (Gravier 1900, Westheide 1974, San Martín 1984), a circumtropical species, also present in temperate waters; *B. pacifica* Rioja, 1941 (Rioja 1941), from the Pacific coasts of Mexico; *B. diazi* Rioja, 1958 (Rioja 1958), from the Caribbean coast of Mexico; and *B. abranchiata* Hartmann-Schröder, 1965 (Hartmann-Schröder 1965) from Samoa. A table summarizing the main characters of all these species is provided in Hartmann-Schröder (1978) and San Martín (1984). *Branchiosyllis lorenae*, n. sp. is easily distinguished from *B. oculata*, *B. pacifica* and *B. abranchiata* because these three species have only claw-shaped seta, and lack unmodified ones. *Branchiosyllis lorenae* differs from *B. diazi* in lacking a dorsal branchia on each parapodium and in the shape of anterior compound setae. The most similar species is *B. exilis*; however, *B. lorenae* differs in having compound setae on anterior parapodia with long, curved, blades, with the distal tooth small, shorter than the proximal tooth; this kind of blade is very unusual and *B. lorenae*, n. sp., is the only member of this genus with this kind of seta.

Etymology.—The species is named in honor of Lorena Galindo, who collaborated in the collection of the samples and separation of specimens.

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Parvidrilus strayeri, a new genus and species, an enigmatic interstitial clitellate from underground waters in Alabama

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Abstract.—An exceedingly small oligochaete, *Parvidrilus strayeri*, a new genus and species, is described from a streambed in northern Alabama, U.S.A. The species is up to 1.4 mm long (with up to 33 segments) and has several unusual features. In ovigerous specimens, a clitellum is developed as a pair of lateral rows of a few, large, swollen epidermal cells in segments (IX–) X–XII (–XIII, –XIV). Chaetae are absent from segment II. Otherwise, in the anterior part of the body, there are long hair chaetae as well as small crotchet chaetae in both dorsal and ventral bundles. Furthermore, the chaetal bundles are situated posteriorly in each segment. It is unclear whether gonads are paired or unpaired; testes (testis?) are in segment XI, ovaries (ovary?) in XII. The other reproductive organs include a U-shaped muscular 'genital body' in segment XII and a V-shaped 'copulatory organ' in segments XII–XIII; the exact nature and function of these structures are unknown. The genus is proposed to be classified as the single member of Parvidrilidae, new family. It appears to be most closely related to two, largely Southern Hemisphere, aquatic clitellate families, Capilloventridae and Phreodrilidae. A possible relationship to the monotypic, South American taxon, Narapidae, is also discussed.

In the course of a study of the underground fauna of a crystal clear, spring fed stream in Alabama (Strayer et al. 1995), specimens of an exceedingly small, undescribed, oligochaete were encountered. Dr. David L. Strayer (Institute of Ecosystem Studies, Millbrook, New York, U.S.A.) placed the material at the present author's disposal. It is described as the type species of a new genus, *Parvidrilus*, in the present paper. The phylogenetic affinities of the new species, which appears to represent a new higher level taxon of the Clitellata, are also discussed.

Material and Methods

The worms were collected at a single site in Hendrick Mill Branch, northern Alabama, in October 1990 (Strayer et al. 1995). They were fixed in buffered formalin, stained with Rose Bengal, sorted under a dissecting microscope, and stored in 70% ethanol. The material was then sent to the present author, who stained several individuals in alcoholic paracarmine and mounted them whole in Canada balsam on microscope slides. Most of the measurements in the description refer to this whole-mounted material, examined under a light microscope. Due to the small dimensions, however, the details of the chaetae could not be observed even when using a high-resolution 100× oil immersion lens. Therefore, external traits were also investigated by means of scanning electron microscopy. Since the animals were too small for the perforated containers available for critical point drying, they were simply dehydrated in 99% ethanol, transferred to butyl acetate, and air-dried. This is a rough method, but thanks to their sturdy cuticle and small size the worms maintained the body shape acceptably, at least in a comparison with individuals prepared for light microscopy. Three specimens were mounted on double-sided tape, coated with gold and examined with SEM.

The holotype and some paratypes of the new species, *Parvidrilus strayeri*, are deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., additional paratypes in the Swedish Museum of Natural History (SMNH), Stockholm.

Parvidrilidae, new family

Etymology.—Family name (-idae) based on *Parvidrilus*, new genus (type genus).

Diagnosis.—Until additional species are found, the new family is characterized by the features of the type species of the type genus. They can be summarized as follows:

Meiofaunal freshwater oligochaetes, about 1 mm long. Chaetal bundles situated posteriorly in each segment, but completely absent from segment II. In anterior part of body, both dorsal and ventral bundles with very long hair chaetae as well as short crotchet chaetae; dorsal crotchets single-pointed, ventral ones bifid. In posterior part of body, dorsal bundles similar to anterior dorsal ones, ventral bundles with bifid crotchets only. In ovigerous specimens, clitellum developed as a pair of lateral rows of large, swollen, transparent, cells in segments (IX–) X–XII (–XIII, –XIV). Alimentary canal simple, without diverticula. It is unclear whether gonads are paired or unpaired; testes (testis?) in segment XI, ovaries (ovary?) in XII. Reproductive organs complex, including U-shaped muscular 'genital body' in XII and V-shaped 'copulatory organ' in XII–XIII.

Parvidrilus, new genus

Etymology.—A combination of *parvus* (Latin for 'small') and *drilus* (Greek for 'worm').

Diagnosis.—As for family.

Type species.—*Parvidrilus strayeri*, new species.

Other species.—None.

Parvidrilus strayeri, new species
Figs 1–2

Oligochaeta n. sp.: Strayer et al. 1995:506.

Holotype.—USNM 185769, whole-mounted specimen.

Type locality.—A hyporheic site in a sand-gravel bar, in Hendrick Mill Branch, a spring-fed stream about 20 km NE of Pinson, Blount Co., Alabama, U.S.A., 33°52′12″N, 86°33′57″W, 4 Oct 1990, coll. D. L. Strayer. At this site, the stream is 3–6 m wide and runs through a hardwood forest in a limestone terrain. The bottom varies from sand to exposed bedrock, with a predominance of coarse sand, angular gravel and small (10–15 cm) stones. Generally the alluvium is thin, but a large deposit of sand and gravel is held in place by a dam about 3 m high. At the time of collection, the emergent part of this deposit was 3–4 m wide, about 30 m long, and reached about 0.5 m above the stream water level. Because the dam leaked from the base, water flowed down into and through the bar. Subsamples were taken from 16 wells in the bar, using a Bou-Rouch pump (Bou 1974), all wells yielded water freely. Dissolved oxygen was 0–8.0 ppm, with most readings 2–6 ppm. Other chemical characteristics (means of several subsamples): Ca 22.2 ppm; Mg 11.6 ppm; K 0.5 ppm; Na 0.7 ppm; NO_3 0.9 ppm; SO_4 1.8 ppm; Cl 1.2 ppm; Dissolved Organic Carbon (DOC) 0.5 ppm (Strayer et al. 1995; Strayer, pers. comm.).

Paratypes.—USNM 185770–185776-000000, seven whole-mounted specimens; SMNH Type coll. 5085–5092, eight whole-mounted specimens; SMNH Type coll. 5093, three specimens mounted on a SEM stub; all from type locality.

Etymology.—Named for Dr. David L. Strayer, who collected the material and was the first to realize that the species was a

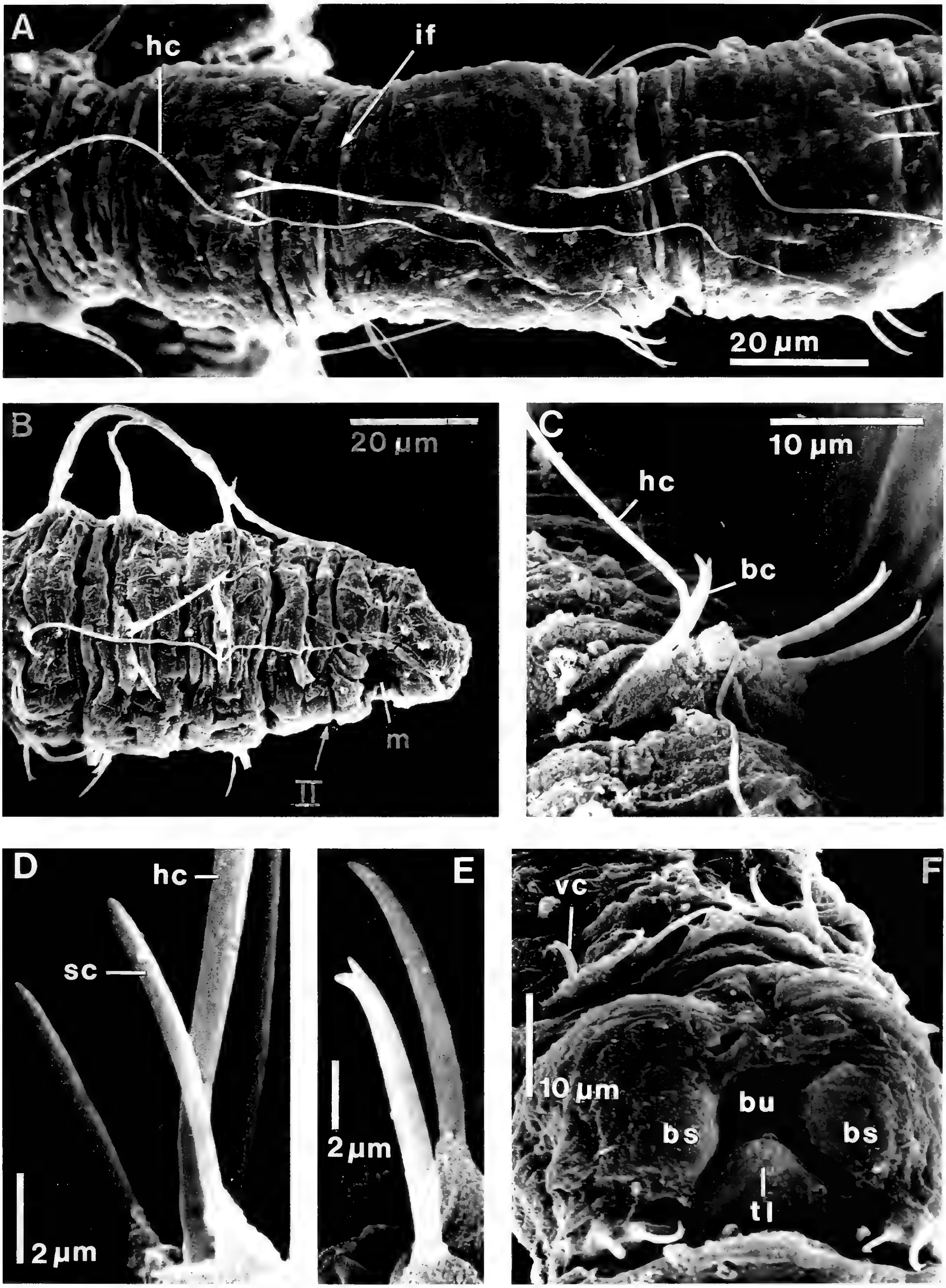

Fig. 1. *Parvidrilus strayeri*, new genus and species; SEM micrographs. A, postclitellar part of body, showing dorsal hair chaetae (hc) ventral bifid chaetae (in bottom part of figure), and intersegmental furrows (if); note the posterior location of bundles in the segments; B, anterior end of body showing mouth (m), achaetous segment II (II), and dorsal (top of figure) and ventral chaetae (middle and bottom of figure) of segments III–V; C, bundle of ventral chaetae of segment IX, showing hair chaeta (hc) and bifid crotchets (bc); D, bundle of dorsal chaetae of segment X, showing hair chaeta (hc), and single-pointed crotchets (sc); note also thin outer part of hair chaetae of another segment; E, bundle of ventral chaetae of postclitellar segment, showing two bifid crotchets; F, ventral view of genital bursa (bu) in segment XII, showing lateral bulbous swellings (bs), posterior triangular lappet (tl), and ventral chaetae (vc).

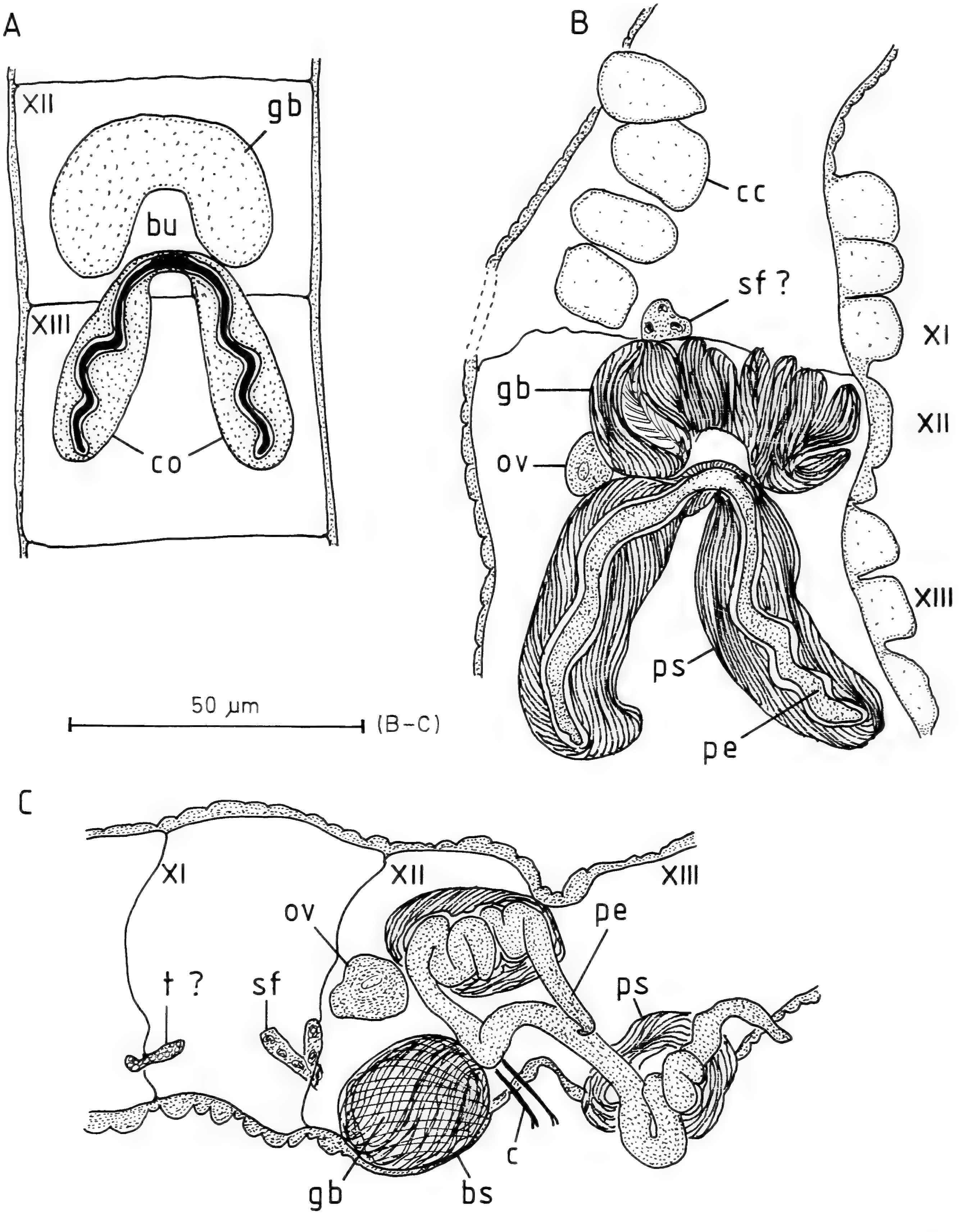

Fig. 2. *Parvidrilus strayeri*, new genus and species. A, schematical, horizontal view of segments XII and XIII, showing general outline of 'genital body' and 'copulatory organ'; B, somewhat horizontal view of segments XI–XIII of one paratype; C, somewhat lateral view of segments XI–XIII of another paratype. Abbreviations: bs, bulbous swelling (of body wall); bu, location of genital bursa (cf. Fig. 1F); c, chaeta; cc, clitellar cell; co, copulatory organ; gb, genital body; ov, ovary; pe, penis/pseudopenis; ps, penial/pseudopenial sac; sf, sperm funnel, t, testis.

new taxon of considerable systematic interest.

Description.—Length (five complete specimens) 0.7–1.4 mm, 18–33 segments. Width at genital region 0.03–0.10 mm. Prostomium rounded, somewhat narrower than and well set off from peristomium; prostomial epidermis with numerous (stained) cell nuclei, probably indicating a glandular or sensory function. Posterior part of body (Fig. 1A) more clearly annulated (i.e., with distinct intersegmental furrows; Fig. 1A, if) than anterior part. Pygidium generally demarcated, somewhat narrower than last (true) segment. Cuticle smooth, but foreign particles often adhering to it here and there along body of worm. Clitellum poorly developed in most individuals; but in ovigerous specimens, a row of large, swollen, transparent, epidermal cells (Fig. 2B, cc) present on each side of worm in segments (IX–) X–XII (–XIII, –XIV).

Chaetal bundles situated posteriorly in each segment (Fig. 1A), but lacking completely in segment II (Fig. 1B). Anterior dorsal bundles each with one to two (occasionally three) long, whip-like, hair chaetae (Fig. 1D, hc), alternating with two or three (occasionally four) single-pointed, smaller crotchet chaetae (Fig. 1D, sc); hairs occasionally up to about 200 μm long (exact length difficult to measure due to strong curvature of hairs and poorly resolved view of tips), entally about 1 μm wide, progressively tapering and only about 0.1 μm wide at ectal end; crotchets 15–25 μm long, about 0.5–0.6 μm thick, with somewhat blunt tips. Postclitellar dorsal bundles each with one or no hair chaeta (Fig. 1A, hc) and two single-pointed crotchets. In anterior segments (at least in III–VII, but generally also including a few additional pre-genital segments, and sometimes even as far back as in XV), ventral bundles each with one hair chaeta (Fig. 1C, hc), and three (occasionally four) bifid crotchets (Fig. 1C, bc); ventral hairs slightly shorter and thinner than corresponding dorsal hairs; bifids about 20–25 μm long, about 0.9–1.4 μm thick, with upper tooth thinner and shorter than lower tooth. Within these bundles, uppermost (most lateral) chaeta bifid, followed by a hair, and these two chaetae clearly separated from two, more ventral, bifids (Fig. 1C). Postclitellar ventral bundles with two to three bifid crotchets (Fig. 1E), similar to anterior ventral bifids. Modified genital chaetae absent.

Ventrally in segment XII, body wall forming a conspicuous, generally somewhat "X"-shaped genital bursa (Fig. 1F); impression of an X facilitated by a pair of large, bulbous, swellings (Fig. 1F, bs), one at each side of bursal opening, and an indistinct, mid-ventral, triangular lappet (Fig. 1F, tl), located immediately posterior to bursal opening.

Spermathecal openings not observed.

Brain located within, and with front end reaching anterior coelomic lining of, peristomium. Nerve cord ventral, of normal microdrile oligochaete appearance. Alimentary system of normal microdrile oligochaete type too: simple pharynx with dorsal pharyngeal bulb, somewhat sinuous esophagus with a few pharyngeal (?) gland cells scattered in segments V–VIII, followed by a narrow, simple intestine; no particular enlargements or diverticula on gut. Large, diffuse cells of chloragogen tissue present along most of gut. Free coelomocytes not observed.

In three specimens, a small lump of cells in anterior end of coelom of segment XI probably an (unpaired?) testis (Fig. 2C, t?); in another worm, a single sperm bundle present in coelom of this segment; otherwise male gonads or developing spermatozoa not observed. In nine specimens, an ovary (apparently developed on one side only) observed in anterior part of segment XII (Fig. 2B, C, ov); three of these worms ovigerous, i.e., with a large mature egg filling whole width of coelom, and extending through one or two segments, in region of XIII–XV. In two specimens (only), a sperm funnel discernible at anterior side of septum between XI and XII (Fig. 2B, C, sf), but its continuation into a vas deferens not seen.

Other internal genitalia (in XII–XIII) complex (Fig. 2), but due to quality of fixation and small dimensions difficult to interpret using conventional oligochaete terminology. Two conspicuous structures present, here referred to as the 'genital body' and the 'copulatory organ', respectively.

Genital body (Fig. 2A–C, gb) a "U"-shaped structure incorporated in ventral body wall in segment XII; the two arms forcing body to bulge considerably, corresponding to two bulbous swellings at lateral sides of genital bursa (Fig. 1F, bs). Arms of genital body more or less oval, 20–35 μm long, 15–23 μm wide, oriented along long axis of worm, and united anteriorly. At early developmental stages, lobes appear to contain a lumen. At full maturity, wall of genital body thick, heavily muscular and folded in complex manner (Fig. 2B, C, gb), with indistinct lumen (lumina?); sometimes densely packed cilia (see Fig. 2B) and/or spermatozoa (?) visible inside. At late stages of development, lobes tend to break up into a number of secondary, pear-to-spindle-shaped, packages of muscle fibers (as in Fig. 2B). Function of genital body unknown; possibly having something to do with storage and/or ejaculation of sperm, either before (an atrium?) or after copulation (a spermatheca?). Whether genital body has any permanent or temporary opening to the exterior or any connection with the sperm funnels or copulatory organ unknown.

Copulatory organ (Fig. 2A, co) bilobed, somewhat "V"-shaped, consisting of a pair of straight or somewhat curved sacs (Fig. 2B, C, ps), communicating with each other mid-ventrally in most posterior part of segment XII. At point of union of the two sacs, copulatory organ appears anchored in the ventral body wall, in a position corresponding to apex of the mid-ventral, triangular, lappet located in posterior wall of genital bursa (Fig. 1F, tl; see above). Inner ends of sacs extending obliquely and freely backwards into coelom of XIII. Each sac 25–60 μm long, 10–21 μm wide, with thick, muscular, wall, and containing a coiled, slender tube. In one damaged specimen, tubes squashed out from sacs, appearing as long penes (Fig. 2C, pe), but it appears as if tips of these are normally located inside inner ends of sacs rather than at mid-ventral attachment point in body wall. It is thus unknown whether tubes are protrusible (i.e., penes) or eversible structures (i.e., pseudopenes).

Remarks.—Although there is a possibility that the genital body in segment XII is used for storing sperm from a concopulant (see above), typical spermathecae were not observed.

Several points in this description need to be clarified by future studies. Nevertheless, *Parvidrilus strayeri* is easily separated from all other known oligochaete taxa. See Discussion below.

Distribution and habitat.—Known only from the type locality in Alabama, USA. Interstitial groundwater.

Discussion

Parvidrilus strayeri is clearly a clitellate. It appears to be hermaphroditic (the genitalia of all specimens look the same) with gonads in specific segments, and it has an eversible, thickened, pharynx roof, a brain located behind the prostomium, and large glandular epidermal cells in the genital region suggesting the existence of a clitellum (see Purschke et al. 1993). In a traditional sense, the worm is a member of the Oligochaeta; but there is now increasing evidence that this taxon is paraphyletic unless leeches and leech-like groups are included (Purschke et al. 1993, Brinkhurst 1994, Siddall & Burreson 1996, Ferraguti & Erséus 1999). A formal phylogenetic analysis to establish the more specific systematic position of *Parvidrilus* within the Clitellata, is not meaningful until some uncertainties in the description have been clarified. As there is yet no strong indication as to which clitellate subgroup the new species belongs, outgroups for such an analysis would need to be selected from outside the Clitellata, implying that most ingroup and outgroup character states would not be comparable.

In some ways, however, the new species is unusual and unique (see Table I). First, it is one of the smallest clitellates known. With a body length of about 1 mm it resembles only the smallest *Chaetogaster* spp. (Naididae) (see Sperber 1948), an undescribed freshwater species tentatively assigned to *Capilloventer* (Capilloventridae) from Western Australia (Pinder & Brinkhurst 1997b); and a miniature terrestrial species of Enchytraeidae from Italy, *Marionina eleonorae* Rota, 1995. Some marine oligochaetes are just slightly longer. Examples within the 1.5–2.5 mm range are numerous species of the subfamily Phallodrilinae (Tubificidae; see, e.g., Erséus 1980, 1989, 1990, 1992), and *Randiella caribaea* Erséus & Strehlow, 1986 and *R. minuta* Erséus & Strehlow, 1986 (Randiellidae; see Erséus & Strehlow 1986, Erséus 1997). To my knowledge, there is no freshwater tubificid that is even close to the 0.7–1.4 mm range that characterizes *Parvidrilus*.

Second, in *Parvidrilus strayeri*, the four chaetal bundles of each segment are located in a more posterior position within the segment than in other oligochaetes. Third, the clitellar cells are large in relation to the body diameter, few in number, and restricted to two lateral rows, one at each side, through a few segments of the worm. These features are likely to be autapomorphies of *Parvidrilus* or of a group including as yet unknown taxa.

Although complete male ducts have not been observed in *Parvidrilus*, the position of the genital bursa indicates that male pores (or an unpaired male pore?) are present in segment XII. In this respect the new taxon bears resemblance to four other microdrile families, Enchytraeidae, Propappidae, Capilloventridae and Phreodrilidae, and a few representatives of the Lumbriculidae. Capilloventridae and Phreodrilidae are regarded as endemic to the Southern Hemisphere (although a few phreodrilids occur north of the equator), but a further comparison with them is pertinent here as both (see Harman & Loden 1984; Erséus 1993; Pinder & Brinkhurst 1997a, 1997b) are characterized by absence of chaetae in segment II (for phreodrilids, at least with regard to the dorsal chaetae; Pinder & Brinkhurst 1997a), and presence of hair chaetae in the other segments, i.e., two striking similarities with the chaetal pattern in *Parvidrilus* (Table I).

The additional feature of ventral hair chaetae is, within the Clitellata, shared only by *Parvidrilus* and Capilloventridae and may be homologous. However, Capilloventridae, as currently defined (Pinder & Brinkhurst 1997b), is characterized by modified hair-like genital chaetae, spermathecae in segment VII, and a pair of blind ventral sacs (salivary glands?) opening into the mouth cavity (the two first features also known from the Randiellidae; see Erséus and Strehlow 1986). As none of these is present in *Parvidrilus*, inclusion of the new genus in Capilloventridae would imply reductions of all three traits, which is a less parsimonious hypothesis than to regard *Parvidrilus* as a taxon outside Capilloventridae. Moreover, in Capilloventridae but not in *Parvidrilus*, the chaetal bundles of each side are located close together and widely separated from those of the other side, somewhat like the distribution of chaetae on parapodia of polychaetes (Erséus 1993). This could be a plesiomorphic condition reflecting ancestry of the Clitellata among the polychaetes (cf. Westheide 1997), and in which case the Capilloventridae could be the most ancestral group of all Clitellata; alternatively, it is an additional autapomorphy of Capilloventridae.

The Phreodrilidae comprises a total of about 60 species with great morphological variation with regard to chaetae as well as genital organs (Pinder & Brinkhurst 1997a). In phreodrilids, the dorsal chaetal bundles frequently consist of long hair-like chaetae accompanied by short, single-pointed, "lat-

Table 1.—Summary of some morphological features of Parvidrilidae, new family, and some other aquatic clitellate families discussed in the text. Internal genital organs, which are only tentatively described for Parvidrilidae, are excluded; for these structures, comparisons with the other groups are difficult to make. Features that are regarded as likely to be autapomorphic by the author are underlined.

Character	Parvidrilidae	Capilloventridae	Phreodrilidae	Narapidae	Tubificidae
Size, approx. range	1 mm	1–5 mm	3–40 mm	3–5 mm	2–185 mm
Chaetae	present	present	present	absent	present
Chaetae in II	absent	absent	sometimes absent	(not applicable)	present
Position of chaetae in segment	posterior	in middle	in middle	(not applicable)	in middle
Chaetal bundles of each side	widely separated	close together	widely separated	(not applicable)	widely separated
Hair chaetae	dorsal and ventral	dorsal and ventral	dorsal, if present	(not applicable)	dorsal, if present
Dorsal crotchet chaetae	single-pointed, protuberant	single-pointed or bifid, protuberant	single-pointed, not protuberant	(not applicable)	bifid or pectinate, protuberant
Genital hair-like chaetae	absent	present	absent	(not applicable)	absent
Ventral chaetae, no. per bundle	2–4	1–5	2	(not applicable)	highly variable
Clitellar cells	as lateral rows	surrounding body	surrounding body	surrounding body	surrounding body
Male pores	in XII	in XII	in XII	in VI	in XI
Spermathecae	absent?	in VII	in XIII	in VII	in X
Ventral buccal sacs	absent	present	absent	absent	absent

eral support chaetae", an arrangement similar to that found in *Parvidrilus strayeri* (but also similar to the dorsal 'hairs and needles' in species of Naididae and Opistocystidae). The crucial point would then be to what extent the curious genital body and copulatory organ of the new species are homologous to phreodrilid genital structures. They show some superficial resemblance to the atria and eversible pseudopenes, respectively, of the species of *Phreodrilus* Beddard (see Pinder & Brinkhurst 1997a), although in *Parvidrilus* the two kinds of structures do not appear to be continuous with each other as the atria and pseudopenes are in *Phreodrilus*. Moreover, the phreodrilid atria are filiform invaginations, lying freely in the coleomic cavity, whereas the *Parvidrilus* genital body is in very close contact with (merely as a pair of swellings of) the body wall. There are also other differences between Phreodrilidae and *Parvidrilus* (Table I). In phreodrilids, the general body size is one order of magnitude larger than that of *Parvidrilus*, the ventral chaetae are consistently paired, there is a thin clitellum of normal microdrile type and it is generally restricted to segments XII–XIII, there are spermathecae in segment XIII, and if hairs are present, the lateral support chaetae do not usually project from the chaetal sacs. Many of these features are shared with other aquatic clitellate taxa, but the lateral support chaetae, the position of the spermathecae (in segment XIII), and the well developed tubular atria mentioned above, are likely to be autapomorphies supporting monophyly of the Phreodrilidae. Thus, it does not appear appropriate to place *Parvidrilus* in the Phreodrilidae.

Narapa bonettoi Righi & Varela, 1983, the single representative of the family Narapidae and known only from the Paraná River in Argentina (Righi & Varela 1983, Brinkhurst & Marchese 1989), is another aquatic oligochaete taxon with an unclear systematic position. It shows some curious resemblance to *Parvidrilus*. Although lacking chaetae completely and having its genital system in a more anterior position (Table I), *Narapa* has a male gonoduct (in segment VI) (Righi & Varela 1983:figs 4–6) with an outline comparable to one possible interpretation of the reproductive system in *Parvidrilus*. In *Narapa*, the sperm funnel is followed by a short vas deferens (not yet observed in *Parvidrilus*), leading to a ventral glandular, tubular atrium (possibly corresponding to a lateral arm of the 'genital body' in *Parvidrilus*), followed by a posteriorly bent-over penial sac with a winding lumen (possibly corresponding to a copulatory sac in *Parvidrilus*). It is also noteworthy that the ovary (in VII) is reported to be unpaired in *Narapa*; in none of the specimens of *Parvidrilus strayeri* was more than one ovary observed. It is an open question whether these similarities are synapomorphic or convergent, but Narapidae and Parvidrilidae are both monotypic and each possesses its own autapomorphies (Table I). As currently defined, they can, therefore, at most be regarded as sister taxa.

However, relevant comparisons with other aquatic microdrile taxa have still not been exhausted. For instance, it could be suggested that the U-shaped genital body of *Parvidrilus strayeri* is a derivative of a pair of atria of the kind found in the family Tubificidae, and that its position in segment XII is merely an autapomorphic rearward shift of a tubificid male system. Following this line of reasoning, the copulatory organ of *Parvidrilus* (Fig. 2C) could be interpreted as an indication of a close relationship with, e.g., *Teneridrilus flexus* Erséus & Hiltunen, 1990 (in Erséus et al. 1990). The latter is a North American Great Lakes freshwater tubificid (reported also by Stacey & Hubley 1994), with small, convoluted, tubular penial organs contained within muscular sacs (Erséus et al. 1990:fig. 2D, E). However, these similarities are probably coincident and convergent. As noted above, the chaetal pattern and the segmental position of the genitalia strongly suggest that *Parvidrilus* is more closely related to the Capilloventridae and Phreodrilidae than to the Tubificidae

(Table I). Furthermore, the tubificid atria extend freely into the coelom, rather than being incorporated in the body wall as is the case with the genital body of *Parvidrilus*.

To conclude, it seems justified to establish a higher level taxon, Parvidrilidae, new family, for *Parvidrilus* on the basis of the available morphological evidence. This classification is not likely to render any of the other clitellate families paraphyletic. Several features of *Parvidrilus*/Parvidrilidae are probably autapomorphic: the extreme miniaturization, the chaetal bundles situated posteriorly in each segment, the clitellum modified into two lateral rows of a few large glandular cells, and the unique, complex, genital organs surrounding a conspicuous mid-ventral bursa in segment XII.

In its area of distribution, *Parvidrilus* is part of a particular association of invertebrates ('stygobionts') adapted to life in interstitial groundwater, an association which also includes the polychaete *Troglochaetus* sp., aeolosomatids (Annelida, Aphanoneura), smaller lumbriculid (e.g., *Stylodrilus wahkeenensis* Rodriguez & Coates, 1996) and naidid oligochaetes, bathynellacean crustaceans, microcerberid isopods and numerous benthic cyclopoid copepods (Rodriguez & Coates 1996, Strayer et al. 1995, Strayer & Reid in preparation, Reid et al. in preparation). Although still greatly overlooked, this rich stygobiont fauna appears to characterize a vast area of unglaciated ancient terrain in eastern North America. Some authors (e.g., Wägele et al. 1995, Reid 1998) have already pointed out that many endemic interstitial microcrustaceans of this region appear to represent an old continental fauna, with closely related, but anatomically distinct Eurasian counterparts. It is possible that *Parvidrilus* is a northern representative of a group of aquatic clitellates, which also contains the Southern Hemisphere families, Capilloventridae, Phreodrilidae and, possibly also, Narapidae.

Parvidrilus was common at Hendrick Mill (D. L. Strayer, pers. comm.) and is probably not a rare animal, once the right habitats are searched.

Parvidrilus strayeri deserves further attention. New material needs to be studied by methods that would enable a detailed scrutiny of the true nature of its miniature genital organs, which may throw additional light on its systematic position. Molecular systematic analyses of this enigmatic taxon may contribute towards the same end.

Acknowledgments

I am indebted to Dr. David L. Strayer, for generously placing the material at my disposal, and for sharing published and unpublished information; to Dr. Anders Warén (SMNH) for invaluable assistance with scanning electron microscopy; to Ms. Barbro Löfnertz (University of Göteborg), Mrs. Anna Hedström and Ms. Christine Hammar (both SMNH), for technical assistance; to Dr. Ralph O. Brinkhurst (Hermitage, TN, USA) and Dr. Kathryn A. Coates (Bermuda Biological Station for Research, Inc), for constructive criticism of the text; and the Swedish Natural Science Research Council, for financial support.

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On the entocytherid ostracods of the Brazos River basin and adjacent coastal region of Texas

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Abstract.—New records of entocytherid ostracods infesting crayfishes are recorded from the Brazos River basin in southeastern Texas, which extend the ranges of *Ankylocythere ancyla*, *A. sinuosa*, *Entocythere harrisi*, *E. reddelli*, and *Uncinocythere simondsi*. A review of the variations in the copulatory complex of *A. ancyla* is provided and the synonymy of *A. tiphophila* with *A. sinuosa* is proposed.

Upon the completion of his study of the crayfishes of the Brazos River basin and nearby areas, Douglas W. Albaugh (1973, 1975; Albaugh & Black 1973) sent sediments from the containers in which his specimens were preserved to the Smithsonian Institution. This report is based on the ostracods contained in these samples which were made available to us through the kindness of the late Horton H. Hobbs, Jr.

Five species of entocytherid ostracods were retrieved from 118 samples collected between 21 February and 8 March 1973. Hosts, which were identified by Dr. Albaugh (the subgeneric assignments were provided by Horton H. Hobbs, Jr.), include the following: *Cambarellus* (*Dirigicambarus*) *shufeldtii* (Faxon), *C.* (*Pandicambarus*) *ninae* Hobbs, *C.* (*P.*) *puer* Hobbs, *Fallicambarus* (*Creaserinus*) *fodiens* (Cottle), *Procambarus* (*Capillicambarus*) *brazoriensis* Albaugh, *P.* (*C.*) *hinei* (Ortmann), *P.* (*C.*) *incilis* Penn, *P.* (*Girardiella*) *simulans* (Faxon), *P.* (*Ortmannicus*) *a. acutus* (Girard), *P.* (*O.*) *texanus* Hobbs and *P.* (*Scapulicambarus*) *clarkii* (Girard). Insofar as we have been able to determine, all of the collections were made from open water; no crayfishes were taken from burrows. The ostracods, locality data, host and entocytherid identifications are deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Ankylocythere ancyla Crawford
Figs. 1a–h, 2a–h, 4

Ankylocythere ancyla Crawford, 1965:148, 149, 152, 153, figs. 1–3, 6, 7 [Type locality: "... in the city limits of Greensboro, Guilford County, North Carolina." Types: holotype, allotype, morphotype, and dissected male paratype USNM; paratypes in the collection of E. A. Crawford, Jr., and USNM. Host: *Cambarus latimanus* (LeConte) (=*Cambarus* (*Depressicambarus*) *catagius* Hobbs & Perkins, 1967)].

Ankylocythere species g Hobbs III, 1969: 32–34, figs. 4d–g, l.

Ankylocythere species h Hobbs III, 1969: 34–36, figs. 4h–k, l.

Except for the omission of the references to Hobbs III (1969), Andolshek & Hobbs (1986:10) included a compilation of all references in the literature to this ostracod.

Diagnosis of Texas material.—Shell length of male 336 to 378 (avg. 357) μm; shell height 196 to 224 (avg. 218) μm. Peniferum truncate to tapering with acute antero- and posteroventral angles. Clasping apparatus L-shaped with vertical ramus lon-

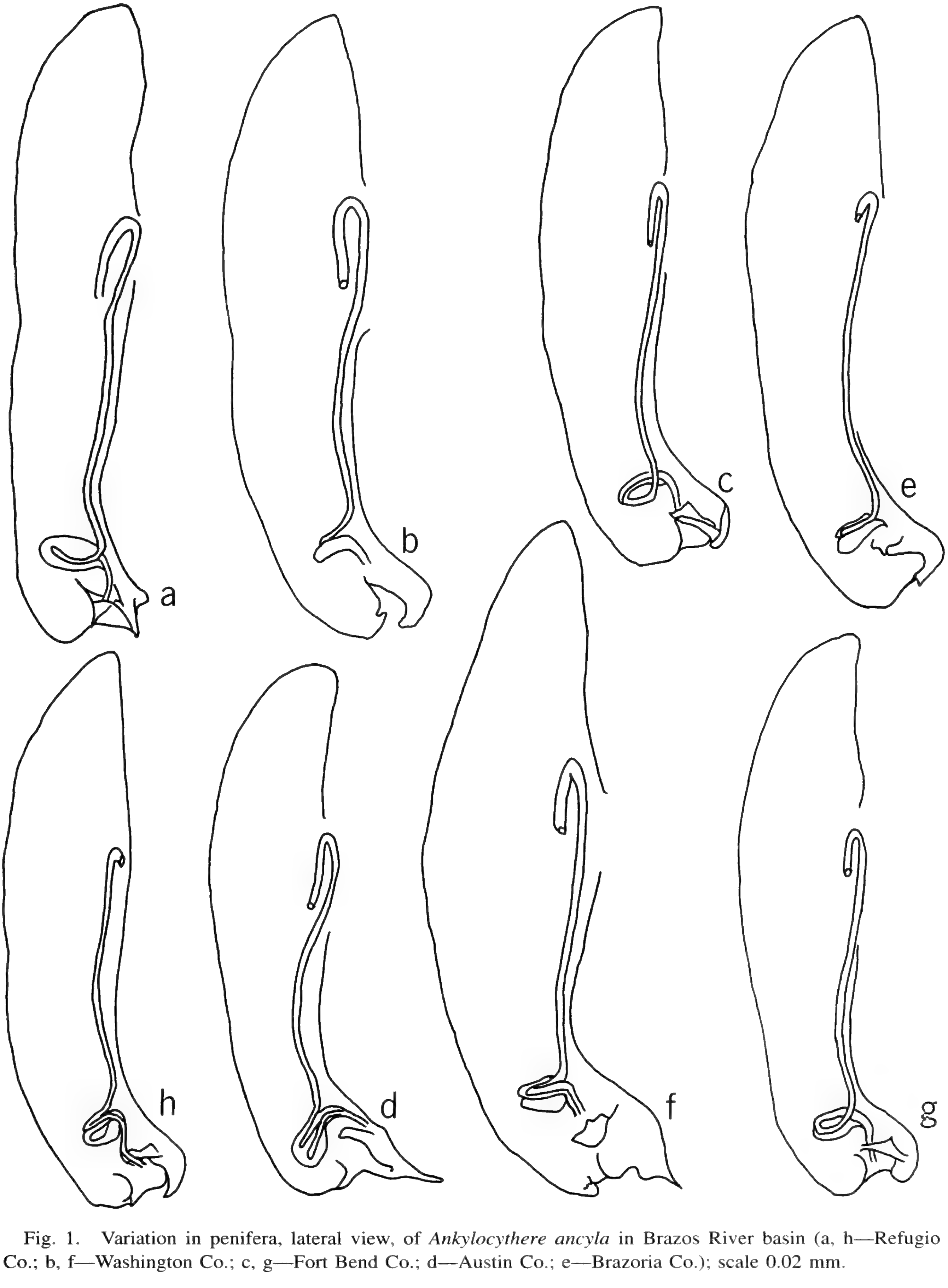

Fig. 1. Variation in penifera, lateral view, of *Ankylocythere ancyla* in Brazos River basin (a, h—Refugio Co.; b, f—Washington Co.; c, g—Fort Bend Co.; d—Austin Co.; e—Brazoria Co.); scale 0.02 mm.

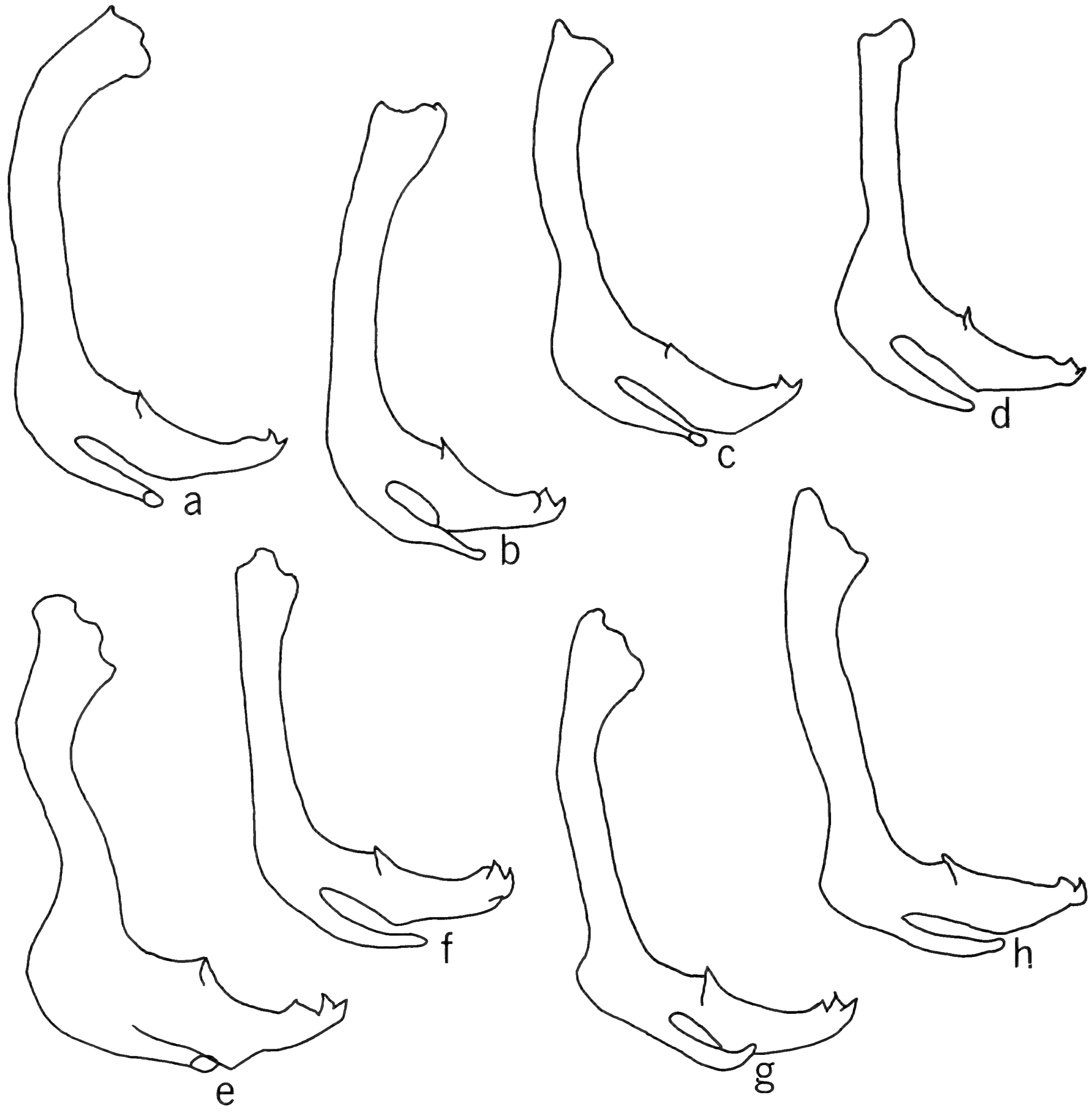

Fig. 2. Variation in clasping apparatus, lateral view, of *Ankylocythere ancyla* in Brazos River basin (a, h—Refugio Co.; b, e, g—Washington Co.; d—Fort Bend Co.; f—Austin Co.; c—Brazoria Co.); same scale as Fig. 1.

ger than horizontal ramus; latter with tooth on preaxial border near midlength, and postaxial border with long, curved talon reaching to midway between preaxial tooth and apex of ramus; extreme apical part of talon sometimes strongly curved mesially. Apex of clasping apparatus with 2 denticles.

Range.—Andolshek & Hobbs (1986) quoted the range of the species as cited by Hobbs & Peters (1977) as extending "... along the Atlantic and Gulf slopes from the Mobile River drainage in Alabama and Mississippi northeastward to the Potomac drainage in Virginia and in the New River Basin of North Carolina." The locality records established herein extend the westward limits some 750 kilometers to the Brazos basin in Texas.

Southeastern Texas records (Fig. 4).—Nineteen localities from the following counties: Austin (2), Brazoria (2), Brazos

(2), Calhoun (3), Fort Bend (2), Matagorda (1), Refugio (6), and Washington (1).

Remarks.—In his study of the entocytherids infesting burrowing crayfishes in the coastal plain between extreme eastern Texas and the Apalachicola Basin in Alabama and Florida, Hobbs III (1969) recognized 12 species belonging to the genus *Ankylocythere*. Specimens of two of these, *A.* species "g" and "h" were lent to us by Dr. Hobbs, and, after comparing them with representatives of *A. ancyla* from throughout its range, we are convinced that they are referable to this species. Thus there are few gaps in its known range. Andolshek & Hobbs (1986:14) reviewed available data on the size of the shell of this ostracod and found that the smallest individuals occurred in southeastern Georgia and the largest in Virginia. Those in North Carolina were, on the average, intermediate in size. The range in size of the material from along the coasts of Florida, Alabama, Mississippi, Louisiana, and Texas reported herein falls within that cited for the species in southeastern Georgia (length, 315 to 399 μm; height 175 to 245 μm). Thus it appears that the shells of southern populations of *A. ancyla* are smaller than those occurring in the more northern parts of the range.

A cursory examination of the ventral part of the peniferum would suggest that a dimorphic condition exists in this appendage, one in which the anteroventral extremity is produced in a subspiculiform prominence (Fig. 1d), and in the other, subtruncate (Fig. 1e). That the difference is more in the angle from which the penifera are viewed rather than due to morphological variation becomes apparent when those of a number of specimens are compared. In this ostracod, the basic structure of the ventral extremity of the peniferum is more clearly observed in specimens from the eastern part of the range where a broad concavity exists between the acute cephloventral and rounded posteroventral extremities (See fig. 4a in Andolshek & Hobbs (1986)). In specimens from the Brazos region, the anteroventral angulate extension often appears to be more strongly produced, and its base to bear a thickened, sclerotized prominence, which when viewed at some angles, seems to project posteriorly or posteroventrally; also the anteroventral apex of the posteroventral prominence is procurved, diminishing the maximum diameter of the concavity, and is frequently rather strongly sclerotized. (For variations compare Fig. 1b, c, e, g, h). Thus, whereas the ventral extremity of the penifera of the eastern and western members of the species appear to be markedly different, the contrast is less marked than seems apparent when only a superficial comparison is made.

Among other variations noted in the copulatory complex of this ostracod are the thickness of the junction of the horizontal and vertical rami of the clasping apparatus and the curvature of the vertical ramus. In specimens from Washington County, TX, males were found that possess a sinuous vertical ramus (Fig. 2e), and in the area of the junction of the rami there occurs a conspicuous thickening (Fig. 2e). Even though different, this variance must be considered to be within the range of variation in the species. For example, in one specimen one of the pair of clasping apparati exhibits such a thickening and the other resembles the more frequently observed apparatus (Fig. 2f, g). Considerable variation occurs in the curvature of the vertical ramus and in that of the talon (Fig. 2a–h).

Hosts.—In the Brazos Basin, *A. ancyla* is known to infest *F.* (*C.*) *fodiens*, *C.* (*P.*) *ninae*, and *P.* (*S.*) *clarkii*, and has been retrieved from collections containing all of the crayfishes known to occur in the area except *C.* (*P.*) *texanus*, *P.* (*C.*) *hinei*, and *P.* (*C.*) *brazoriensis*; rarely, however, was it found in collections containing representatives of *C.* (*P.*) *puer*, *C.* (*D.*) *shufeldtii*, and *P.* (*C.*) *incilis*.

Entocytherid associates.—In the 19 localities in which this ostracod was found, it was the only one infesting the crayfishes in nine sites. Its most frequent associate (in 9 localities) was *A. sinuosa*, and only rarely was it found with *E. reddelli* (2), and *U. simondsi* (1).

Ankylocythere sinuosa (Rioja)
Figs. 3, 5

Entocythere cambaria.—Hobbs, 1941:4 [in part].

Entocythere (Cytherites) heterodonta sinuosa Rioja, 1942a:203, 204, figs. 5, 6 [Type locality: La Cueva Chica, San Luis Potosi, Mexico. Types: not extant. Host: *Procambarus acutus cuevachicae* Hobbs 1941.]; 1953:287.

Entocythere (Cytherites) sinuosa.—Rioja, 1942b:688, 689, 695, 696, fig. 20; 1943a: 564; 1943b:576.

Entocythere sinuosa.—Hoff, 1944:330, 332, 356.—Rioja, 1949:321, 322 [in part], figs. 13, 14; 1951:170; 1953:291, 292.—Tressler, 1954:138; 1959:731, fig. 28.190.—Hobbs, 1957:431.—Crawford, 1959:173, 178.

Ankylocythere sinuosa.—Hart, 1962:127; 1964:246.—Crawford, 1965:149.—Reddell, 1965:156; 1970:395; 1971:18; 1981: 82.—Hobbs, 1966:70, fig. 18; 1971:34–35, fig. 22.—Ferguson, 1968:501.—Hobbs & Walton, 1968:246.—Baker, 1969:293.—Reddell & Mitchell, 1969:6; 1971:142.—Young, 1971:399–409.—Hart & Hart, 1974:1, 2, 14, 21, 22, 29–31, 34, pl. 3: figs. 11–13, pl. 41.—Hobbs III, 1969:5, 14, 20–22, 27, 30, 32–35, 39, 41, 43, 46, 55, 65, 66, 71, 74, 78, 79, fig. 5a–k; 1975:281, 290; 1978:506; 1982: 2.—Hobbs & Peters, 1977:13; 1991:66, 67.—Hobbs & McClure, 1983:773.

Entocythere tiphophila Crawford, 1959: 150, 151, 173–178, 180, 181, figs. 31–37 [Type locality: roadside ditch 9.1 miles (14.6 km) SE of University of South Carolina stadium, Richland County, South Carolina, on St. Rte. 48. Types: USNM. Hosts: *Fallicambarus* (*C.*) *uhleri* and *Procambarus* (*F.*) *troglodytes*].—Hart, 1962:123, 128.

Ankylocythere tiphophila.—Hart, 1962:128; 1964:245.—Crawford, 1965:149.—Hobbs, 1966:71, fig. 16.—Ferguson, 1968:501.—Peters, 1974:74; 1975:iii, 5–8, 10, 13, 20, 22, 23, 27, 45, figs. 2c, 6k, 14.—Hart & Hart, 1974:15, 20, 33, pl. 4: figs. 6–8, pl. 45.—Hobbs & Peters, 1977: iii, 3–7, 9, 12, 16, 19–22, 28, 40, 41, 43, 46, 49–54, 70, fig. 5, map 5.—Hobbs, 1981:140, 499, 501.—Hobbs & McClure, 1983:773.

Ankylocythere tiphophyla.—Hobbs, Holt, & Walton, 1967:77 [erroneous spelling].

Diagnosis of Texas material.—Shell length of male 329–378 (avg. 350) μm; shell height 168–210 (avg. 191) μm. Peniferum varying from deeply cleft to truncate with tapering acute anteroventrally projecting prominence. Clasping apparatus L-shaped with vertical ramus longer that horizontal ramus; latter with truncate, almost straight, anteroventrally projecting talon situated slightly proximal to midway between preaxial tooth and apex of ramus; apex of apparatus with 2 denticles.

Range.—On the Gulf of Mexico versant, from the Cordillera volcanica Transversal along the Gulf and Atlantic (lower piedmont and coastal plain) slope to the York River Basin in Virginia. Hart and Hart (1974:33) also reported it from two localities in Ohio, records that should be confirmed.

Southeastern Texas records (Fig. 5).—This ostracod is the most widespread of the entocytherids within the study area, occurring in 94 of the 118 localities represented among the collections examined.

Hosts.—In southeastern Texas this ostracod was associated with three crayfishes: *P.* (*O.*) *a. acutus*, *P.* (*S.*) *clarkii* and *P.* (*G.*) *simulans*, but has been found in collections containing specimens of all of the other species in the area. In the collections from 94 localities where the ostracod was found, *P.* (*O.*) *a. acutus* was a potential host in 60 of them, *P.* (*S.*) *clarkii* in 52, *P.* (*G.*) *simulans* in 31, *P.* (*C.*) *incilis* in 17, and *F.* (*C.*) *fodiens* in 14. All of the other crayfish-

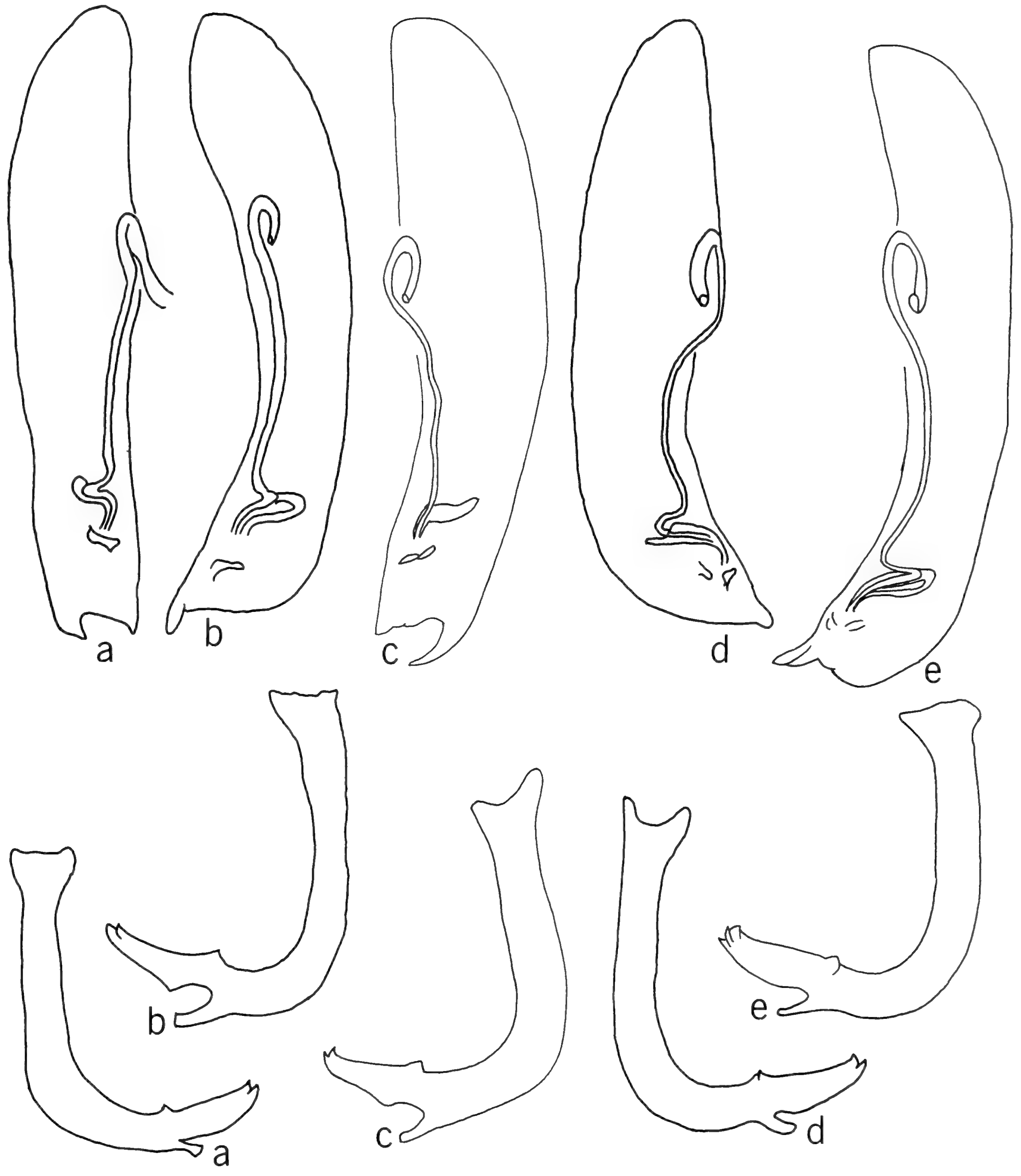

Fig. 3. Variation in male copulatory complex, lateral view, of *Ankylocythere sinuosa* (a—Tamaulipas, Acequia, Mexico; b—Burleson Co, TX; c—Robertson Co., Texas) and *Ankylocythere tiphophila* (d—Dorchester Co., South Carolina; e—Newport News, Virginia); same scale as Fig. 1.

es were present in fewer than 10 of the collections.

Entocytherid associates.—In the 94 localities where *A. sinuosa* was found, it was the only ostracod infesting the crayfish(es) in 57 of them. In 26 localities it shared the host(s) with *E. reddelli*, in eight with *A. ancyla*, and two each with *E. harrisi* and *U. simondsi*.

Remarks.—There is nothing remarkable concerning the size of the animals or in the structures employed in distinguishing this

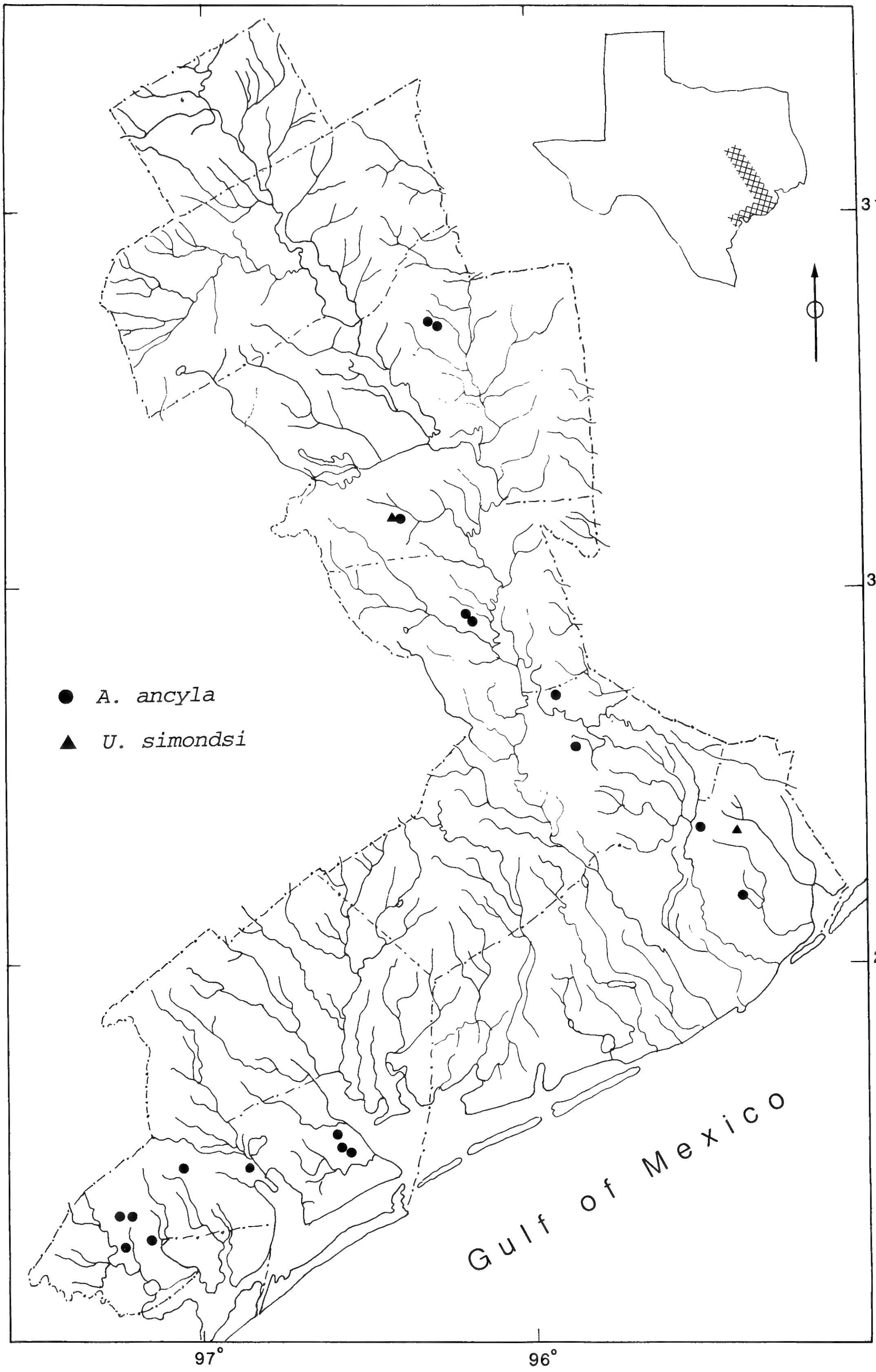

Fig. 4. Distribution of *Ankylocythere ancyla* and *Uncinocythere simondsi* in the Brazos River drainage.

ostracod from its congeners. The length of the shells of males ranges from 329 to 378 μm and the height from 168 to 210 μm. Hobbs (1971), in reporting on this ostracod in Mexico, cited similar ranges in size: 0.34 to 0.37 mm and 0.19 to 0.22 mm, respectively.

Perhaps because of the apparent discon-

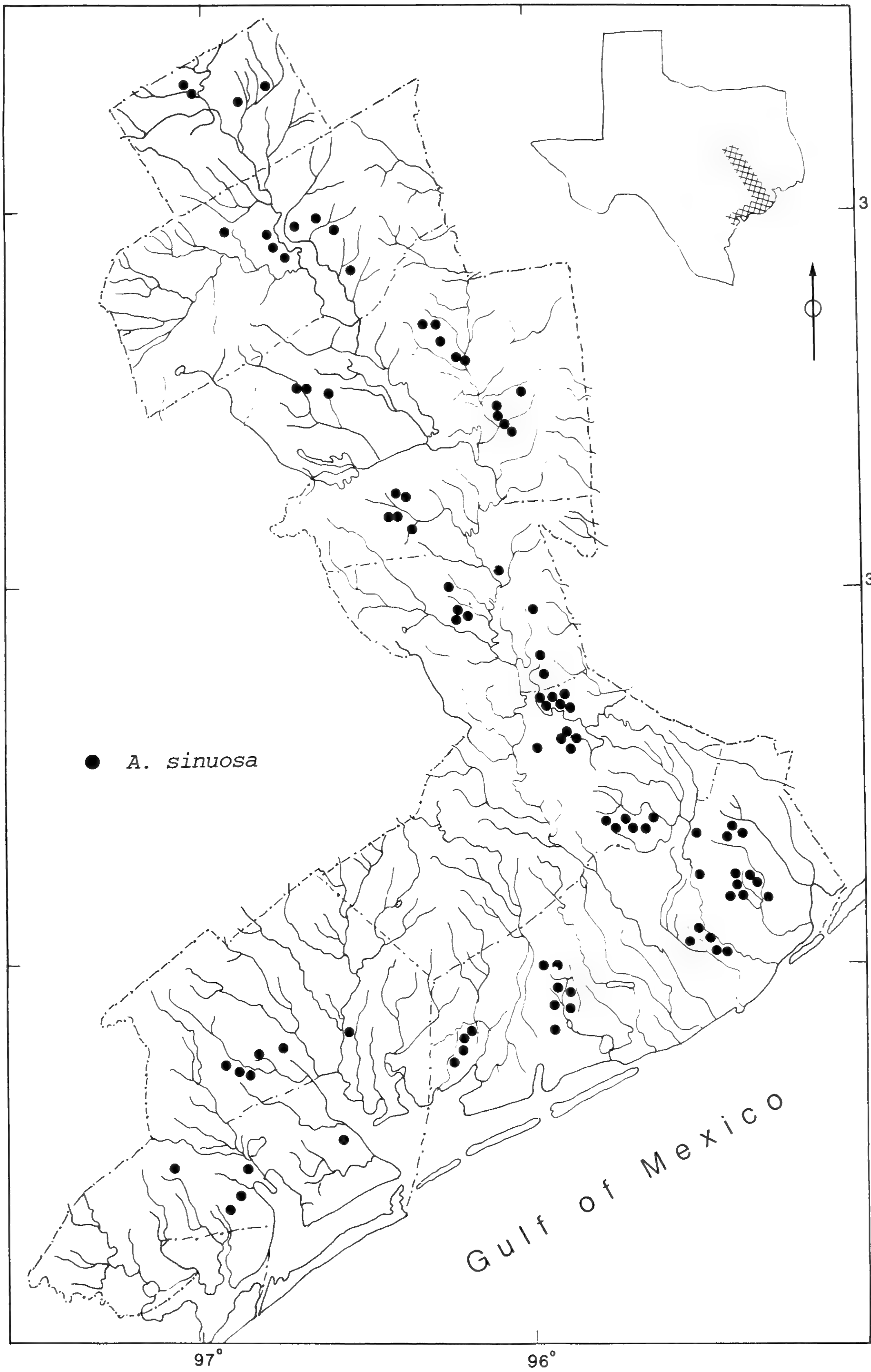

Fig. 5. Distribution of *Ankylocythere sinuosa* in the Brazos River drainage.

tinuity between the ranges of *A. sinuosa* and *A. tiphophila* and the seemingly consistent presence of a cleft peniferum in the range of the former and its absence in that of the latter, there seemed to be no reason to suspect that they represented two forms of a single species. With the acquisition of collections almost merging the ranges of the two species, we were prompted to compare specimens from Mexico to Virginia (Fig. 3) and found that in the Gulf Coastal area forms with a cleft peniferum, the only feature that has served consistently to separate the two (Fig. 3a, c), occur in localities in which some of the males were lacking a cleft (Fig. 3b, d, e). Moreover, in specimens from Bleckley County, Georgia (see Andolshek & Hobbs, 1986:fig. 12a), the peniferum is distinctly excavate, tending toward the cleft condition. In view of the discovery of an almost continuous range and no character that can be relied upon invariably to separate the two, we propose that *A. tiphophila* be considered a synonym of Rioja's *Entocythere sinuosa.*

Reinforcing this proposal is the seemingly subparallel clinal distribution with respect to the size of the shell. Andolshek & Hobbs (1986:25) reviewed in tabular form the shell size reported for *A. tiphophila* revealing that the largest specimens occur in North Carolina (410 μm) and Virginia (390 μm), smaller ones in South Carolina (346 μm), and the smallest in southeastern Georgia (321 μm). Perhaps significant are the sizes reported by Hobbs III (1969:74) for *A. sinuosa* occurring from eastern Texas to the panhandle of Florida. The mean shell length is 323 μm as compared with one of 321 μm in the material from southeastern Georgia. The cline, however, seems to be reversed between eastern Texas and Mexico, for the mean shell length for specimens from Mexico was reported by Hobbs (1971: 36) to be 350 μm.

Entocythere harrisi Peters
Fig. 6

Entocythere harrisi Peters, 1975:32–33, figs. 5a, 6e, f, 7a [Type locality: Rocky Creek 4.3 mi (6.9 km) E of U.S. Hwy 29 on U.S. Hwy 60, Amherst County, Virginia. Types: holotype and allotype, USNM; paratypes, USNM, H.H. Hobbs III, and DJP. Hosts: *Cambarus* (*C.*) *bartonii bartonii* (Fabricius), *C.* (*Hiaticambarus*) *longulus* (Girard), and *C.* (*P.*) *acuminatus* Faxon].—Hobbs & Peters, 1977:iv, 5, 9, 12–14, 21, 29, 33, 36, 41, 45, 47, 51, 52, 54, 55, 60, 61, 64, fig. 25; 1982:314; 1989:328.—Andolshek & Hobbs, 1986:30. [The references cited here constitute a complete bibliography for the species.]

Diagnosis.—Shell length of male 441–570 (avg. 477) μm; shell height 210–300 (avg. 244) μm. Peniferum truncate distally. Clasping apparatus "with postaxial border [slightly] bowed into heellike prominence at junction of horizontal and vertical rami, junction thickened; mesial surface of area of junction without flange; horizontal ramus without oblique ridges on mesial surface" (Hobbs & Peters 1977:51).

Range.—The most recent summary of the range of this ostracod was that of Hobbs & Peters (1977:52) who based their records, except for the type locality, on female specimens. In the present study we have become convinced that the characters they used for distinguishing between the females of this species and those of their *E. internotalis* (=*E. elliptica* Hoff, 1944) are not reliable. This conclusion is based upon the observation that in two collections of *E. harrisi* (one from Pike County, Arkansas, and another from Angelina County, Texas) containing several male and females, none of the latter possess the type of genital apparatus similar to those that were identified with that species in North Carolina and Virginia. Instead, the genital apparatus of the Arkansas and Texas females are indistinguishable from those of *E. elliptica* and *E. reddelli.* Thus we believe this ostracod is represented in collections only by the holotype (from Amherst County, Virginia) and the specimens cited herein from the Brazos River basin, Texas.

Remarks.—With the new records cited herein for the males of this species, we are inclined to propose a clinal distribution in size with respect to shell height. As the largest member is reported from Virginia

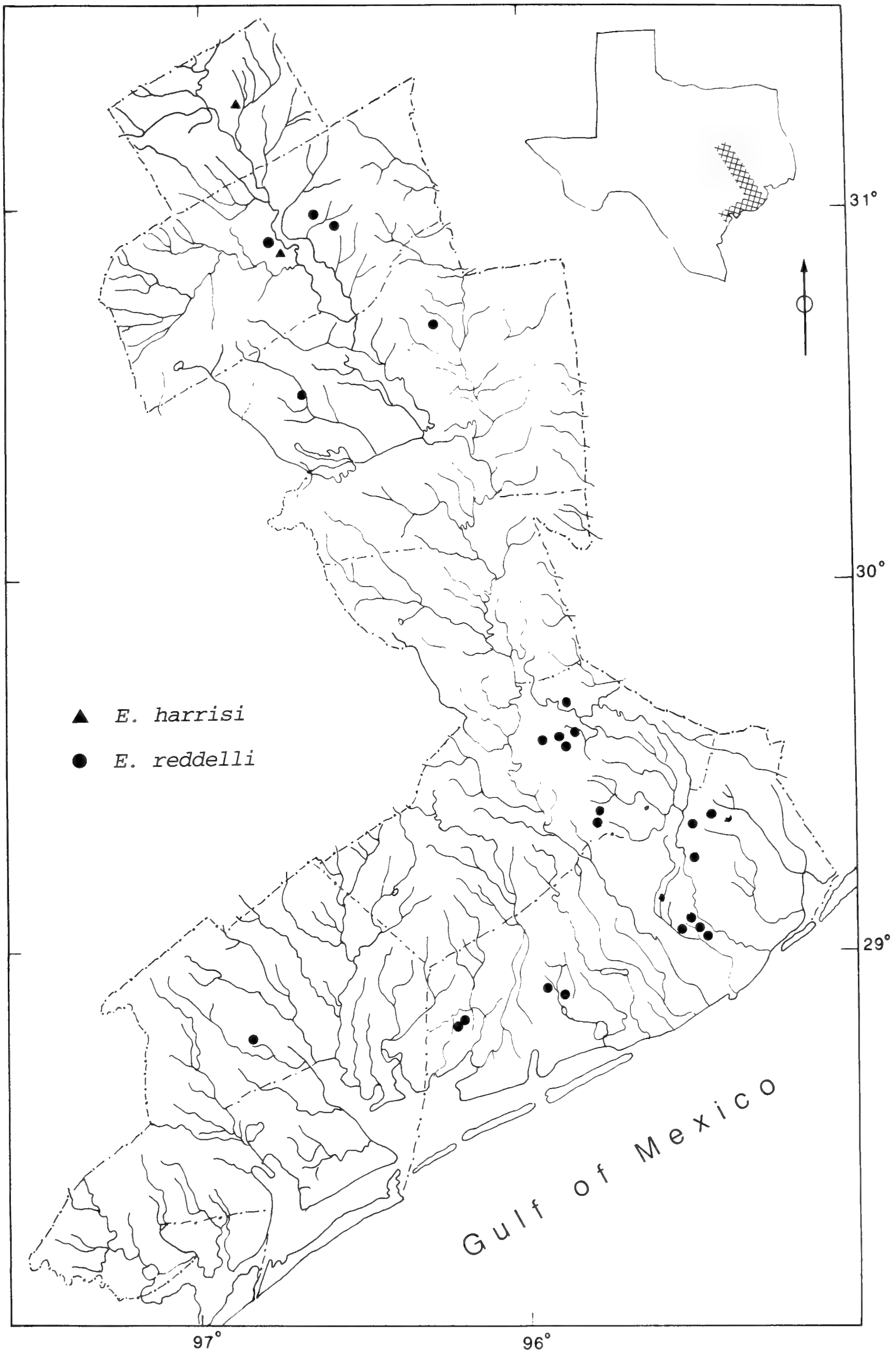

Fig. 6. Distribution of *Entocythere harrisi* and *Entocythere reddelli* in the Brazos River drainage.

(300 μm), smaller members occur from Pike Co., Arkansas (265 μm) and the Brazos River drainage (256 μm), with the smallest (224 μm) appearing in Angelina, Texas. However, when the shell length is compared, the largest member remains in Virginia (570 μm) and the smallest (456 μm) in Angelina, Texas, whereas members from

the Brazos River basin (490 μm) and Arkansas (476 μm) appear reversed. This may be due to the small number of specimens available for examination.

Southeastern Texas records (Fig. 6).—A male from each of the following localities: 4.0 mi (6.4 km) E of Marlin, Falls County, and McLaughlin Creek, 12.5 mi (20 km) E of Cameron on U.S. 90 at Branchville, Milan County.

Hosts.—In both localities this ostracod was found on *P.* (*G.*) *simulans* and *P.* (*O.*) *a. acutus.*

Entocytherid associates.—A. sinuosa was present in the two Brazos localities.

Entocythere reddelli Hobbs & Walton
Fig. 6

Entocythere reddelli Hobbs & Walton, 1968:243–246, fig. 2a–d [Type locality: Golden Fawn Cave, 8 mi (12.8 km) NNE of Boerne, Kendall County, Texas. Types: holotype, allotype, and paratypes, USNM; paratypes, Academy of Natural Sciences of Philadelphia and H.H. Hobbs III. Host: *P.* (*S.*) *clarkii* (Girard)].—Reddell & Mitchell, 1969:6.—Reddell, 1970: 395.—Hobbs, 1971:40.—Hart & Hart, 1974:83, 92–93, pl. XXVII: figs. 11–15, pl. LII.—Hobbs III, 1975:281.—Hobbs & Peters, 1977:iv, 5–7, 9–10, 12, 14, 29, 36, 41, 43, 45, 47, 52, 54, 55, 73; 1982: 313.—Andolshek & Hobbs, 1986:30. [These references constitute what we believe to be a complete bibliography for the species.]

Diagnosis.—Shell length of male 546–581 (avg. 564) μm; shell height 280–294 (avg. 287) μm. Peniferum subtruncate ventrally and possessing rounded antero- and posteroventral extremities. "Clasping apparatus with postaxial border at junction of horizontal and vertical rami produced in heellike prominence and junction thickened; mesial surface of area of junction with angular flange, apex of angle reaching level proximal to proximal tooth on preaxial margin of horizontal ramus, horizontal ramus lacking long oblique ridge extending across mesial surface. Female genital apparatus composed of ventrally directed subspiculiform projection arising from bipartite base, latter embedded in amorphous mass" (Hobbs & Peters 1977:55), second antenna with appendix at base of terminal claws conspicuously enlarged, pectinate, bearing 2 or 3 broad teeth or as many as 6 finely divided denticles.

Range.—In addition to its presence in Kendall County, Texas, Hart & Hart (1974: 93) reported its occurrence in Greene County, Arkansas, and Sumner County, Kansas. Hobbs & Peters (1977:55) also reported it from the Catawba, French Broad, and Hiwassee basins in North Carolina. Twenty-five localities in the Brazos River basin of southeastern Texas are cited here.

Southeastern Texas records (Fig. 6).—Twenty-five localities from the following counties: Brazoria (8), Brazos (1), Burleson (1), Fort Bend (7), Matagorda (4), Milan (1), Robertson (2), and Victoria (1).

Remarks.—Except for the distribution of this ostracod in the Brazos River basin, its range is poorly known. The total absence of records in what appears to be the central part of its range is disturbing, but there is little reason to suspect that the type locality lies on its western limit, and if and where its range and that of *E. cambaria* Marshall and *E. illinoisensis* Hoff meet or intersect to the north have not been determined.

Hosts.—In the Brazos basin, *E. reddelli* was found infesting *P.* (*O.*) *a. acutus* and *P.* (*S.*) *clarkii.* It also occurred in collections containing one or both of these crayfishes along with one or more of the following: *C.* (*D.*) *shufeldtii*, *C.* (*P.*) *ninae*, *C.* (*P.*) *puer*, *C.* (*P.*) *texanus*, *F.* (*C.*) *fodiens*, *P.* (*C.*) *brazoriensis*, *P.* (*C.*) *incilis*, and *P.* (*G.*) *simulans.*

Entocytherid associates.—In all 25 localities in which this ostracod was found, it was associated with *A. sinuosa*, and in one of them *A. ancyla* (hosts: *P.* (*O.*) *a. acutus* and *P.* (*S.*) *clarkii*) was also present; in another of these localities *U. simondsi* was infesting the same two host species.

Uncinocythere simondsi Hobbs & Walton
Fig. 4

Entocythere simondsi Hobbs & Walton, 1960:17, 20–21, figs. 1–10 [Type locality: Dunn Creek, 1.9 mi (3 km) west of Fighting Town Creek on Hell's Hollow Road, Fannin County, Georgia. Hosts: *C.* (*C.*) *bartonii* and *C.* sp. (=*C.* (*D.*) *latimanus*)].

Uncinocythere simondsi.—Hart, 1962:138. [A complete bibliography for the species is presented by Andolshek & Hobbs, 1986:39.]

Diagnosis.—Shell length of male 329–343 (avg. 336) μm; shell height 154–196 (avg. 175) μm. Copulatory complex of peniferum terminating distally in bifid tip. Clasping apparatus L-shaped with preaxial border bearing 3 distinct teeth; postaxial border entire, lacking any excrescence; distal extremity with 3 denticles.

Range.—From Illinois, Kentucky, and North Carolina southward to Brazoria and Washington counties, Texas, and northern Florida, previously known no farther west than Mississippi (Hart & Hart 1974; Hobbs & Peters 1977, 1982; Andolshek & Hobbs 1986).

Southeastern Texas records (Fig. 4).—This ostracod was found in the following localities: 2 mi (3.2 km) N, 2 mi (3.2 km) E of Brenham on St Rte 90, Washington County; and 1.25 mi (2 km) E of Rosharon on Farm Rd 1462, Brazoria County.

Hosts.—*Procambarus* (*S.*) *clarkii* was one of the hosts in both of the Brazos collections in which this ostracod was found. In one of them, *P.* (*O.*) *a. acutus* was also present, and in the other, *P.* (*G.*) *simulans* was in the container from which the ostracods were removed.

Entocytherid associates.—In both of the localities in which this ostracod was found, *A. sinuosa* and *E. reddelli* also were present. In the collection from Washington County, *A. ancyla* also was found with them.

Acknowledgments

We extend our thanks to the late H. H. Hobbs, Jr. who encouraged us in this endeavor and provided the materials, guidance, and insight for this study. We are also grateful to Horton Hobbs III for his criticism of the manuscript and to Brian Kensley, Ray Manning, and Karen Reed for their assistance.

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A new genus, *Neodoxomysis* (Crustacea: Mysidacea: Mysidae: Leptomysini), with description of two new species

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Abstract.—A new genus, *Neodoxomysis*, is established for two new species, *N. elongata* and *N. sahulensis*, collected from Sahul Shelf. The new genus is closely related to *Doxomysis*, but is different from the latter genus in having only a single strong, modified seta on the exopod of the fourth male pleopod, as compared with two in *Doxomysis*. *Doxomysis littoralis* Tattersall, 1922, is transferred to the new genus.

A single male specimen identified by Ii (1964) as *Doxomysis littoralis* Tattersall, 1922, is quite different from the other *Doxomysis* species in having a single strong modified seta on the exopod of the fourth male pleopod. The exopod in all other *Doxomysis* species is armed with two strong modified setae.

During a cruise to southeastern Asian seas (KH-72-1) by the R/V *Hakuho Maru* of the Ocean Research Institute, University of Tokyo, two undescribed species, which were similar to *D. littoralis* with respect to the morphology of the fourth male pleopod, were collected. This morphological character is distinct these species from those of the genus *Doxomysis*. Therefore, a new genus is established to receive these three species, and two new species are described. The type specimens are deposited in the National Science Museum, Tokyo (NSMT).

Neodoxomysis, new genus

Diagnosis.—Carapace produced anteriorly into triangular rostral plate with rounded apex. Antennal scale lanceolate with rounded apex, armed with setae on whole margins. Eye functionally normally developed, without papilliform process on eyestalk. Maxilla with second segment of endopod wider than long, expanded distally, with about 10 strong spines on distal margin. Labrum with rounded frontal margin. Endopods of third to eighth thoracic limbs with propodus divided into 2 subsegments. Endopod of uropod with row of numerous spines along inner margin. Telson with lateral margin armed with spines throughout, apical cleft deep, armed with marginal spinules and pair of plumose setae arising from anterior end. Exopod of fourth pleopod of male modified, longer than endopod, ultimate segment small, with 1 or 2 short simple setae, penultimate segment with single strong seta.

Type species.—*Neodoxomysis elongata*, new genus, new species.

Etymology.—Derived from its relationship to *Doxomysis*. It is feminine in gender.

Remarks.—The new genus *Neodoxomysis* closely resembles *Doxomysis* Hansen, 1912, except for the fourth male pleopod. In the new genus, the exopod of the fourth male pleopod is armed with only a single, strong, modified seta arising from the penultimate segment, while in *Doxomysis* as well as eight related genera in the tribe Leptomysini (Talbot 1997), the exopod is armed with two strong modified setae, one arising from the penultimate segment and the other from the antepenultimate segment.

Among 11 *Doxomysis* species in which the exopod of the fourth male pleopod has been described, only *D. littoralis* bears a single strong modified seta on the exopod. This species was established on specimens from the Andaman Islands by Tattersall (1922); later the male was described from the South China Sea by Ii (1964). Accordingly, *D. littoralis* should be transferred to the new genus. The new genus *Neodoxomysis* comprises a total of three species.

Neodoxomysis elongata, new species
Figs. 1, 2

Type series.—Holotype (NSMT-Cr 12487), adult male (5.3 mm), allotype (NSMT-Cr 12488), adult female with embryos (4.9 mm), paratypes (NSMT-Cr 12489), 6 adult males (6.1–6.8 mm) and 3 adult females (4.5–5.0 mm); Sahul Shelf, 12°37.3′S, 124°33.9′E to 12°36.0′S, 124°36.4′E; 74–78 m; 25–26 June 1972; plankton net installed in mouth of 3-m beam trawl.

Other material.—8 adult males, 3 adult females, 15 immature males and 19 immature females; collection data same as type series.

Description.—Body somewhat slender. Carapace produced anteriorly into triangular rostral plate with rounded apex extending beyond basal margin of antennular peduncles, leaving whole eyes uncovered (Fig. 1A, B); anterolateral corner rounded; posterior margin slightly emarginate, leaving last thoracic somite exposed.

Eye developed, relatively large; cornea occupying more than half of whole organ, spherical, wider than eyestalk; eyestalk hispid on anterior and posterior surfaces, without papilliform process (Fig. 1A, B).

Antennular peduncle of male more robust than that of female, first segment with several setae at outer distal corner and 1 seta at inner distal corner, second segment short, narrower than preceding one; third segment as long as first, wider than preceding two segments, with 1 straight and 4 short curved setae at inner distal corner; processus masculinus large, hirsute (Fig. 1A). Antennular peduncle of female slender; first segment as long as succeeding 2 segments together; second segment short, narrow, with 1 seta at inner distal corner; third segment with 1 seta at distal third of inner margin and 5 setae on inner distal margin (Fig. 1B).

Antennal scale extending beyond distal margin of third segment of antennular peduncle for about ⅓ of its length (Fig. 1A, B), lanceolate, 6.3 times as long as broad, outer margin slightly concave, distal segment $\frac{1}{10}$ of length of scale (Fig. 1C). Antennal peduncle short, reaching proximal third of antennal scale, 3-segmented, third segment longest; sympod with thorn at outer distal corner (Fig. 1C).

Mandible with well developed masticatory edge. Mandibular palp 3-jointed, second segment elongated oval, third segment 0.52 of second in length, outer margin with 2 series of setae, proximal setae longer, barbed on proximal half, distal setae barbed on whole length (Fig. 1D). Maxillule: inner lobe with 9 setae on inner margin, 5 setae on outer margin, 3 setae on ventral surface and 3 stout and 1 slender setae on distal margin; outer lobe with about 10 spines on apical margin and 3 setae on ventral surface (Fig. 1E). Maxilla: second segment of endopod expanded distally, wider than long, distal margin slightly convex, 2.5 times as wide as at base, armed with 10 stout spines, which are rounded and flattened at tip, outermost spine longer than others, inner 6 spines, especially 2 innermost ones armed with short setae on margins; exopod rather rectangular in shape, extending beyond distal margin of first segment of endopod (Fig. 1F). Labrum with frontal margin rounded (Fig. 1G).

Endopod of first thoracic limb robust, dactylus wider than long, with strong terminal claw (Fig. 1H). Endopod of second

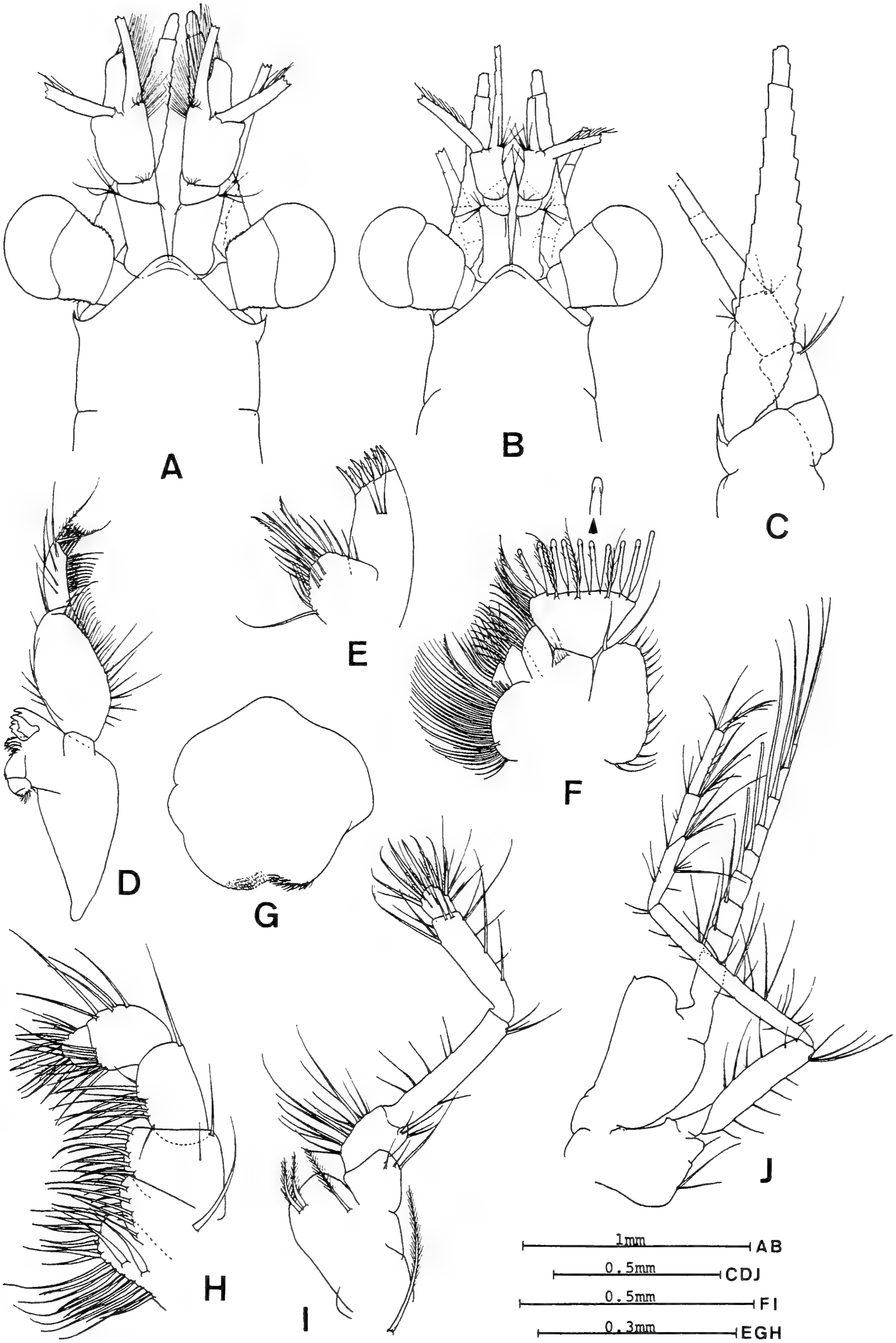

Fig. 1. *Neodoxomysis elongata*, new species; A, C–J: holotype; B: allotype. A, anterior end of adult male; B, anterior end of adult female; C, antenna; D, mandible and mandibular palp; E, maxillule; F, maxilla; G, labrum; H, endopod of first thoracic limb; I, endopod of second thoracic limb; J, sixth thoracic limb.

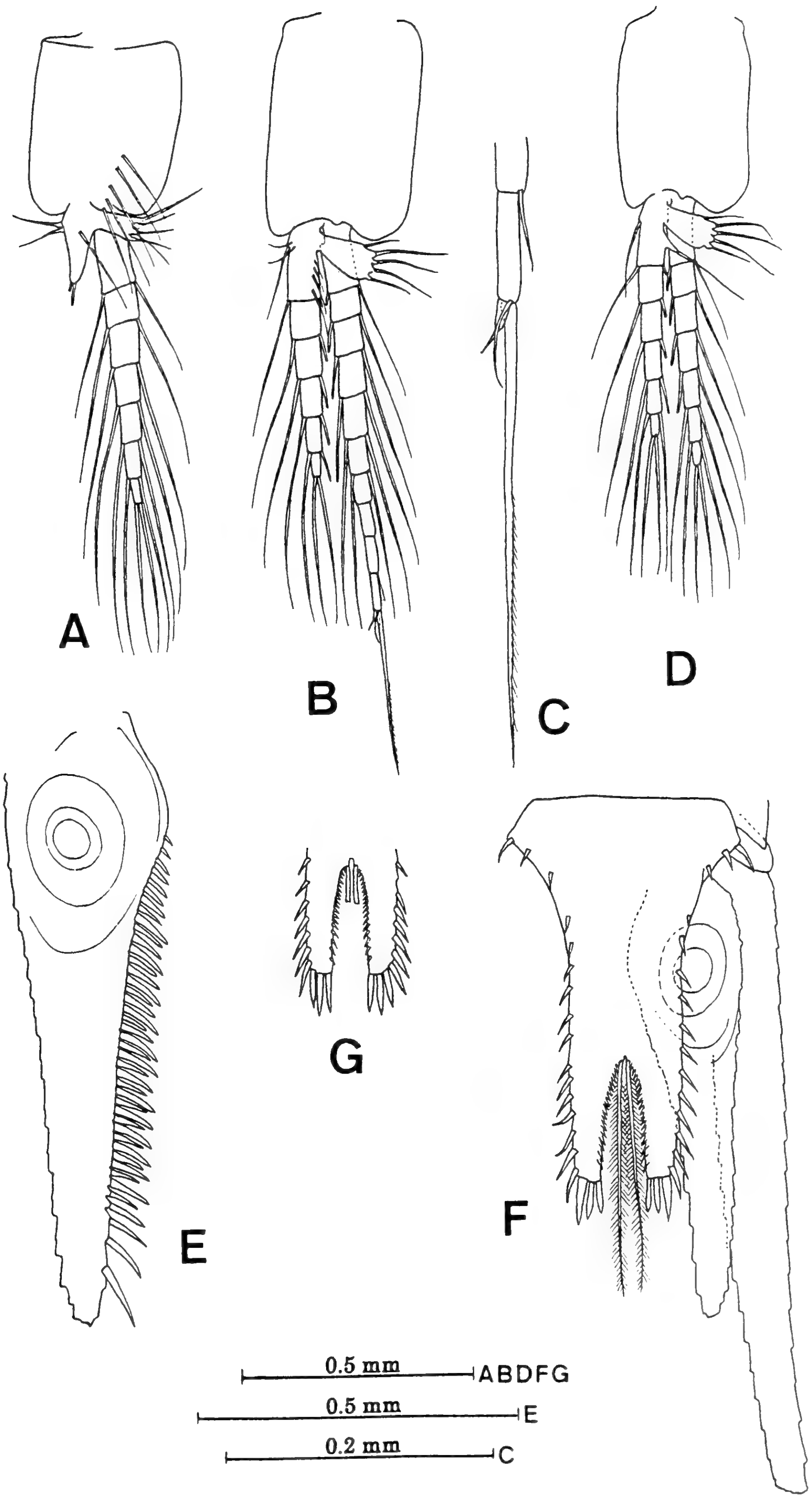

Fig. 2. *Neodoxomysis elongata*, new species; A–F: holotype; G: allotype. A, first male pleopod; B, fourth male pleopod; C, distal part of fourth male pleopod; D, fifth male pleopod; E, endopod of uropod; F, uropod and telson; G, distal part of telson.

thoracic limb slender, basis with inner lobe developed, ischium with long setae on inner margin, merus as long as carpopropodus and dactylus combined, dactylus with terminal claw and 6 barbed setae (Fig. 11).

Endopod of sixth thoracic limb slender, carpus separated obliquely from 2-subsegmented propodus, distal propodal subsegment longer than proximal, equal to carpus in length; dactylus small, with slender terminal claw (Fig. 1J). Exopods of thoracic limbs with basal plate armed with small acute process at outer distal corner, flagelliform part 8-segmented in first and eight limbs, 9-segmented in second to seventh limbs (Fig. 1J).

Abdomen consisting of 6 somites, first 5 somites subequal, sixth somite 1.7 times longer than fifth.

Male pleopods well developed, natatory. First pair with 7-segmented exopod and unsegmented endopod (Fig. 2A). Second and third pairs with 7-segmented exopod and 6-segmented endopod extending to distal margin of sixth segment of exopod. Fourth pair: exopod 1.6 times longer than endopod, 11-segmented, seventh and eighth segments unarmed with setae, ninth segment with 1 short seta at outer distal end, tenth segment with 2 setae on distal end, longer one extremely long, 0.4 of exopod in length, straight, feathered in distal half, shorter one simple, 0.2 as long as longer one, terminal segment very small, ⅓ of preceding one in length, with 1 short seta; endopod 6-segmented, reaching distal end of sixth segment of exopod, without modified setae (Fig. 2B, C). Fifth pair: exopod 7-segmented, longer than endopod, endopod 6-segmented, with triangular lobe tipped with seta on outer margin of first segment (Fig. 2D).

Exopod of uropod slender, long, slightly curved outwardly, extending beyond distal end of telson for its distal half (Fig. 2F). Endopod of uropod extending beyond distal end of telson for distal third, armed along inner margin from statocyst region to near apex with about 42 spines which are made up with longer and shorter ones arranged alternately, except several spines in distal and proximal portions (Fig. 2E, F).

Telson slightly longer than last abdominal somite, 1.7 times as long as broad at base, abruptly narrowing near base, parallel-sided in middle part, then gradually narrowing towards distal end, cleft at apex for ⅓ of telson length; lateral margin armed along whole length with about 16 spines, sparsely in proximal third and densely in distal ⅔; each apex of distal lobes rather truncate, with 3 somewhat obtuse spines, outermost one longest in male and middle one in female; cleft with small notch at anterior end, each side with about 16–18 spinules along whole length except for posterior short distance naked, pair of plumose setae arising from anterior end of cleft (Fig. 2F, G).

Etymology.—The name *elongata* refers to the slender body.

Remarks.—*Neodoxomysis elongata* is considerably different from the other two species of the genus, *N. sahurensis* and *N. littoralis*, in the following aspects: The antennal scale is 6.3 times as long as broad in this species, while it is about 5 times as long in the other two species; the exopod of the fourth male pleopod is 11-jointed in this species as compared with 7 in the other two species; and, spines on the second endopod segment of the maxilla are rounded and flattened distally in this species, while these are sharply or obtusely pointed in the other two species.

Neodoxomysis sahulensis, new species
Figs. 3, 4

Type series.—Holotype (NSMT-Cr 12490), adult male (5.0 mm); allotype (NSMT-Cr 12491), adult female (4.0 mm); paratypes (NSMT-Cr 12492), 2 adult females (3.7, 4.0 mm), 1 adult male (divided into two parts); Sahul Shelf, 12°17.3′S,

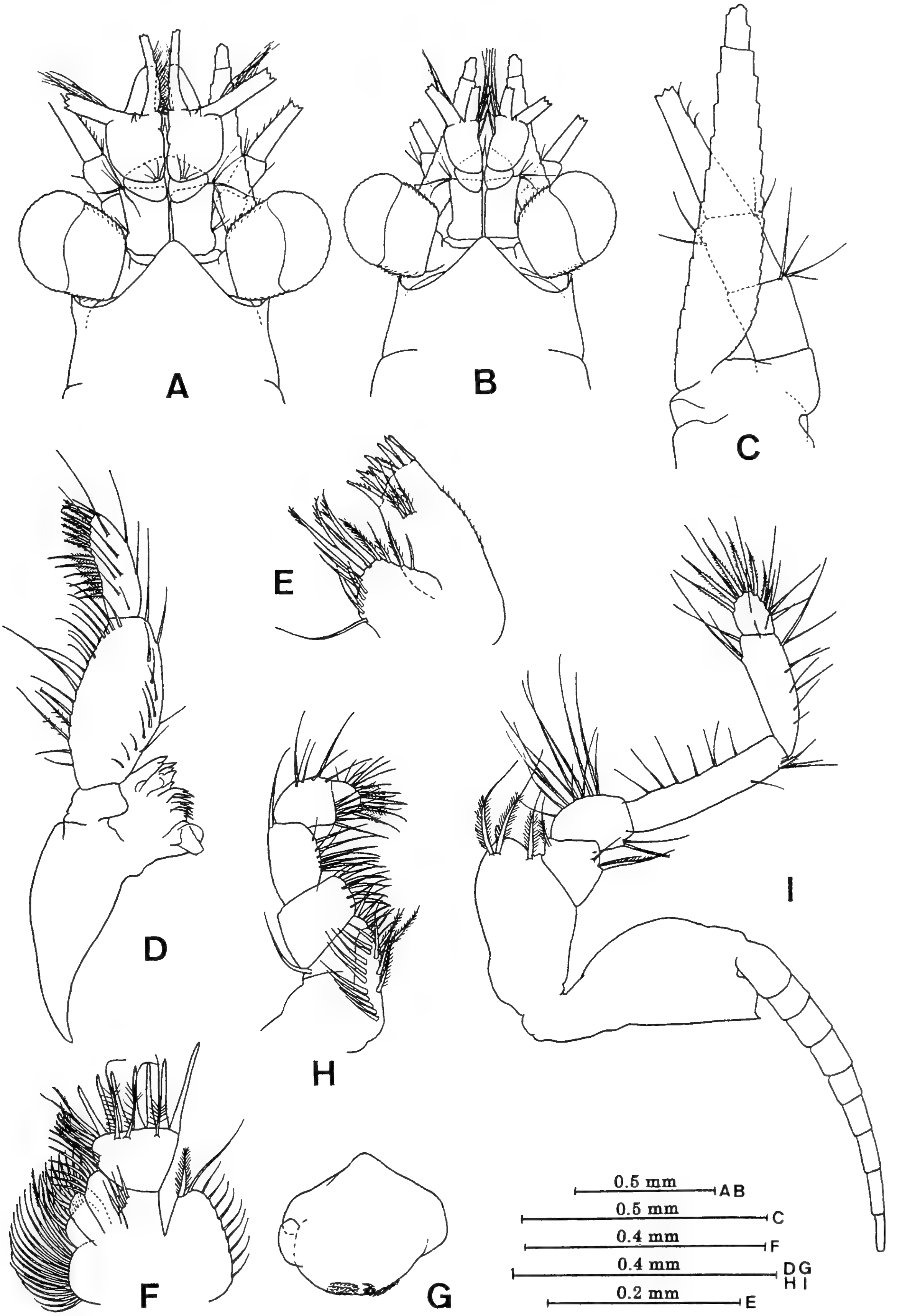

Fig. 3. *Neodoxomysis sahulensis*, new species; A, C–G: holotype; B: allotype. A, anterior end of adult male; B, anterior end of adult female; C, antenna; D, mandible and mandibular palp; E, maxillule; F, maxilla; G, labrum; H, endopod of first thoracic limb; I, second thoracic limb.

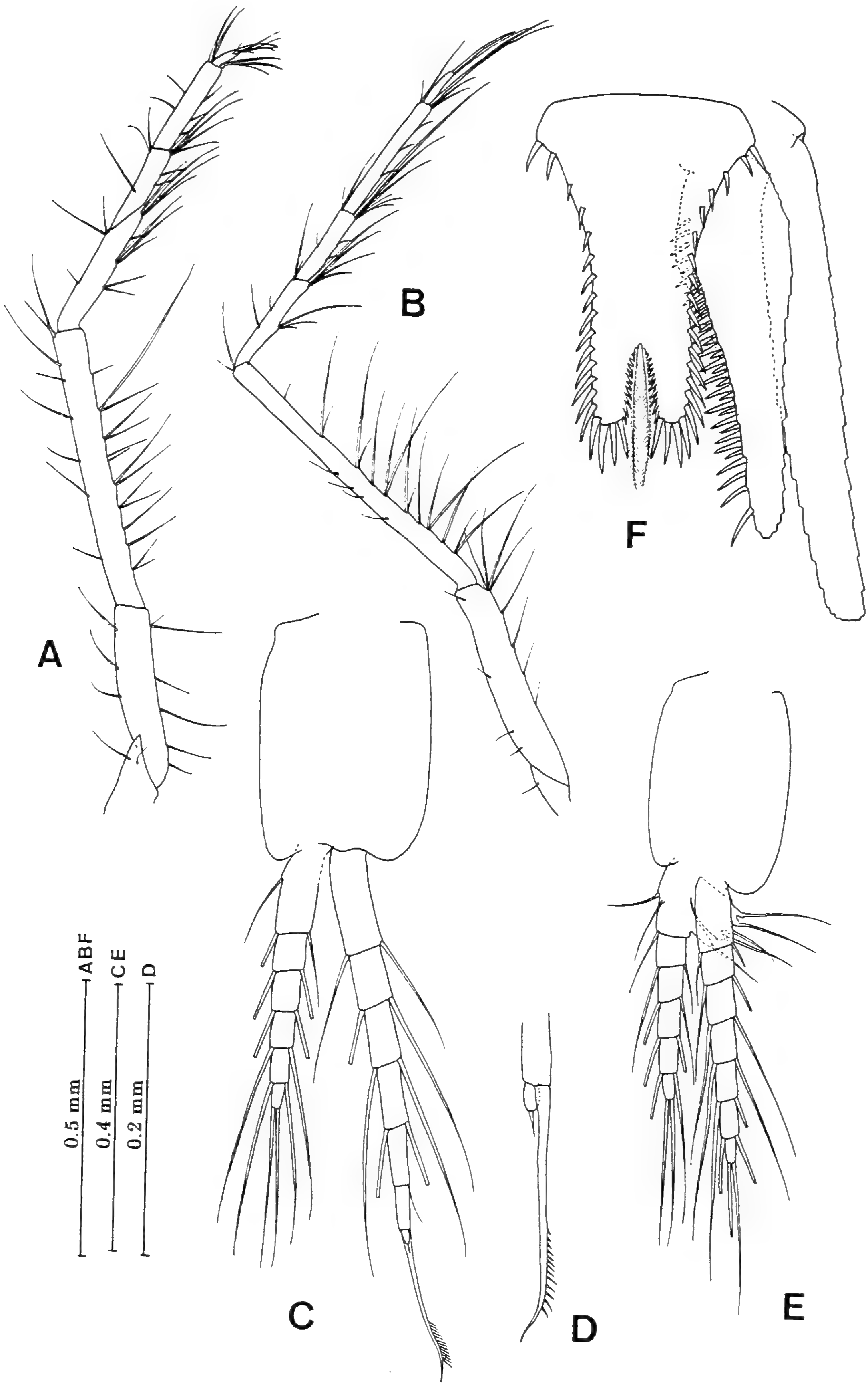

Fig. 4. *Neodoxomysis sahulensis*, new species; A: allotype; B–F: holotype. A, endopod of one of posterior thoracic limbs; B, endopod of eighth thoracic limb; C, fourth male pleopod; D, distal part of exopod of fourth male pleopod; E, fifth male pleopod; F, uropod and telson.

129°40.9′E to 12°17.2′S, 129°41.8′E; 49–52 m; 24 June 1972; plankton net installed in mouth of 3-m beam trawl.

Description.—Carapace with anterior margin produced in triangular rostrum with narrowly rounded apex and almost straight lateral margins, leaving whole eyes exposed (Fig. 3A, B); anterolateral corner rounded; posterior margin somewhat emarginate, leaving last thoracic somite uncovered.

Eye moderately developed; cornea occupying about half of whole eye, slightly wider than stalk; stalk hispid on anterior and posterior surfaces (Fig. 3A, B).

Antennular peduncle of male more robust than that of female, first segment as long as third, with anterolateral corner slightly produced anteriorly, armed with several setae, second segment short and narrow, third segment wider than preceding segments, with 1 short seta at distal third of inner margin and 2 setae at anteromedian corner; processus masculinus large (Fig. 3A). In female, first segment longer than and as wide as third, second segment with 1 seta at anteromedian corner, third segment with 1 seta at distal third of inner margin and 4 setae at anteromedian corner (Fig. 3B).

Antennal scale setose on whole margins, overreaching distal end of antennular peduncle for ⅓ of its length (Fig. 3A, B), more than 5 times as long as broad, outer margin nearly straight, inner margin convex in proximal half, distal segment ⅑ of length of scale (Fig. 3C). Antennal peduncle short, barely extending to middle of antennal scale, composed of 3 segments, distal 2 equal in length, longer than proximal one; antennal sympod with long, acute process at outer distal corner (Fig. 3C).

Mandible with well developed masticatory edge; mandibular palp with second segment elongated oval, third segment 0.6 as long as second, outer margin with 2 series of setae, proximal setae longer, barbed on proximal half, distal one barbed along whole length (Fig. 3D). Maxillule: inner lobe with 7 setae on inner margin, 4 setae on outer margin and 3 stout and 1 slender setae on apical margin; outer lobe with about 10 spines on apical margin, about 10 spinules on middle part of outer margin and 3 setae on ventral surface (Fig. 3E). Maxilla: distal segment of endopod expanded distally, wider than long, distal margin slightly arched, 2.5 times as wide as at base, armed with 7 strong spines of which outer one is longer than others; exopod extending to distal end of first endopod segment (Fig. 3H). Labrum with frontal margin rounded (Fig. 3G).

First thoracic endopod robust, ischium wider than long, with developed inner lobe, merus relatively slender, dactylus wider than long, with stout, straight claw (Fig. 3H). Second thoracic endopod rather slender, basis with developed inner lobe, ischium with about 8 long setae on inner margin, merus as long as carpopropodus and dactylus together, dactylus longer than wide, with 1 barbed claw and 6 barbed setae (Fig. 3I). Third to eighth thoracic endopods becoming more slender towards posterior pairs, carpus articulated obliquely with propodus but in eighth limb articulation is nearly transverse, propodus divided into 2 subsegments, in eight limb distal subsegment 1.6 times longer than proximal (Fig. 4A, B). Exopods with flagelliform part 9-segmented in middle pairs; basal plate with outer distal corner pointed (Fig. 3I).

Abdomen with sixth somite longest, 1.3 times as long as fifth.

Male pleopods well developed, biramous. First pleopod with 7-segmented exopod and unsegmented endopod. Second and third pleopods with 7-segmented exopod longer than 6-segmented endopod. Exopod of fourth pleopod modified, 7-segmented, nearly 1.5 times longer than endopod, terminal segment very small, ⅓ of preceding segment in length, armed with 1 tiny seta at distal end, penultimate segment with 1 strong spinose seta which is nearly 4 times longer than segment supporting it, antepenultimate segment armed with 1 short feeble seta at distal end of outer margin; endopod 6-segmented, normal, without

Table 1.—Morphological differences between *Neodoxomysis sahulensis* and *N. littoralis.*

	N. sahulensis	*N. littoralis*
Second segment of endopod of maxilla	With 7 acute, simple spines	With 9 slender, bluntly pointed spines
Exopod of 4th pleopod of male	7-jointed, with 1 seta at distal end	7-jointed, with 2 setae at distal end
Endopod of 4th pleopod of male	Extending to middle of 4th segment of exopod	Extending to distal end of 5th segment of exopod
Endopod of 5th pleopod of male	Extending to distal end of 5th segment of exopod	Extending to distal end of 6th segment of exopod
Telson	1.5 times as long as broad, lateral margin with 16–17 spines; cleft ¼ as long as telson, with 11–12 spines on each side	1.75 times as long as broad, lateral margin with 16 spines; cleft $^2\!/_7$ as long as telson, with 16–19 spines on each side

modified setae (Fig. 4C, D). Fifth pleopod with exopod 7-segmented, 1.2 times longer than 6-segmented endopod; endopod with first segment with digitiform projection tipped with 1 seta on outer margin in addition to usual side lobe (Fig. 4E).

Endopod of uropod extending beyond distal end of telson for ⅓ of its length, inner margin from statocyst region to near apex with 34 spines, which are composed of longer and shorter spines arranged alternately except for several spines on proximal and distal portions, distal 4 spines long and acute, other spines obtuse (Fig. 4F). Exopod of uropod overreaching endopod for ⅕ of its length (Fig. 4F).

Telson as long as last abdominal somite, 1.5 times as long as broad at base, deeply cleft at apex; lateral margin furnished with 16–17 rather long spines along whole length, distal 10 spines gradually increasing in length towards apex; each apex of distal lobes armed with 3 spines, outer one of which is slightly longer than others; apical cleft ¼ as long as telson, furnished with 11–12 spinules on each side and pair of plumose setae arising from anterior end (Fig. 4F). Spination on telson in female similar to that of male.

Etymology.—The name *sahulensis* refers to the locality in which the specimens were collected.

Remarks.—Neodoxomysis sahulensis is closely similar to *N. littoralis* (Tattersall, 1922) in many respects, but distinguished from that species as shown in Table 1.

In the new species the outer lobe of the maxillule is furnished with a row of spinules on the middle part of the outer margin. Such a character has been observed in *Doxomysis quadrispinosa* by Pillai (1973) and *D. australiensis* by Tattersall (1940).

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First record of the family Gynodiastylidae Stebbing, 1912 (Crustacea: Malacostraca: Cumacea) from Antarctic waters with the description of *Gynodiastylis jazdzewskii*, a new species

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Abstract.—An adult male of an undescribed gynodiastylid cumacean was collected in a Menzies trawl sample taken at a depth of between 388 and 399 m in the Ross Sea (76°01.5′–76°01.0′S, 179°49.9′–179°52.3′E) during February 1972. The specimen, which had lost its third maxillipeds and the last four articles of the first pereopods, is placed in the genus *Gynodiastylis* Calman, 1911. *Gynodiastylis jazdzewskii*, new species, the first member of its family reported from Antarctic waters, can be distinguished from the 59 previously described species of *Gynodiastylis* and members of the other five gynodiastylid genera by a combination of characters, including the finer, more irregularly wavy, longitudinal ridges, and the length and setation of the telson, on the carapace, the shape and terminal setation of the telson, the length of telson in relation to that of the last abdominal somite and uropodal peduncles, and the setation and relative length of the uropodal rami.

An examination of the Cumacea collected by the R/V *Eltanin* in the Ross Sea, revealed a single adult male specimen of an undescribed gynodiastylid. The specimen was damaged (third maxillipeds and the four distal articles of the first pereopods missing), but can be reliably assigned to the genus *Gynodiastylis* Calman, 1911 and represents the first record of the family Gynodiastylidae from the Antarctic region.

Gynodiastylis jazdzewskii, new species
Figs. 1–2

Material examined.—Holotype: adult male (USNM 243765); Ross Sea, between 76°01.5′S–179°49.9′E and 76°01.0′S–179°52.3′E; depth 388–399 m; 08 February 1972; Menzies trawl; R/V *Eltanin*, Cruise 51, Sta. 5761; Coll., Smithsonian Oceanographic Sorting Center.

Diagnosis.—Gynodiastylidae. Adult male. Carapace with numerous (approximately 17) fine, irregular, wavy, longitudinal ridges, many coalescing (especially anteriorly). Exopods on pereopods 1–4. Telson linguiform, distinctly longer than sixth abdominal somite, extending to distal ¾ of uropodal peduncle, armed with 2 distinct, closely set, terminal spine-setae. Uropods relatively long, attenuated; peduncle with 4 spine-setae along inner distal margin; endopod and exopod with 2 articles, endopod (excluding terminal setae) slightly longer than exopod, exopod with 2 long terminal setae, innermost about as long as rest of exopod, outer seta about ⅔ length of inner one.

Description.—adult male holotype (Fig. 1), carapace length 0.9 mm, total length 3.2 mm. Carapace nearly ⅓ of total length; having numerous (approximately 17) fine, irregular, wavy, longitudinal ridges (or striations), many coalescing anteriorly; ocular lobe well-developed, eyes obscure, unpig-

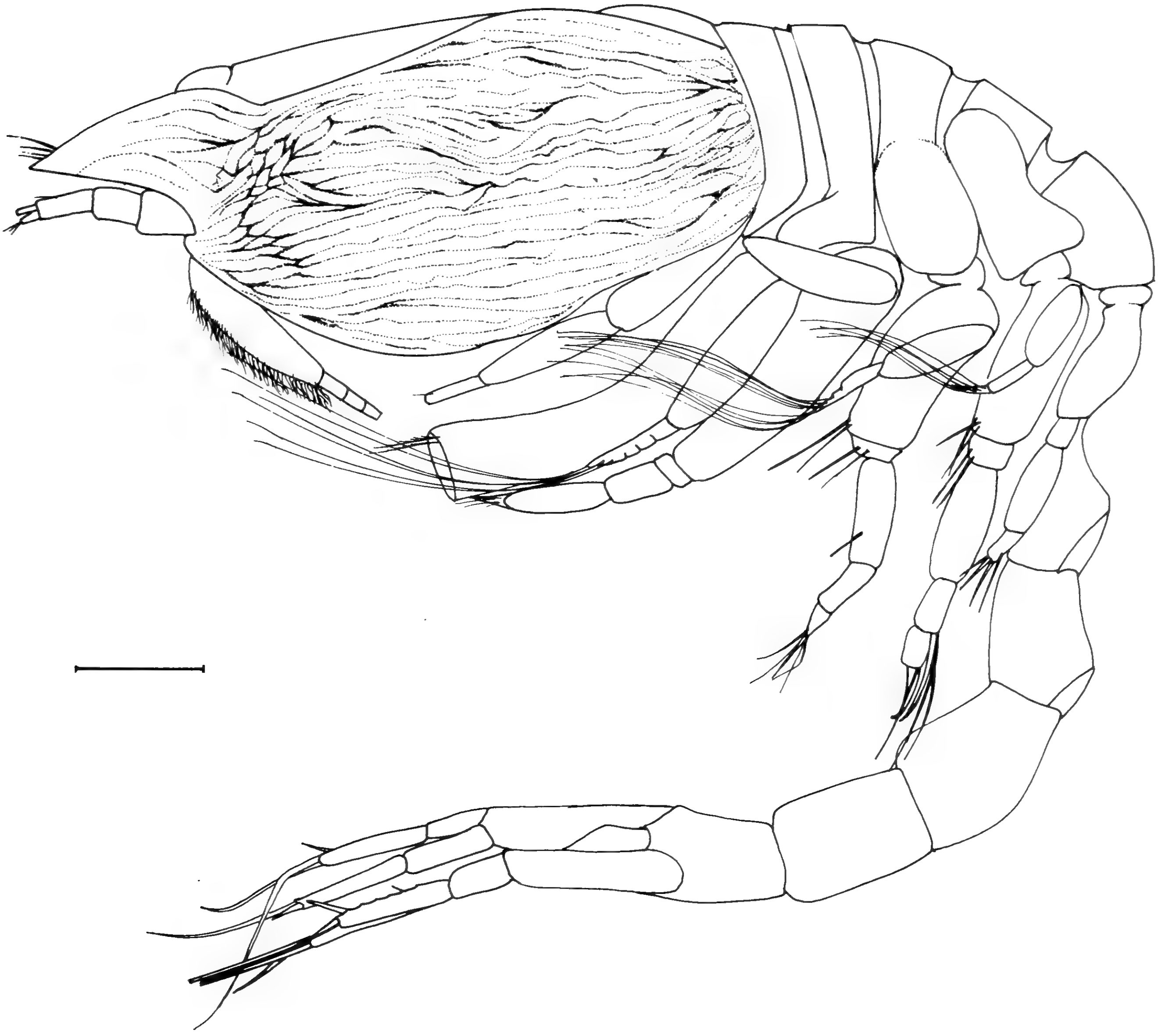

Fig. 1. *Gynodiastylis jazdzewskii*, n. sp. Lateral view of male holotype. Scale = 0.2 mm.

mented; pseudorostrum strongly developed, acutely pointed, slightly decurved, extending well beyond ocular lobe. Antennal notch broad, not defined ventrally by sharp tooth. Thoracic somites 3–5 as illustrated (Fig. 1). Abdomen (Fig. 1) subequal in length to carapace; somites of similar length. Telson (Fig. 2J) linguiform, distinctly longer than sixth abdominal (telsonic) somite, extending to distal ¾ of uropodal peduncle, armed with 2 distinct, closely set, terminal spine-setae. First and second antennae (not dissected), appearing similar to those of other described members of genus. Mandible (Fig. 2A): with well developed incisor and molar. First maxilla (Fig. 2B): outer endite with 14 terminal or subterminal, stout, spine-setae. Second maxilla (fig. 2E): characterized by well-developed, stout comb setae. Maxilliped 1 (Fig. 2D): branchial lobe (not illustrated) lacking branchial processes; siphon long, twisted distally, terminating in bent acute tip; endopod with well-developed specialized setae and spine-setae on inner plate, coxa, and propodus (Fig. 2D, enlargements). Second maxilliped (Fig. 2C): carpus nearly twice as long as propodus; propodus more than twice as long as dactyl; dactyl terminating in 3 well developed, simple spine-setae. Third maxillipeds: lost. Pereopods 1–4: bearing exopods, exopods decreasing in size posteriorly

Fig. 2. *Gynodiastylis jazdzewskii*, n. sp. A, left mandible: incisor (on left), all spine teeth, except distal most broken off; molar (on right); B, first maxilla; C, second maxilliped (terminal articles); D, first maxilliped (excluding damaged branchial lobe) showing enlargement of setal types; E, second maxillia F, second pereopod (exopod not shown); G, third pereopod; H, fourth pereopod (exopod not shown); I, fifth pereopod; J, sixth abdominal (telsonic) somite, uropods, and telson. Scale a = 0.1 mm for F, G, H, I; Scale b = 0.3 mm for A, B, C and 0.1 mm for J.

(Fig. 1). First pereopod (Fig. 1) damaged, only basis present; basis strongly developed, extending anteriorly past midlength of carapace, nearly as long as entire second pereopod. Second pereopod (Fig. 2F), basis subequal to combined length of other articles; ischium distinguishable; carpus longer than merus; propodus subequal in length to dactyl. Third pereopod (Fig. 2G), merus well developed, subequal in length to basis; carpus approximately as long as propodus, nearly as wide as long with 3 well developed distal setae, 1 extending to tip of dactyl and 2 extending well beyond dactyl; dactyl about as long as propodus. Fourth pereopod (Fig. 2H) similar to third, but having more slender carpus. Fifth pereopod (Fig. 2I), basis relatively short, subequal in length to combined lengths of ischium, merus, and carpus; merus broad, slightly longer than carpus; carpus longer than propodus; propodus with long, stout, distal seta extending well past dactyl; dactyl shorter than propodus. Uropods (Fig. 2J): relatively long, approximately equal to combined length of abdominal somites 5 & 6, attenuated; peduncle with 4 spine-setae along inner distal margin; inner ramus with 2 articles, longer than outer ramus, proximal article with inner margin bearing 3 spine-setae, distal article longer than proximal, inner margin with 3 spine-setae, 2 terminal setae present, outer seta distinctly longer than distal article and over 4 times longer than inner seta; outer ramus with 2 articles, distal article with one relatively short subterminal seta on inner margin and 2 long terminal setae, innermost approximately as long as rest of exopod, outer seta about ⅔ length of inner.

Etymology.—This species is named in honor of Professor Krzysztof Jażdżewski (University of Łódź, Poland) in recognition of his many significant contributions to Antarctic biological research.

Comparisons.—*Gynodiastylis jazdzewskii* can be distinguished from the previously described species of the genus by the fine, irregularly wavy, longitudinal ridges on the carapace, the shape and terminal setation of the telson, the relative length of the telson in relation to that of the last abdominal somite and the uropodal peduncles; and by the setation and relative length of the uropodal rami.

Of the known species of *Gynodiastylis*, four (*G. costata* Calman, 1911; *G. turgida* Hale, 1928; *G. lata* Hale, 1946; *G. lineata* Day, 1980) have carapaces with longitudinal ridges or striations. Of these, *G. jazdzewskii* appears to be most closely related to *G. costata*, the only other member of the genus having numerous, fine, irregular striations on its carapace. *Gynodiastylis costata* was originally described from Gulf of Siam at depths ranging from 9 to 37 m. It was later reported from "night surface plankton" in Japanese waters by Gamô (1968).

Gynodiastylis jazdzewskii is readily distinguishable from the comparable males of *G. costata* sensu Calman (1911) and Gamô (1962) by having: (1) a longer and more acutely tipped rostrum, (2) a distinctly longer telson (approximately ¾ the length of the uropodal peduncle), and (3) two long terminal setae on the tip of uropodal exopod. Based on Calman's (1911) and Gamô's (1962) descriptions and illustrations (plate 36, figs. 1–10 and fig. 40, respectively) the telson of male *G. costata* is half or less the length of the uropodal peduncle. There is only a single long inner terminal seta on the uropodal exopod of *G. costata*, the outer terminal seta being weakly developed (less than ⅕ the length of the inner).

The variously modified peduncular articles of the first antennae of *Allodiastylis* Hale, 1936 and *Sheardia* Hale, 1946 distinguish *G. jazdzewskii* from the species of these two genera. The presence of uropodal endopods with two articles distinguishes *G. jazdzewskii* from the species of the genus *Dicoides* Hale, 1946, which are characterized by uropodal endopods with three articles. The members of the remaining two gynodiastylid genera, *Halina* Day, 1980, and *Zimmeriana* Hale, 1946, all lack the fine, longitudinal, carapace ridges that characterize *G. jazdzewskii.*

Discussion.—In her revision and reinstatement of the family Gynodiastylidae, Day (1980) recognized six genera, *Gynodiastylis*, *Allodiastylis*, *Dicoides*, *Haliana*, *Sheardia*, and *Zimmeriana*. Based on the summary works by Day (1980) and Băcescu (1992), records for all previously described gynodiastylids appear to be confined to the Indo-West Pacific region between 40°N (Japan) and 43°S (New Zealand).

Because present day gynodiastylids have predominantly tropical and temperate distributions, *G. jazdzewskii* might represent a relic species whose ancestral stock was present in cold Antarctic waters before the break up of Pangaea over 180 million yr ago. Based on its similarity to other warmer water species like *G. costata*, *G. jazdzewskii* could have split off from the same stock that gave rise to the rich present day gynodiastylid fauna. Following this reasoning, present day gynodiastylids may have evolved from a small group of cold water, Antarctic progenitors and then underwent rapid speciation and dispersal as Australia and South Africa slowly drifted northward into the warmer latitudes. There, however, are some problems with this hypothesis. For example, if the origin of gynodiastylids was the cold water of the Antarctic Ocean, their apparent absence from continental waters of South America is puzzling. Recently, however, Les Watling (pers. comm) informed us that he has collected gynodiastylids from waters off Chile.

There is the additional possibility that, due to their small size and specialized habitat requirements, the lack of previous records for the family in Antarctic waters also may be due to an artifact of sampling. However, if populations of gynodiastylids are common in the shelf waters of Antarctica, at least some additional specimens should have been collected in studies conducted in the waters adjacent to the Antarctic Peninsula. There has been considerable benthic sampling in this region, and the cumaceans from the resulting collections have been identified (Lowry 1975, Richardson & Hedgpeth 1977, Ledoyer 1993, Błażewicz & Jażdżewski 1995, R. Heard, personal observations).

A third plausible option is that gynodiastylids originated in the warm temperate waters of the Indo-Pacific (Day 1980). If so *G. jazdzewskii* might simply be a pioneer species, representing a relatively recent and isolated dispersal event for the family in Antarctic waters.

The occurrence of *G. jazdzewskii* at a depth between 388 and 399 m represents the second deepest record for the genus and family. A southern African species, *G. profondus* Day, 1980, was reported from depths of 68 to 680 m by Day (1980).

The description of any new species, based on a single damaged specimen, is tenuous. Notwithstanding, *G. jazdzewskii* is readily distinguishable from all previously described gynodiastylids and represents an important zoogeographic record for the family in Antarctic waters.

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A new genus and species of sphaeromatid isopod (Crustacea) from Atlantic Costa Rica

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Abstract.—*Beatricesphaera ruthae,* a new genus and species of sphaeromatid isopod inhabiting shallow water along the Atlantic Costa Rican coast is described. This small species is placed into a new genus as the combination of characters which describe it precludes inclusion into any known sphaeromatid genus. It is best recognized by these character states: short epistome, flattened antenna 1 peduncle articles 1 and 2, robust setose pereopods, lamellar uropods, simple pleopods 4 and 5, short and unfused penes and an elongate basally attached appendix masculina. It is not readily allied to any genus or group of genera within the Sphaeromatidae.

Costa Rican shores boast every major tropical coastal marine habitat, from rocky shores and sandy beaches, to mangrove lagoons and coral reefs. In a joint project between Universidad de Costa Rica and the Los Angeles County Natural History Museum, the Cahuita Reef (9°18′N, 82°7′W) at Parque Nacional on the Caribbean coast of Costa Rica was surveyed and monitored between April 1986 and August 1987 for habitat degradation resulting from upland deforestation. This national park includes a small 240 hectare barrier reef (Wellington 1974; Risk et al. 1980; Cortés et al. 1984; Guzman & Cortés 1984a, 1984b; Murillo & Cortés 1984; Cortés & Risk 1985).

Knowledge of the Pacific Costa Rican isopod fauna rests with Brusca & Iverson's 1985 summary. The greater Caribbean region is covered by the publications of Kensley (1984), the field guide of Kensley & Schotte (1989) and miscellaneous other contributions, notably by Müller (e.g., 1993a, 1993b). This new genus and species of marine sphaeromatid isopod brings the total number of sphaeromatid genera known from the Caribbean to 17.

Bruce (1993, 1995, 1997) discusses some of the taxonomic difficulties of the Sphaeromatidae (e.g., high levels of homoplasy and the certain lack of monophyly of many larger genera) when compared to other flabelliferan families. The Sphaeromatidae are remarkable for their morphological diversity and are highly speciose. To date almost 100 genera have been described (Bruce 1995), and the latest count reports over 600 described species (see Kensley & Schotte, USNM Isopod List on the WWW at: ⟨URL: http://nmnhwww.si.edu/gopher–menus/Isopods.html⟩). For the Caribbean, Kensley & Schotte (1989) reported 32 species in 13 genera, and White (1996 unpublished) reports 7 described sphaeromatids from the Cahuita reef and two undescribed species.

Methods and terminology.—Coral rubble and algal samples from the intertidal to 12 m were collected and rinsed in fresh water and sieved through a 240 μm mesh screen. All material was fixed and preserved in 95% ethyl alcohol. Material was examined with dissecting, compound, and scanning electron microscopes. Appendages were drawn with the aid of a camera lucida. Setal and spine nomenclature as well as the nomenclature of appendage orientation follows Brusca et al. 1995. Abbreviations used are: LACM—Los Angeles County Museum of Natural History, Los Angeles, California; MOV—Museum of Victoria, Melbourne, Australia; SDNHM—San Diego Natural History Museum, San Diego, California; UCR—Universidad de Costa Rica, San Jose, Costa Rica; USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.; PMS, plumose marginal setae; SEM, scanning electron microscope.

Systematics

Order Isopoda Latreille, 1817
Suborder Flabellifera Sars, 1882
Family Sphaeromatidae
Milne Edwards, 1840
Beatricesphaera, new genus

Type species.—*Beatricesphaera ruthae*, new species, here designated.

Diagnosis of male.—Body vaulted, about twice as long as wide, widest at pereonites 5 and 6; body with translucent, flexible membrane-like covering; body margins with setose fringe, membrana cingula (see Buss & Iverson 1981). Cephalon lacking rostral point, lateral margins not expanded; eyes lateral, distinctly faceted. Pereonites 2–6 of about equal length, pereonites 1 and 7 longest; pereonite 7 not extending to lateral margins, laterally overlapped by pereonite 6; coxae without coxal keys (see Bruce 1994a, Figs. 2G, 22D), sutures absent. Pleon consisting of 1 segment. Pleotelson anterolateral margins extending to full body width, posterior margin narrowed, with distinct dorsal foramen, posterior margins of which contact posteriorly.

Antenna 1 peduncle articles 1 and 2 strongly flattened, anteriorly expanded; article 2 with anterodistal lobe; anterior margins of article 1 and 2 contiguous; article 3 slender, not expanded; flagellum short, slightly longer than article 3. Antenna 2 peduncle article 1 shortest, article 5 longest, articles 2–4 progressively increasing in length.

Epistome short, not laterally narrowed or constricted, with blunt median point; not separating antennule bases; lateral margins narrow, encompassing labrum. Right mandible incisor blade-like, narrow, unicuspid; without spine row and lacinia mobilis; left mandible incisor similar to right, but with lacinia mobilis and spine row of 2 spines; both mandibles with robust molar provided with proximal marginal teeth, gnathal surface smooth. Maxilla 1 outer lobe with 10 spines, outer 5 smooth, inner 5 weakly serrate, inner lobe with 4 feathered spines and 2 short simple spines. Maxilla 2 with 3 subequal lobes, provided with setae. Maxilliped palp articles 2 and 3 with short distinct distomedial lobes, article 4 and 5 quadrate; endite flat, distal margin subtruncate, with acute and blunt spines.

Pereopods robust, ambulatory, accessory unguis of dactylus simple. Pereopod 2 markedly slender in comparison to pereopod 1, pereopods 3–7 more robust than 1 and 2, posterior margins of pereopods with fringe of simple and plumose setae on ventral margins of merus, ischium, and propodus.

Paired short flattened penes present on posterior of sternite 7, not extending to pleopod rami.

Pleopods 1–3 rami with PMS, 4–5 without PMS. Pleopod 1 rami almost subequal in length, neither indurate nor operculate. Pleopod 2 endopod about 1.5 times as long as exopod; appendix masculina on basal lobe, nearly twice (1.8) as long as endopod, apically acute. Pleopod 3 endopod without suture; pleopods 4 and 5 without ridges or folds; pleopod 5 exopod with 3 scale patches. Uropods lamellar, extending just beyond posterior of pleotelson, not meeting at midline; exopod prominent, about half as long as endopod.

Female.—Mouthparts not metamorphosed; pleotelson posterior margin entire, without exit channel; oostegites absent;

eggs apparently held within pereon; otherwise similar to male.

Remarks.—This small species of sphaeromatid presents a combination of characters that prevents its inclusion in any known sphaeromatid genus, and furthermore, cannot readily be allied to any group of genera within the Sphaeromatidae. We therefore regarded it as incertae sedis. Superficially it is perhaps most similar to the "*Cassidinidea* group" discussed by Bruce (1994b), but it lacks the large dorsally visible epistome, fused penes, laterally extended cephalon, and also has short rather than elongate pleopod 1 rami. In common with that group, it has an elongate appendix masculina which is set on a basal lobe, the marsupium is composed of anterior and posterior pockets (see Harrison 1984, Kensley & Schotte 1989: 205 for terminology), the pleon consists of a single segment entirely without sutures, and pleopods 4 and 5 are similar to those of *Cassidinidea* (all of these characters mentioned might be considered possible apomorphies). The significance of the shared characters is uncertain as all of these states are known to occur in other sphaeromatid genera. In common with the "*Leptosphaeroma* group" (sensu Bruce 1994b) are the short epistome and short penes, but the genera of this group are otherwise distinct. What is remarkable, if the affinities of this new genus do lie with *Cassidinidea* and related genera, is that this is the first instance of a perforate pleotelson in that group of genera.

There is, as mentioned earlier, a superficial resemblance to the genus *Cassidinidea* Hansen, 1905 (reviewed in Bruce 1994b). That genus is immediately distinguished by the dorsally visible epistome, narrow antennule peduncle articles, expanded lateral margins of the head, and fusion of the penial processes (Kensley & Schotte's 1989 statement that the penes are "elongate, separate" is in error, applying only to "*Cassidinidea*" *mosaica* Kensley & Schotte, 1987, a species incorrectly placed in the genus). In addition both male and female *Cassidinidea* have the pleotelson posterior margin entire, whereas it is perforate in the male of *Beatricesphaera* new genus. A "gel-layer" occurs in *Cassidinella* (Bruce 1994a) as well as other genera, but seems easily lost, and is usually not recorded, so its significance is entirely uncertain. It was not observed in *Beatricesphaera*.

Lack of thickened ridges or folds on pleopods 4 and 5 has repeatedly been shown to be a character of dubious phylogenetic significance (most recently Bruce 1995, 1997) that can vary within genera, and the flattened antennule peduncle article(s) can also vary within genera (e.g., *Cassidinella*, Bruce 1994a). Another character state that is not widely distributed in the family is the marked slenderness and elongation of the second leg in comparison to the first. This is also known to occur in some genera and species of the *Ischyromene*-group (Bruce 1995) as well as some species of *Dynamenella* (e.g., *D. nuevitas* Kensley et al. 1997). Lamellar uropods, which occur in most genera formerly placed in the subfamily Cassidininae, are also to be found in other genera such as *Exosphaeroma* for example. Without a full phylogenetic analysis of the genera with the associated identification of informative characters and resolution of the evidently high level of homoplasy in the family (Bruce 1993, 1995, 1997), problems such as the one that this genus presents will continue to plague taxonomists working on the Sphaeromatidae.

Of the other sphaeromatid genera known from the Caribbean region, none is particularly similar, and the genus can best be identified by the characters of short epistome, flattened antenna 1 peduncle articles 1 and 2, robust setose pereopods, lamellar uropods, simple pleopods 4 and 5, short and unfused penes and an elongate basally attached appendix masculina. Females can be identified by the antenna 1, epistome and pereopod characters. The prominent bosses on pereonite 7, while not included as a generic character, further serve to identify the genus and species.

Etymology.—During her tenure at the SDNHM, RW had the great pleasure of working with and benefiting from two tremendously wise women (Beatrice Koepnick and Ruth Kantor), whose efficacy, insight, and hard-earned wisdom left an indelible impression on all they met. It is the energy that these two women gave to so many scientific projects that this new genus and species honors. The *new genus* honors Bea who passed away April 1995 and unfortunately before this manuscript was completed. The generic name is feminine, as the second element, *sphaera*, is a feminine Latin noun.

Beatricesphaera ruthae, new species
Figs. 1–6

Material examined.—Male holotype (LACM 86-196.4), Atlantic, Costa Rica, Limon Province, Parque Nacional Cahuita, Punta Cahuita Reef, 9°44.18′N, 82°48.7′W, inner reef flat, brown algae wash, 1–3 m depth. 29 Oct 1986. Coll. R. C. Brusca and P. M. Delaney, LACM 86-196. Ovigerous female allotype (LACM 86-202.3) Parque Nacional Cahuita, Punta Cahuita Reef, 9°40.3′N, 82°45′W, outer reef crest, algae and algae holdfast washes, 1–8 m depth. 30 Oct 1986. Coll. R. C. Brusca and P. M. Delaney, LACM 86-202. Paratypes (2 mature males, 2 juvenile males) (LACM 86-196.7), Parque Nacional Cahuita, Punta Cahuita Reef, 9°44.18′N, 82°48.7′W, inner reef flat, brown algae wash, 1–3 m depth. 29 Oct 1986. Coll. R. C. Brusca and P. M. Delaney, LACM 86-196. Paratypes (1 male, 1 female, 1 juvenile) (LACM 86-202.4), Parque Nacional Cahuita, Punta Cahuita Reef, 9°40.3′N, 82°45′W, outer reef crest, algae and algae holdfast washes, 1–8 m depth. 30 Oct 1986. Coll. R. C. Brusca and P. M. Delaney, LACM 86-202. Paratypes (2 males, 3 females) (LACM 87-3.2), Parque Nacional Cahuita, Punta Vargas, 9°44.18′N, 82°48.7′W, inner reef lagoon, algae washes, 1–3 m depth. 8 Jan 1987. Coll. R. C. Brusca and R. Wetzer, LACM 87-3. Paratype (1 male, dissected and figured appendages) (LACM 86-122.4), Limon Province, north of Puerto Viejo, 9°40.8′N, 82°45.53′W, coralline algae rock wash, offshore algae ridge, 1–3 m depth, CRA-86-13. 27 Jul 1986. Coll. G. L. Hendler, LACM 86-122. Paratypes (5 males, 5 females) (USNM 286886), Parque Nacional Cahuita, Punta Vargas, 9°44.18′N, 82°48.7′W, inner reef lagoon, algae washes, 1–3 m depth. 8 Jan 1987. Coll. R. C. Brusca and R. Wetzer, LACM 87-3. Paratypes (4 males, 4 females) (MOV J45491 through J45498), Parque Nacional Cahuita, Punta Cahuita Reef, 9°40.3′N, 82°45′W, outer reef crest, algae and algae holdfast washes, 1–8 m depth. 30 Oct 1986. Coll. R. C. Brusca and P. M. Delaney, LACM 86-202. Paratypes (2 males, 3 females) (UCR-2248), Parque Nacional Cahuita, Punta Cahuita Reef, 9°40.3′N, 82°45′W, outer reef crest, algae and algae holdfast washes, 1–8 m depth. 30 Oct 1986. Coll. R. C. Brusca and P. M. Delaney, LACM 86-202.

Other material examined: Atlantic, Costa Rica, specimens: Limon Province, Parque Nacional Cahuita, Punta Cahuita Reef, 9°44.35′N, 82°48.7′W, approximately 500 m from shore, algae and coral rubble washes, 3–4 m depth. 3 Apr 1986. Coll. R. C. Brusca and P. M. Delaney, LACM 86-98, 2 mancas. Parque Nacional Cahuita, Punta Cahuita Reef, 9°44.35′N, 82°48.7′W, approximately 500 m from shore, brown algae washes, 3–4 m depth. 4 Apr 1986. Coll. R. C. Brusca, P. M. Delaney, and R. Wetzer, LACM 86-100, 9 specimens. Limon Province, north of Puerto Viejo, 9°40.8′N, 82°45.53′W, coralline algae rock wash, offshore algae ridge, 1–3 m depth, CRA-86-13. 27 Jul 1986. Coll. G. L. Hendler, LACM 86-122, 24 specimens. Limon Province, north of Puerto Viejo, 9°40.8′N, 82°45.53′W, outer reef crest, coralline algae on *Sargassum* reef, 6–11 m depth. 27 Jul 1986. Coll. R. Wetzer, LACM 86-128, 2 specimens each attached to a walking leg of brachyuran crab: *Acanthonyx petiverii.* One specimen attached to left 3rd walking leg; second specimen attached to left 2nd walking leg. Limon Province, Parque Nacional Cahuita, Punta Cahuita Reef, 9°44.18′N, 82°48.7′W, inner reef flat, brown algae wash, 1–3 m depth. 29 Oct 1986. Coll. R. C. Brusca and P. M. Delaney, LACM 86-196, 40+ specimens. Limon Province, Parque Nacional Cahuita, Punta Cahuita Reef, 9°40.3′N, 82°45′W, outer reef crest, algae and algae holdfast washes, 1–8 m depth. 30 Oct 1986. Coll. R. C. Brusca and P. M. Delaney, LACM 86-202, 64+ specimens. Limon Province, Parque Nacional Cahuita, Punta Vargas, 9°44.18′N, 82°48.7′W, inner reef lagoon, algae washes, 1–3 m depth. 8 Jan 1987. Coll. R. C. Brusca and R. Wetzer, LACM 87-3, 70+ specimens. Limon Province, Parque Nacional Cahuita, Punta Vargas, 9°44.18′N, 82°48.7′W, inner reef lagoon, coral rubble washes, 1–12 m depth. 8 Jan 1987. Coll. R. C. Brusca and R. Wetzer, LACM 87-4, 2 females. Limon Province, Parque Nacional Cahuita, Punta Vargas, 9°44.18′N, 82°48.7′W, inner reef lagoon, rock, coral rubble, and algae washes, 1–13 m depth. 8 Jan 1987. Coll. R. C. Brusca and R. Wetzer, LACM 87-5, 2 mancas. Limon Province, Parque Nacional Cahuita, Punta Vargas, 9°44.5′N, 82°48.37′W, inner reef lagoon, skimming *Thallassia* bed off point, intertidal to 1 m depth. 8 Jan 1987. Coll. R. C. Brusca and R. Wetzer, LACM 87-7, 1 male. Limon Province, Parque Nacional Cahuita, Punta Vargas, 9°44.18′N, 82°48.7′W, inner reef lagoon, broken coral and rubble washes, 1–3 m depth. 8 Jan 1987. Coll. R. C. Brusca and R. Wetzer. LACM 87-8, 1 molt. Limon Province, Puerto Viejo, 9°40.3′N, 82°45′W, forereef crest and along sand bottom junction, algae and gorgonian washes, 1–6 m depth. 9 Jan 1987. Coll. R. C. Brusca and R. Wetzer, LACM 87-9, 34 specimens. Limon Province, Parque Nacional Cahuita, Punta Cahuita Reef, 9°44.37′N, 82°48.7′W, rock, coral, and algae holdfast washes, 0.9–3 m depth. 19 Aug 1987. Coll. R. C. Brusca and R. Wetzer, LACM 87-158, 21 specimens. Limon Province, Parque Nacional Cahuita, Punta Cahuita Reef, 9°44.52′N, 82°48.37′W, rock, coral, and algae holdfast washes, 0.5–10 m depth. 20 Aug 1987. Coll. R. C. Brusca and R. Wetzer, LACM 87-165, 64 specimens.

Description.—Adult male: Body strongly vaulted, limpet-like, about 2.3 times as long as wide (Figs. 1A, B, 2A). Antennular peduncle articles, lateral body margins, uropods, and pleotelson with conspicuous setal fringe, *membrana cingula* (Figs. 1A, B, C, 3A). Frontal margin of cephalon without rostral process (Fig. 1A). Dorsum of pereonite 7 elevated into large dome-like conical tubercle, with lateral notches on posterior margin. Single free pleonite also with tubercle, somewhat smaller than tubercle on pereonite 7; with lateral projections on posterior margin. Pleotelson acute; pleotelsonic foramen dorsally directed, triangular, entirely enclosed (Figs. 1A, B, 2B). A thin membrane visible with SEM overlie the dorsal cuticle of entire body including antennular peduncle articles and appears finely granular with small, numerous, evenly spaced pits; each pit with 1 to 3 simple or palmate setae (Fig. 2A, B, C). Coxal sutures indistinct dorsally and ventrally. Eyes round, well developed, slightly elevated, with facets and pigmentation, deeply immersed in pereonite 1. Pereonite 1 longest, pereonites 2–6 subequal, pereonite 7 longer than preceding pereonites. First pleonite subequal in length to pereonites 2–6 (Figs. 1A, B, 2A).

Antennae 1 short, extending to posterior margin of pereonite 2 (Fig. 3A). Peduncular articles 1–2 shovel-shaped, dorsoventrally compressed and greatly expanded. Article 1 rectangular, almost twice as long as wide. Last (third) peduncular article narrow, not expanded; about twice as long as wide. Flagellum 6-articulate, article 1 short, article 2 longer, article 3 longest, terminal articles gradually tapering distally. One long, "articulated" aesthetasc on lateral, distal flagellar articles 2, 3, and 4 (Fig. 3A, B).

Antennae 2 extending to anterior margin of pereonite 3; usually not visible in dorsal aspect. Peduncle composed of 4 articles, 1

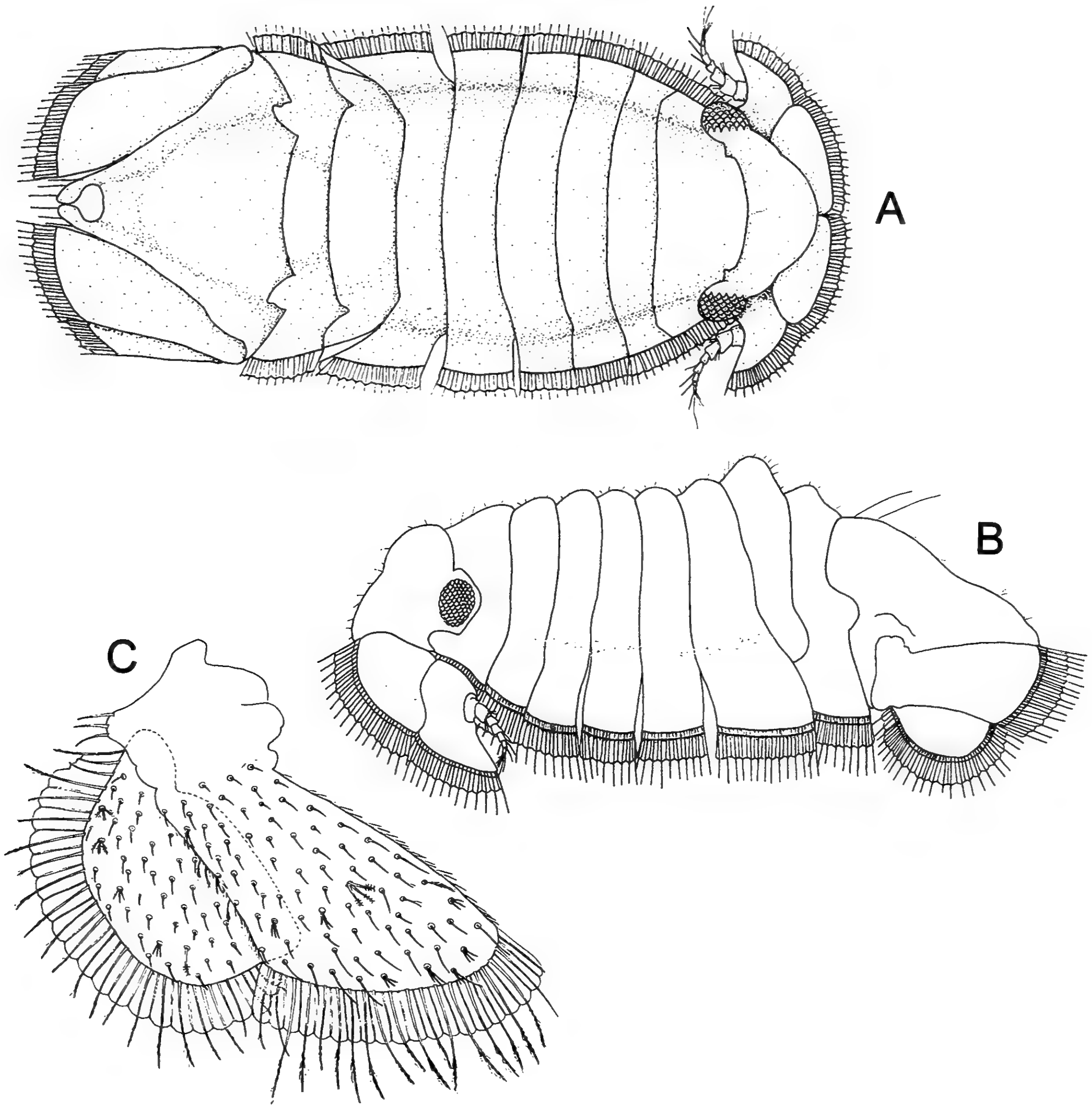

Fig. 1. *Beatricesphaera ruthae*, new species. A, dorsal view, adult male, holotype LACM 86-196; B, lateral view, adult male, holotype LACM 86-196; C, uropod (right), adult male, paratype LACM 86-122.

and 2 subequal in length, article 3 1.6 times as long as 2 and somewhat expanded, article 4 slender and about twice as long as article 1. Simple and palmate setae present on peduncular articles as figured. Flagellum 8-articulate, each article with 2–6 simple setae on margin (Fig. 3C).

Frontal lamina wide, crescent shaped, encompassing clypeus and part of labrum. Labrum with dense short simple setae on medial margin, setae become less dense and longer on lateral margins (Figs. 3D, 4E, F). Clypeus and labrum fused, together forming a subovate structure. Mandibular incisors distally narrow, flattened, unicuspid; lacinia mobilis composed of 2 large bifid spines; spine row composed of 2 comb spines; molar process with proximal marginal teeth; gnathal surface almost smooth; palp 3-articulate, article 2 with 3 stout biserrate setae, article 3 with 6 biserrate robust setae (Figs. 3E, 4A, B, C). Maxilla 1 outer lobe nearly twice as wide as inner lobe, with 5 flattened, smooth robust spines laterally, 4–5 large, serrate spines medially; inner lobe with 4 slender, plumose robust setae (Fig. 3F). Maxilla 2 with 3 subequal lobes; outer lobe with 4 long robust setae; middle lobe with 4 long robust setae; inner lobe with simple, plumose and comb setae, as figured; numerous short, simple setae dispersed along medial margin; endite basis

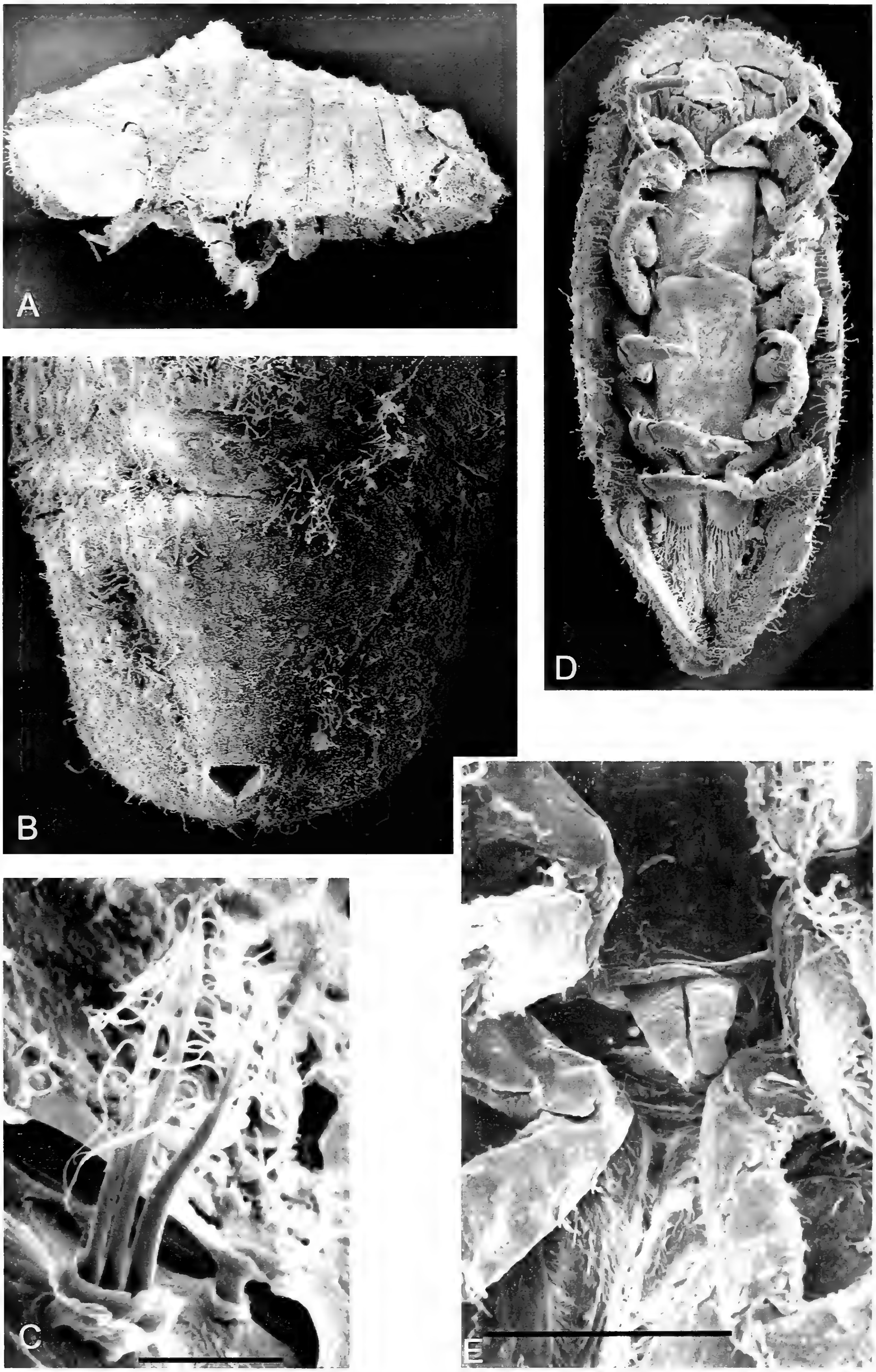

Fig. 2. *Beatricesphaera ruthae*, new species. Scanning electron micrographs. A, adult male LACM 86-122, lateral view; B, adult male LACM 86-122, pleotelson; C, male LACM 87-7 palmate setae on pleotelson, note torn "cuticle;" i.e., membrana cingula, scale bar = 20 μm; D, gravid female LACM 86-122 ventral brood pouch; E, adult male LACM 86-7 penes, scale bar = 200 μm.

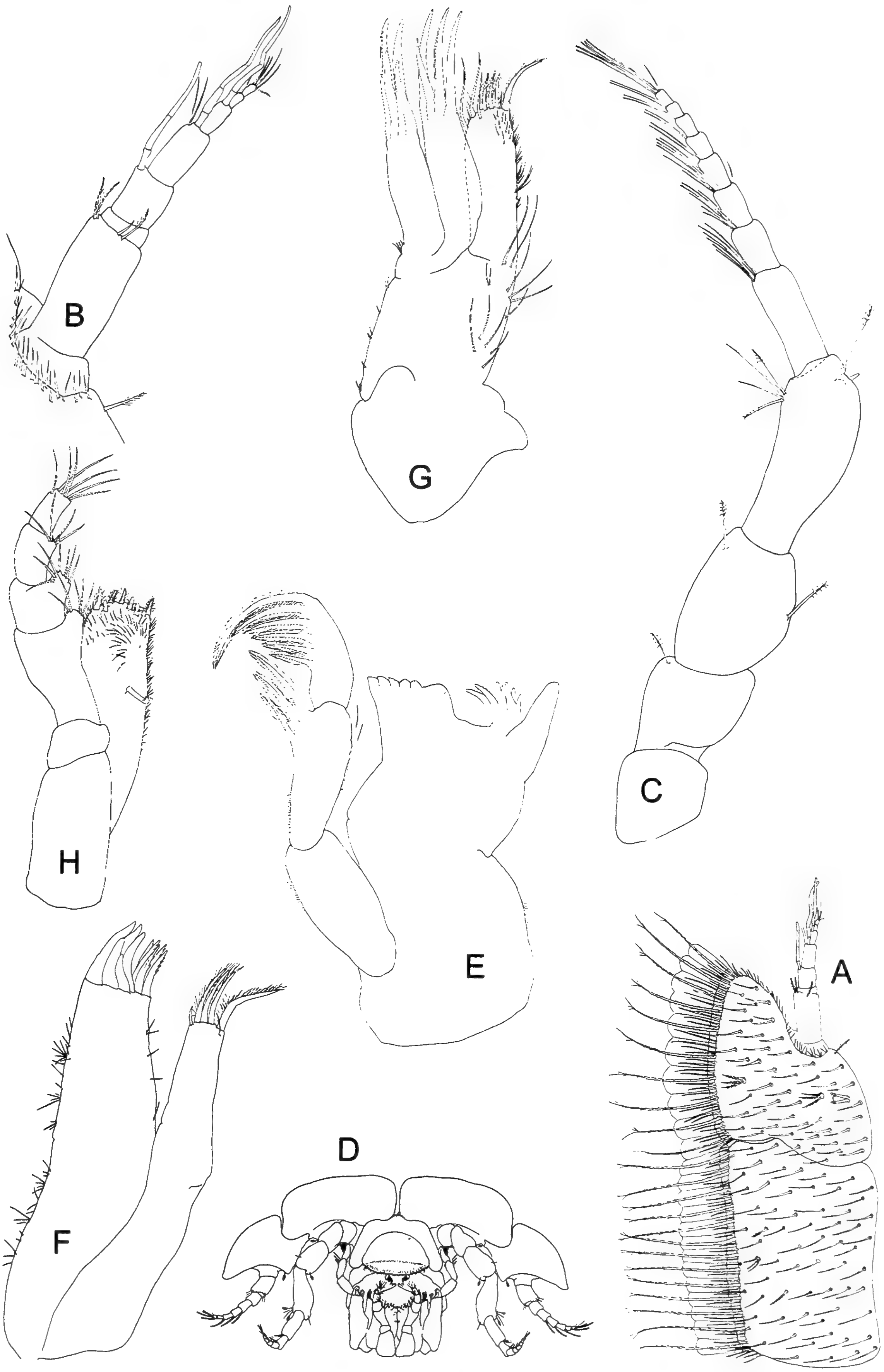

Fig. 3. *Beatricesphaera ruthae*, new species. Adult male paratype LACM 86-122. A, antenna 1 (right); B, flagellular articles antenna 1 (right); C, antenna 2 (right); D, frontal lamina, clypeus, labrum; E, mandible (left); F, maxilla 1 (right); G, maxilla 2 (right); H, maxilliped (right).

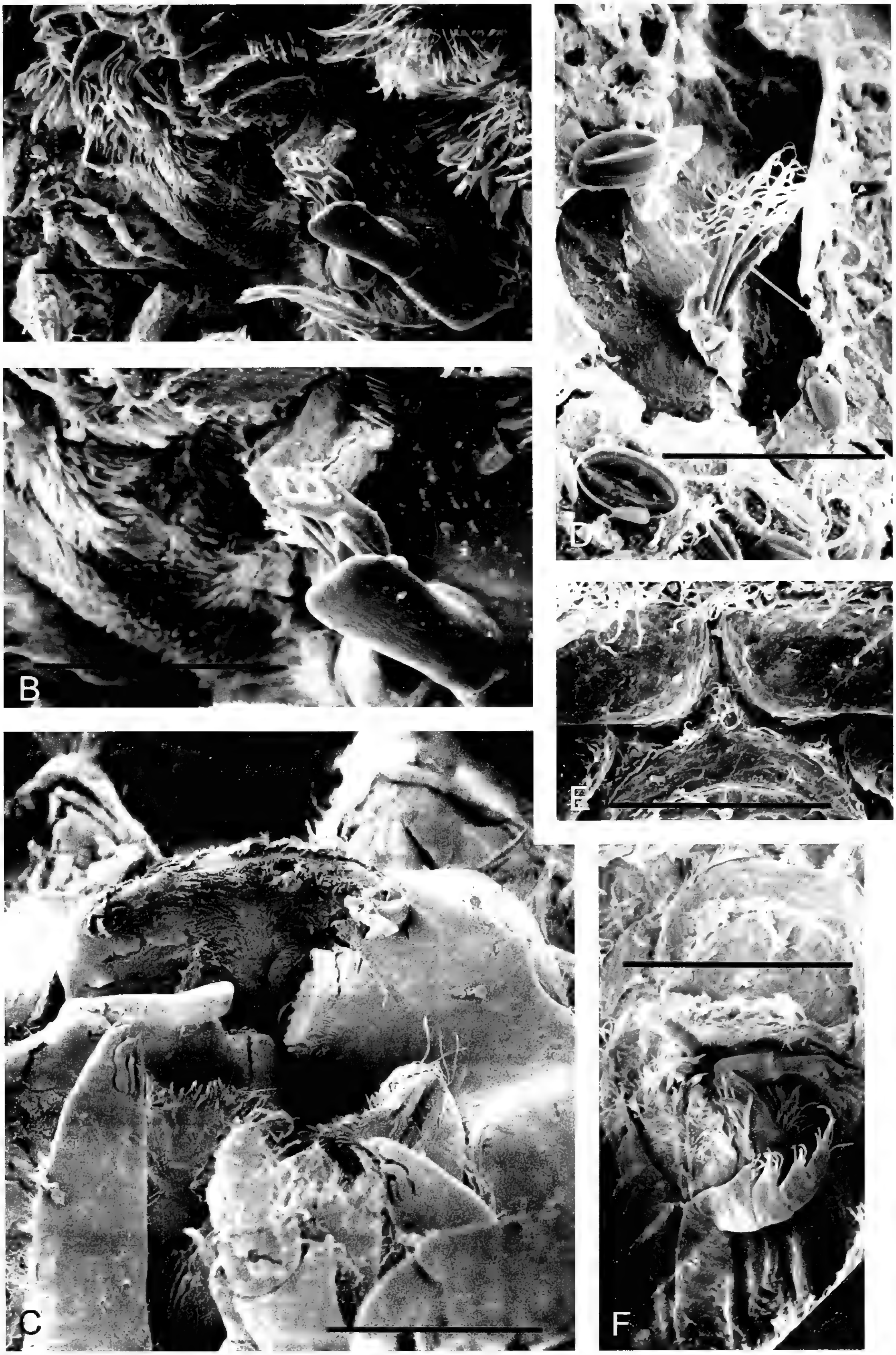

Fig. 4. *Beatricesphaera ruthae*, new species. Scanning electron micrographs. A, male LACM 87-7, mouthfield with right and left molar processes, left incisor, lacinia mobilis, and spine row, scale bar = 100 μm; B, same as A, scale bar = 50 μm; C, male LACM 86-122, mouthfield, frontal view, scale bar = 100 μm; D, male LACM 87-7, palmate setae on pleotelson, membrana cingula torn, discs are diatom symbionts, scale bar = 20 μm; E, male LACM 87-7, peduncular articles of antennules, frontal lamina, scale bar = 200 μm; F, male LACM 87-3, mouthfield with clypeus, labrum, left and right maxillipeds, scale bar = 200 μm.

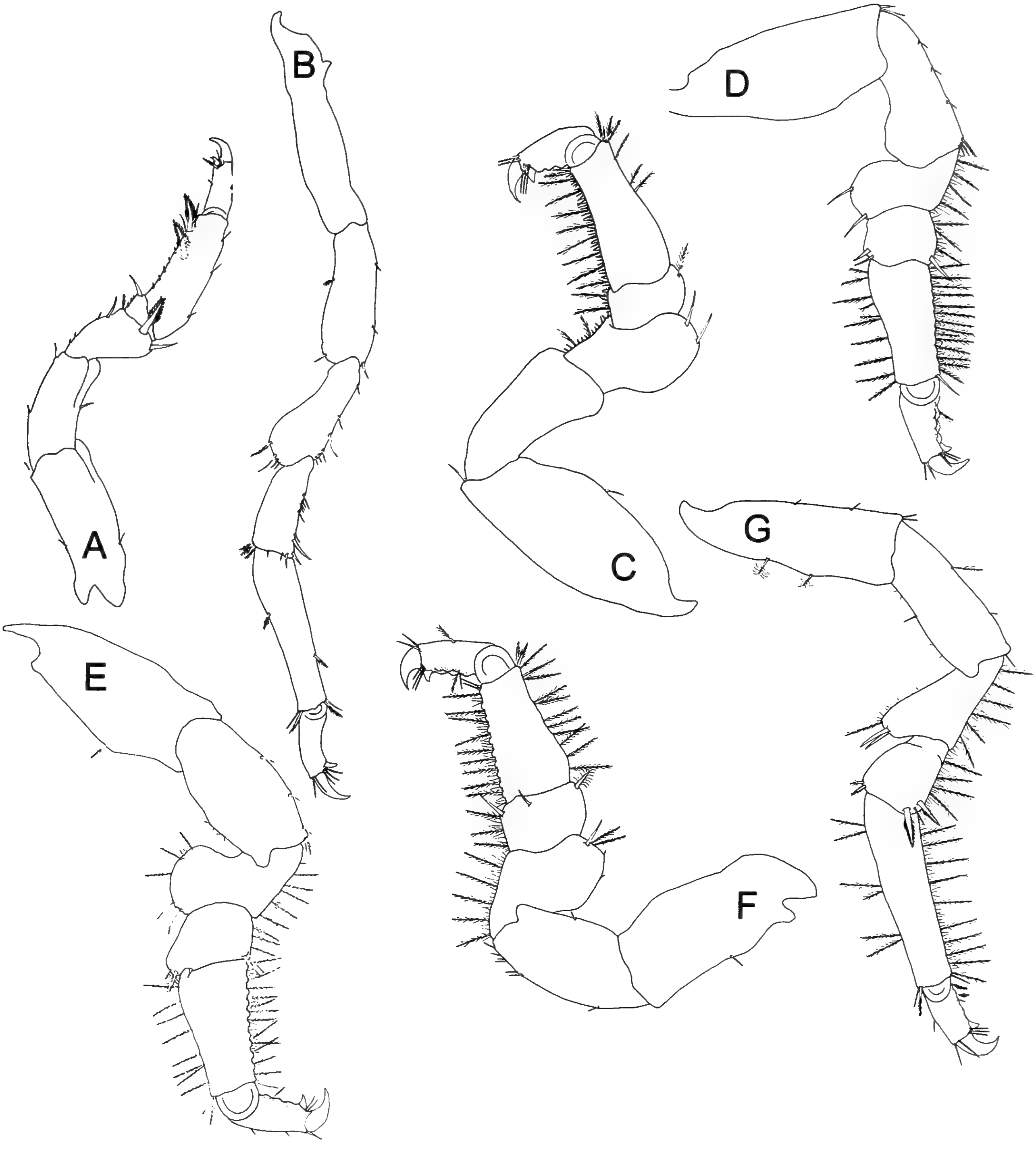

Fig. 5. *Beatricesphaera ruthae*, new species. Adult male paratype LACM 86-122. All appendages from left side of body. A, pereopod 1 posterior surface; B, pereopod 2 anterior surface; C, pereopod 3 posterior surface; D, pereopod 4 anterior surface; E, pereopod 5 posterior surface; F, pereopod 6 posterior surface; G, pereopod 7 posterior surface.

with long setae on dorsal surface, excite basis with very short simple setae on lateral margin (Fig. 3G). Maxillipedal endite extended to middle of palp article 2 (carpus); endite with 4 short, stout, setose robust setae, and 4 acute plumose setae on distal margin; 1 coupling hook present on each maxilliped (Figs. 3H, 4F).

All pereopods with secondary unguis. Ratios of lengths of pereopods 1–7 respectively (relative to pereopod 1): 1.0:1.6:1.3:1.3:1.3:1.4:1.5 (Fig. 5A–G). Pereopod 1

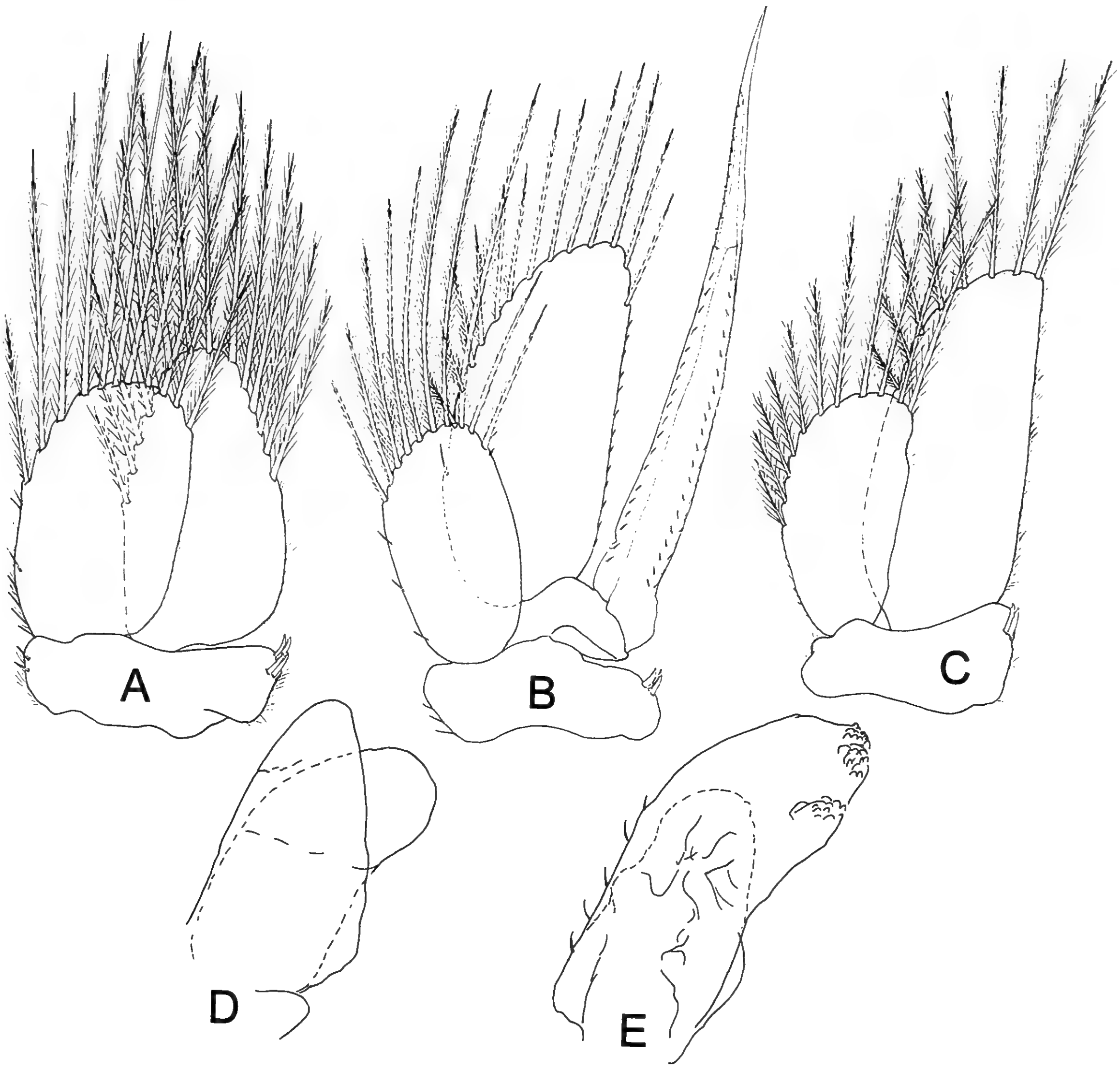

Fig. 6. *Beatricesphaera ruthae*, new species. Adult male paratype LACM 86-122. All appendages from left side of body. A, pleopod 1; B, pleopod 2; C, pleopod 3; D, pleopod 4; E, pleopod 5.

propodus inferior margin with 2 stout serrate setae and one simple distal robust seta; merus and carpus inferior margin each with single simple stout seta; merus anterior superior margin with stout serrate spine (Fig. 5A). Pereopod 2 propodus 2.5 times as long as carpus (Fig. 5B). Pereopods 4–6 with small tubercles on propodal inferior margin; tubercles more prominent on pereopod 5 compared to 4, largest on pereopod 6. Pereopods 3–7 with cuticular scale spines on inferior dactyl surface; with setose fringe on inferior margin of merus, carpus, and propodus; fringe becomes longer, more complex, and denser on posterior pereopods (i.e., fringe composed of variable length simple and plumose setae); simple and plumose setae on superior margins of merus, carpus, and propodus as figured, becoming more abundant on posterior pereopods (Fig. 5C–G).

Penes 2.5 times as long as basal width, conical, separate at base (Fig. 2E).

Pleopods 1–3 endopods and exopods with long plumose marginal setae. Pleopod 1 endopod weakly subtriangular, exopod ovoid, 0.8 times length of exopod; peduncle with 4 coupling spines (Fig. 6A). Pleopod 2 endopod long, 2.4 times as long as wide, 1.5 times as long as exopod; appendix masculina arising basally from endopod and tapering to acute tip, distal ⅓ separated from basal ⅔ by distinct cuticular "interruption," 1.8 times as long as endopod, ornamented with serrations and minute spines; peduncle with 2 coupling spines (Fig. 6B). Pleopod 3 endopod 1.5 times as long as exopod, exopod weakly indurate, peduncle with 2 coupling spines (Fig. 6C). Pleopods 4 and 5 rami without plumose marginal setae (Fig. 6D, E). Uropodal endopod 1.3 times as long as exopod, endopod reaching posterior margin of pleotelson, both rami with setal fringe composed of short and long setae, the latter extending beyond membrana cingula and feathered distally (Fig. 1C).

Adult female: Similar to male, except dorsal tubercles on pereonite 7 and first pleonite less pronounced than in adult males; pleotelson entire, not perforated (pleotelson also entire in juveniles and subadult males). Without oostegites, internal morphology of brood pouches and brood pouch openings not discernible, ventrum of ovigerous females appears entire (see Harrison 1984, fig. 2D).

Remarks.—The thin membrane overlying the cuticle is easily damaged during preservation and subsequent handling and with light microscopy has the appearance of shattered glass, which SEM reveals is torn membrane (Figs. 2C, 4D). In preparing specimens for SEM this membrane covering has a tendency to distort and curl especially on appendage margins (Fig. 2D, evident on distal coxal margins).

Color.—Live color a uniform pink, lost shortly after preservation in ethanol.

Size.—Maximum length to 3.2 mm.

Variation.—Cephalon of some specimens with anterior row of 5 long simple setae and one pair of medial setae on pereonites 2–7. Absent in holotype.

Distribution and ecology.—Habitats from which specimens were collected include seagrass beds, coral rubble, and algal holdfasts in Limon Province, Parque Nacional Cahuita and south to Puerto Viejo. Two specimens were each attached to a walking leg of brachyuran crab *Acanthonyx petiverii.*

Etymology.—The specific epithet honors Ruth Kantor. The name of the new genus is feminine and the specific name of the type species also is feminine because of its derivation; *ruthae* is the Latin feminine genitive singular of a modern feminine noun.

Acknowledgments

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Icelopagurus tuberculosus, a distinct new hermit crab species (Crustacea: Decapoda: Paguridae) from Japan

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Abstract.—A new species of pagurid hermit crab of the genus *Icelopagurus* McLaughlin, *I. tuberculosus*, is described and illustrated. It is the second species in the genus and is distinct in having a large well-calcified, immovable plate that is partially fused with the shield's posterior and posterolateral margins, a transverse row of four prominent protuberances on the dorsal surface of the shield, a pair of similar protuberances on each anterolateral margin of the shield, and a somewhat reduced abdomen. The new species is compared with the only other congeneric species, *I. crosnieri* McLaughlin. Morphological similarities and differences of *Icelopagurus* with selected, specialized pagurid genera are discussed.

In the course of studies of the decapod crustacean fauna from the Ryukyu Archipelago (Okinawa) by Keiichi Nomura of the Kushimoto Marine Park and his coworkers, numerous specimens of hermit crabs were collected and given to the author for identification. A partial account of these hermit crabs was published together with data on other decapod crustaceans (Nomura et al. 1996). However, a number of specimens still remained unidentified, some of which resemble species of *Catapagurus* A. Milne Edwards, 1880 with sabre blade-like dactyls on the ambulatory legs, although the males differ in having a short sexual tube.

McLaughlin (1997) recently established the monotypic genus *Icelopagurus* for *I. crosnieri* McLaughlin, 1994, based on specimens collected from Indonesian waters. *Icelopagurus* is superficially similar to *Catapagurus* but differs in the shortness of the sexual tube in males, which does not curve up over the dorsal surface of the body, and by the distinct development of the telson. The specimens from the Ryukyu Archipelago belong to *Icelopagurus* and represent a new species described herein.

Material and Methods

Collections were made by SCUBA diving on coral reefs of the Kumejima Island, northern part of the Ryukyu Archipelago (Okinawa), Japan. Specimens were fixed in 10% formalin solution and then transferred to 75% alcohol solution for preservation. Specimens were stained with a 5% Methylene Blue solution and examined under a stereoscopic microscope OLYMPUS SZH and using a NIKON UW for high magnification. Drawings were made using a camera lucida attachment. All specimens are deposited in the Natural History Museum and Institute, Chiba, with the registration code CBM-ZC.

Terms used in this study follow McLaughlin (1974) in general, and Lemaitre (1995) for the cephalothorax.

Shield length (SL), measured from the tip of the rostrum to posterior end, is used as indicator of size. The length of segments in chelipeds and cephalic appendages is measured along the dorsomedian line. The length of segments in the second and third pereopods is measured along the lateromedian line.

To evaluate the affinities of the new species, material of the following species was examined: *Icelopagurus crosnieri*, paratypes, 1 ♀, SL = 3.15 mm, 1 ov. ♀, SL = 3.90 mm, 884–891 m, Station CP91, 8°44′S–131°05′E, Tanimbar Islands, Indonesia, 5 Nov 1991, Karubar Cruise, Muséum national d'Histoire naturelle, Paris, MNHN-Pg 5279; *Catapagurus ensifer* Henderson, 1893, syntypes, 2 ♂, SL = 2.40, 2.35 mm, 1 ♀, SL = 2.40 mm, 2 ov. ♀, SL = 2.15, 2.45 mm, Gulf of Martabian, Burma, The Natural History Museum, London, 1888.34; *Catapagurus granulatus* Edmondson, 1951, holotype, ♂, SL = 2.58 mm, 58–79 m, off Bird Island, Hawaii, Bernice P. Bishop Museum, Hawaii, BPBM 5446, paratypes, 2 ♂, SL = 2.05, 2.00 mm, 36–49 m, off the south coast of Oahu, Hawaii, BPBM No. 5514; *Catapagurus japonicus* Yokoya, 1933, syntypes, 3 ♂, SL = 2.10, 2.60, 2.95 mm, st. 324, Bungo Strait, 106 m, 21 Jul 1928, Kitakyushu Museum of Natural History; 1 ♂, SL = 2.20 mm, 65 m, Maruyamadashi, Amadaiba, Sagami Bay, 27 Jul 1958, Biological Laboratory, Imperial Household, Showa Memorial Institute, Tsukuba, BLIH 1474; 1 ♂, SL = 2.65 mm, 84–85 m, Aoyamadashi-Maruyamadashi, Amadaiba, Sagami Bay, 24 Jan 1968, BLIH 3551; 1 ovi. ♀, SL = 3.10 mm, 80–85 m, 2.41 km western southwest off Jyougashima Island, Sagami Bay, 25 Jul 1959, BLIH 1615.

Icelopagurus tuberculosus, new species

Figs. 1A–H, K–M, 2–4

Holotype.—♂, SL = 5.70 mm, CBM ZC 4700, outer side of coral reefs, northern coast of Kumejima (26°20′N, 126°45′E), Shimajiri-gun, Okinawa-ken, Ryukyu Archipelago, SCUBA diving, coll. Yuisho Sakamoto, 16 Aug 1993.

Paratypes.—1 ♂, SL = 4.90 mm, CBM ZC 4701; 1 ♀, SL = 5.10 mm, CBM ZC 4702; same data as holotype.

Type locality.—Kumejima, Ryukyu Archipelago.

Description.—Eleven pairs of phyllobranchiate gills: 2 pairs of arthrobranchiae on either side of coxo-thoracic articulations of third maxilliped and first to fourth pereopods, plus 1 pair of pleurobranchiae on either side of pleural plate of seventh thoracic somite (above fourth pereopod).

Shield (Fig. 1A, B, D) slightly broader than long, 1.12:1.00; anterior margin between rostrum and lateral projections distinctly concave and terraced; anterolateral margins each bearing prominent protuberance armed with numerous often spiniform tubercles on middle portion; lateral margins straight and armed with numerous spiniform tubercles; posterolateral margins irregular; posterior margin truncate. Dorsal surface of shield vaulted and rugose, covered with numerous often spiniform tubercles and scattered with short setae; anterior region with a transverse row of 4 prominent protuberances armed with numerous often spiniform tubercles; posterolateral regions each with 3 distinct incisions. Rostrum broadly rounded, overreached by lateral projections. Lateral projections distinctly produced, triangular, upturned. Anterior faces of shield between rostrum and lateral projections each with 3–5 distinct blunt-tipped spines on ventral margin laterally. Very broad, flat, well-calcified plate surrounding margin of posterior half of shield (Fig. 1A), unarmed, with scattered long setae; partially fused with shield, immovable; lateral and posterior margins straight and edged.

Posterior carapace (Fig. 1A, B) with pair of partially calcified broad bands in areas between cardiac sulci and sulci cardiobranchialis, broader anteriorly; partially calcified, small plate present between cardiac sulci, abutting to medial portion of posterior margin of accessory portion of shield; linea anomurica extending from anterior extremity of accessory portion of shield to subproximal portion of ventrolateral margin of posterior carapace. Branchiostegites (Fig. 1B) not calcified except for somewhat calcified anterodorsal margin; anterodorsal and anterior margins unarmed.

Ocular peduncles (Fig. 1A, D) short, distinctly shorter than shield, 0.30:1.00; each with constriction near base of cornea; strongly tuberculate dorsally and dorsomesially; corneae dilated; basal margins of corneae each fringed with thick, long setae dorsally and mesially. Ocular acicles distinctly shorter than ocular peduncles, 0.40: 1.00; elongated triangular, subacute; separated basally by width of rostrum; mesial margins fringed with few, thick setae; lateral margins with few short, fine setae. Interocular plate rectangular, calcified; separated from surrounding region by soft membrane.

Antennular peduncles (Fig. 1A, E, F) very long, with penultimate segment exceeding ocular peduncle (excluding cornea) by approximately 0.80 own length, when fully extended. Ultimate segment unarmed, with few long setae dorsodistally. Penultimate segment unarmed, with few short setae on dorsal face subdistally. Basal segment slightly produced distomesially, with 1 acute spinule at ventrodistal mesial angle.

Antennal peduncles (Fig. 1A, B, G, H) moderately long, with distal margin of fourth segment reaching beyond base of corneae but not to distal margin, when fully extended; with supernumerary segmentation. Fifth and fourth segments with few scattered long setae. Third segment with ventrodistal angle produced. Second segment with dorsolateral distal angle produced, terminating in strong spine accompanied ventrally by short accessory spine, dorsolateral face with several tubercles, dorsomesial distal angle with acute spine. First segment with strong, hook–shaped spine laterally and strong spine at ventrodistal margin mesially. Antennal acicle moderately short, overreaching ocular peduncles; straight, blunt-tipped, with scattered setae; mesial face slightly tuberculate. Flagella very long, 6.2 times length of shield, scarcely setose.

Mandible (Fig. 2A) without distinguishing characters. Maxillule (Fig. 2B, C) with external endopodal lobe obsolete; internal lobe with 1 apical bristle. Maxilla (Fig. 2D) with moderately broad scaphognathite. First and second maxillipeds (Fig. 2E, F) without distinguishing characters. Third maxilliped (Fig. 2G–1) with 3 acute corneous teeth on basis; ischium with crista dentata well developed, composed of 15–16 corneous teeth and with 1 strong accessory tooth; merus with acute dorsodistal spine.

Sternite of 3rd maxillipeds unarmed, with shallow median cleft.

Right cheliped of male (Fig. 3A–D) larger and stouter than that of left; compressed dorsoventrally. Dactyl distinctly shorter than palm, 0.32:1.00; forming weak hiatus with fixed finger; terminating in strong, curved calcareous claw; dorsal face convex, tuberculate mesially, with tufts of long setae; cutting edge with prominent blunt-tipped calcareous tooth medially. Fixed finger with dorsal surface tuberculate, with tufts of long setae; cutting edge with minute calcareous teeth on distal half. Palm very long, with dorsal surface covered with numerous spiniform tubercles, with 2 faint longitudinal sulci on proximal ⅔, continuing to proximal very deep depression, dorsomesial and dorsolateral surfaces covered with dense tubercles, with proximal angles protruded and strongly armed with spiniform tubercles; ventral surface covered with dense minute tubercles and scattered long setae. Carpus distinctly shorter than palm, 0.56:1.00; swollen distally; dorsal surface flat, with scattered spiniform tubercles, dorsolateral and dorsomesial margins forming distinct ridges, each armed with strong spiniform tubercles; lateral, mesial and ventral surfaces glabrous. Merus with dorsal margin irregular, covered with strong spiniform tubercles and protuberances, and scattered long setae, dorsodistal angle bearing slightly upturned large spine; lateral and mesial faces tuberculate, ventromesial and ventrolateral faces tuberculate with distal angles only protruded. Ischium with very strong, acute spine on ventrodistal margin laterally. Coxa with tubercles on ventromesial distal angle.

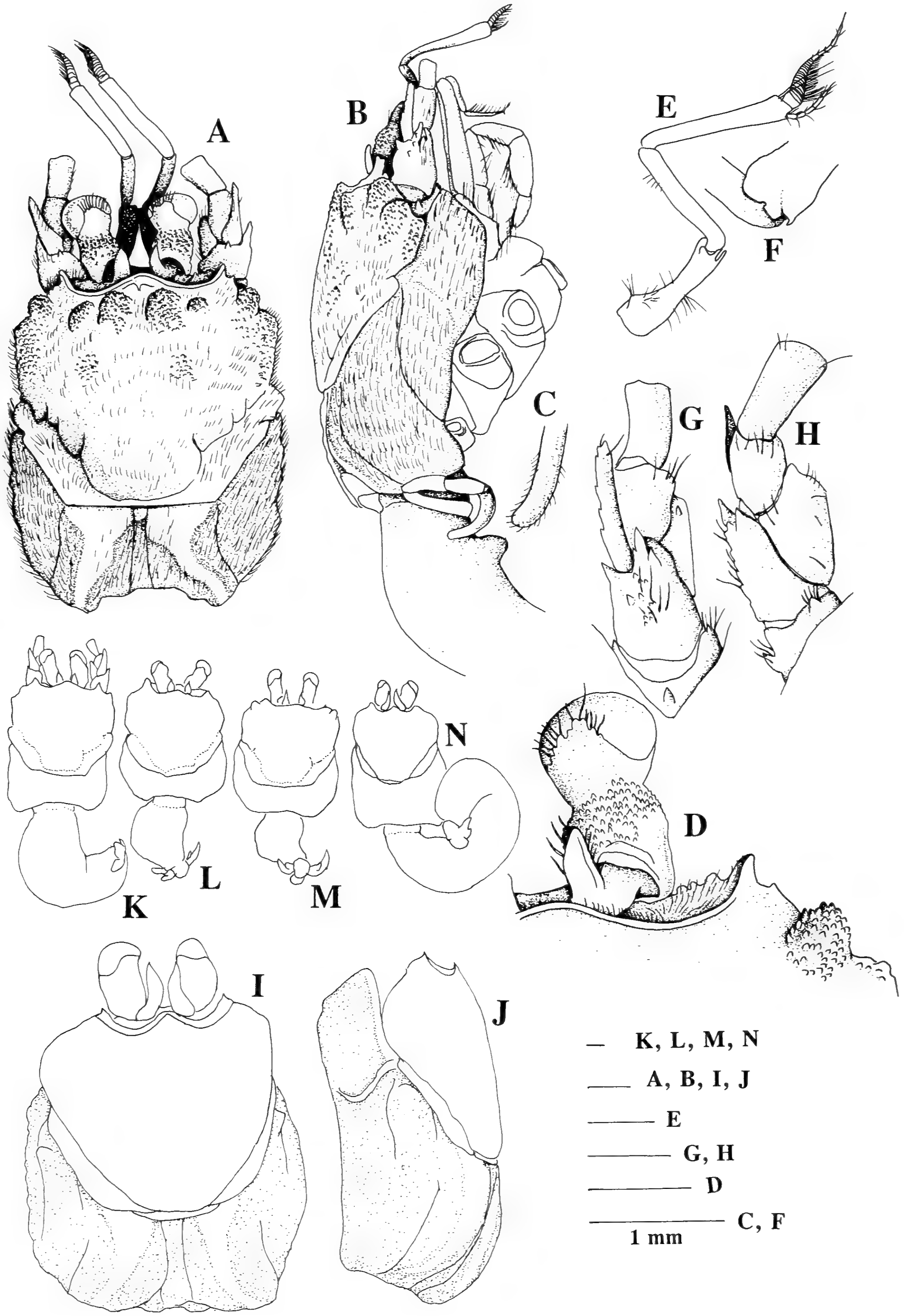

Fig. 1. *Icelopagurus tuberculosus*, new species: holotype male, SL = 5.70 mm, Okinawa, Japan (CBM ZC 4700); A–H, cephalothorax and cephalic appendages: A, whole (dorsal view); B, whole (right lateral view); C, tip of sexual tube arising from coxa of right fifth pereopod; D, ocular peduncle and anterolateral portion of shield (right, dorsal view); E, antennule (right, lateral view); F, same, distal portion of basal segment (mesial view); G, antenna (right, lateral view); H, same (ventral view); K–M, proportion of cephalothorax and abdomen: K, holotype male; L, paratype male, SL = 4.90 mm (CBM-ZC 4701); M, paratype female, SL = 5.10 mm (CBM-ZC 4702). *Icelopagurus crosnieri*

Left cheliped of male (Fig. 3E–G) slightly shorter than that of right, 0.92:1.00; considerably more slender than right, 0.65:1.00 in widest portion of palm and 0.32:1.00 in widest portion of carpus, respectively. Dactyl strongly curved distally, forming large hiatus with fixed finger; approximately equaling palm in length, with tufts of long setae; terminating in strong corneous claw; cutting edge with numerous tiny corneous teeth. Fixed finger tuberculate laterally, with tufts of long setae; terminating in strong recurved corneous claw; cutting edge with numerous tiny corneous teeth. Palm with dorsal surface tuberculate, with very broad faint longitudinal sulcus on proximal half continuing to proximal depression; mesial, lateral and ventral surfaces covered with dense blunt or spiniform tubercles. Carpus moderately long, approximately equaling palm in length; dorsal surface flat, with numerous blunt or spiniform tubercles, dorsolateral and dorsomesial margins distinct, each armed with strong, spiniform tubercles; mesial and lateral faces granular or tuberculate. Merus with dorsal margin strongly tuberculate, dorsodistal angle bearing very large spine; lateral face granular; ventrolateral margin tuberculate, with distal angle bearing blunt-tipped spine, ventromesial distal angle only produced and unarmed. Ischium with strong spine at ventrolateral distal angle.

Second (Fig. 2J–O) and third (Fig. 2P–R) pereopods morphologically similar; third slightly longer than second, 1.09:1.00, especially dactyl of third longer than second, 1.15:1.00, but broader in second than in third (ratio of width/length = 0.17 in second but 0.12 in third). Dactyls slightly shorter than propodi (second), 0.91:1.00, or as long as propodi (third); broad, sabre blade-shaped; each terminating in strong corneous claw; mesial faces concave longitudinally, with scattered long setae; dorsomesial and ventromesial margins each with row of corneous spinules; lateral faces slightly convex longitudinally. Propodi with entire surfaces minutely tuberculate; dorsal margins each with 2 to 5 thick, spine-like setae, dorsodistal margins each with pair of thick, spine-like setae; ventral margins each with 1 or 2 thick, spine–like setae. Carpi each with tiny spinule at dorsodistal angle; dorsal, lateral and mesial surfaces covered with dense tubercles or granules. Meri with dorsal, lateral and mesial surfaces tuberculate; dorsal face tuberculate, dorsodistal angles each only slightly protruded (second) (with tiny spinule on left second of paratype male) or bearing very strong spine (third); dorso-subdistal portion with 1 strong spine (second, but 2 spines in right second of paratype male), or 2 strong spines (third); ventrolateral distal angles each bearing large spine (second) or slightly protruded (third), ventromesial distal angles unarmed; distal half of ventrolateral margins slightly (second) or strongly (third) expanded ventrally, but ventromesial margins not. Female with coxae of third pereopods each with gonopore (Fig. 4N).

Fourth pereopods (Fig. 4A–C) semichelate. Dactyl moderately long, terminating in strong corneous claw; prominent preungual process present, covered with dense short setae; cutting edge with several corneous teeth. Propodus with rasp composed of 1 row of strong corneous scales along 0.80 length of ventral margin; dorsodistal angle unarmed. Carpus with blunt-tipped spine at dorsodistal angle.

Fifth pereopods chelate (Fig. 4D). Dactyls and propodi with well developed rasps. Male (Fig. 1B, C) with right coxa bearing moderately-short sexual tube directed to exterior; sexual tube with blunt-tipped apex, not filamentous, covered with scattered

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McLaughlin, 1997: paratype female, SL = 3.15 mm, Tanimbar Island, Indonesia (MNHN-Pg 5279): I, carapace, dorsal view; J, same, lateral view; N, proportion of cephalothorax and abdomen. Scales = 1 mm.

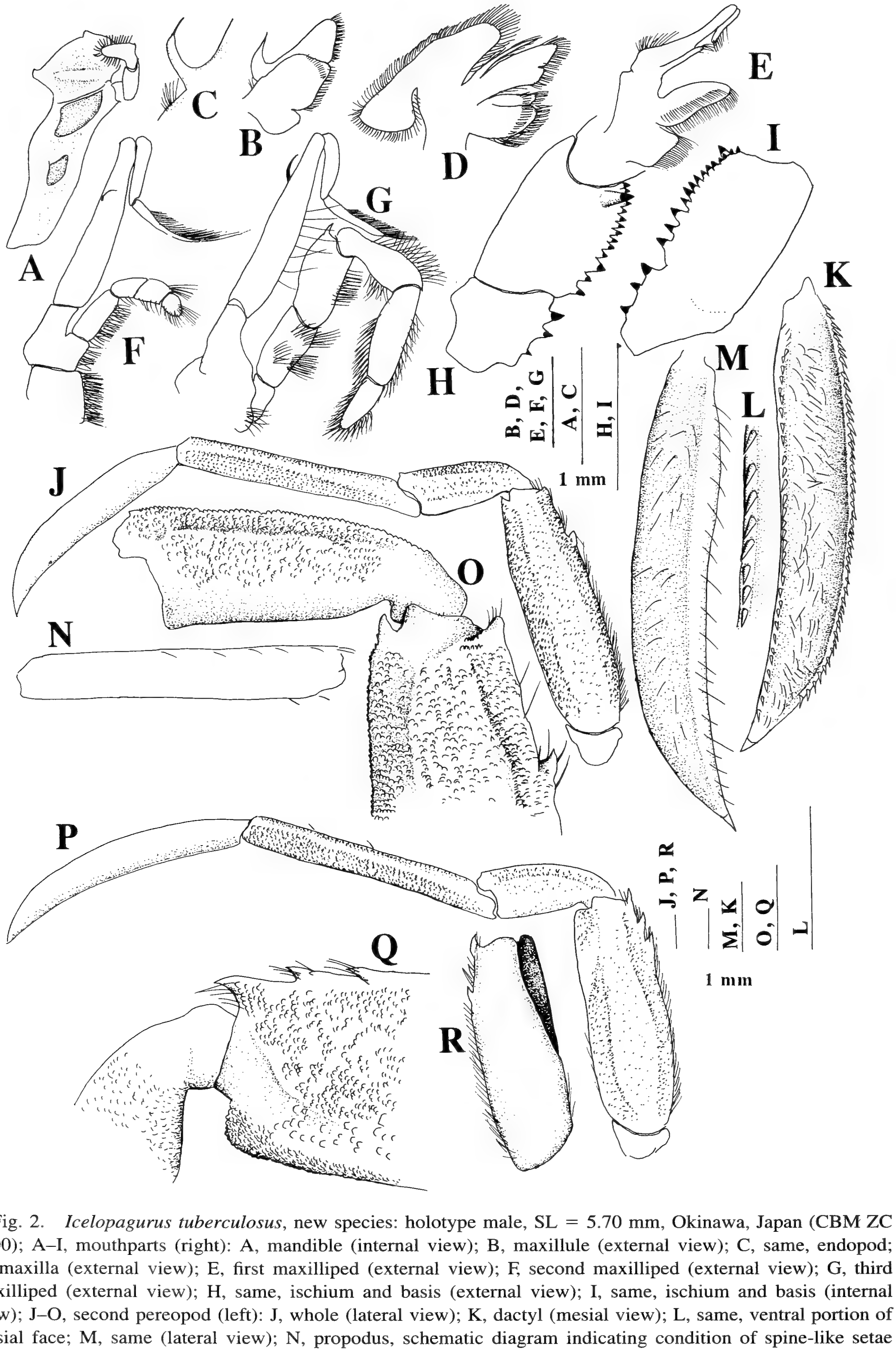

Fig. 2. *Icelopagurus tuberculosus*, new species: holotype male, SL = 5.70 mm, Okinawa, Japan (CBM ZC 4700); A–I, mouthparts (right): A, mandible (internal view); B, maxillule (external view); C, same, endopod; D, maxilla (external view); E, first maxilliped (external view); F, second maxilliped (external view); G, third maxilliped (external view); H, same, ischium and basis (external view); I, same, ischium and basis (internal view); J–O, second pereopod (left): J, whole (lateral view); K, dactyl (mesial view); L, same, ventral portion of mesial face; M, same (lateral view); N, propodus, schematic diagram indicating condition of spine-like setae

short setae apically; gonopore of left coxa (Fig. 4E) with vas deferens only slightly protruded, obscured by dense short setae posteriorly and dense medium-length setae anteriorly. Female with nearly symmetrical coxae (Fig. 4O).

Sternite of second pereopods (Fig. 4F) broad, subrectangular; divided into 2 lobes by longitudinal shallow median groove; anterior margin of each lobe round, unarmed, with long setae. Sternite of third pereopods (Fig. 4F, G) with perpendicular anterior lobe bearing pair of small projections armed with minute tubercles and fringed anteriorly with setae; horizontal posterior plate very broad, with setae anteriorly; subdivided into 2 lobes by longitudinal shallow median groove. Sternite of fourth pereopods (Fig. 4F) as transverse rod, accompanied by setae anteriorly. Sternite of fifth pereopods (Fig. 4E, F) reduced to very narrow transverse rod with pair of round projections with setae; widely separated from preceding sternal plates.

Abdomen (Fig. 1K–M) small in holotype male, comparatively reduced in paratype male, reduced in paratype female; membranous, dextrally twisted. Tergite of first abdominal somite small and chitinous. Tergites of second to fifth abdominal somites not clearly delineated, membranous. Tergite of sixth abdominal somite calcified, subrectangular, unarmed; divided into anterior and posterior lobes by shallow, transverse groove. Male with 3 unpaired left uniramous pleopods (Fig. 4H–J) fringed with long setae, arising from third to fifth abdominal somites. Female with no paired first pleopods modified as gonopods but with 3 unpaired left biramous pleopods (Fig. 4P–R) arising from second to fourth abdominal somites; existence of fourth pleopod uncertain because of damaged abdomen of single female specimen. Uropods (Fig. 4K, L) strongly asymmetrical, left distinctly larger than right; rasps of exopods and endopods well developed; protopods with some tubercles on posterodistal face (right) or unarmed (left). Telson (Fig. 4M) with lateral constrictions; posterior lobes separated by very broad median cleft; terminal margins of left and right lobes round, with short setae mesially.

Variations.—A marked sexual dimorphism is seen in chelipeds. Right cheliped of female (Fig. 3H–L) distinctly more slender and more compressed dorsoventrally than male; dactyl shorter than palm, 0.48:1.00, cutting edge with 2 broad but weak calcareous teeth on proximal half and many small corneous teeth on distal half; fixed finger not forming hiatus with dactyl, cutting edge with minute calcareous teeth on distal half; palm long, with dorsal face flat and weakly granular; carpus long and slender, approximately equaling palm in length, dorsal surface flat, with dorsolateral and dorsomesial margins each forming distinct ridge bearing row of large tubercles; merus with row of large tubercles and long setae on dorsal margin, dorsodistal angle bearing strong spine, ventromesial and ventrolateral distal angles each with blunt-tipped spine. Left cheliped of female (Fig. 2M–P) more slender than male; slightly shorter than right, 0.90:1.00; more slender than right, 0.75:1.00 in widest portion of palm and 0.79:1.00 in widest portion of carpus; dactyl and fixed finger straight, not forming hiatus; palm slender, with dorsal surface minutely tuberculate, median portion flat; carpus longer than palm, 1.46:1.00, slender, dorsal surface flat, dorsolateral and dorsomesial margins forming ridges, each bearing distinct row of granules; merus with dorsal face tuberculate, dorsodistal an-

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(mesial view); O, carpus and distal portion of merus (lateral view); P–R, third pereopod (left): P, whole (lateral view); Q proximal portion of carpus and distal portion of merus (lateral view); R, merus (mesial view). Scales = 1 mm.

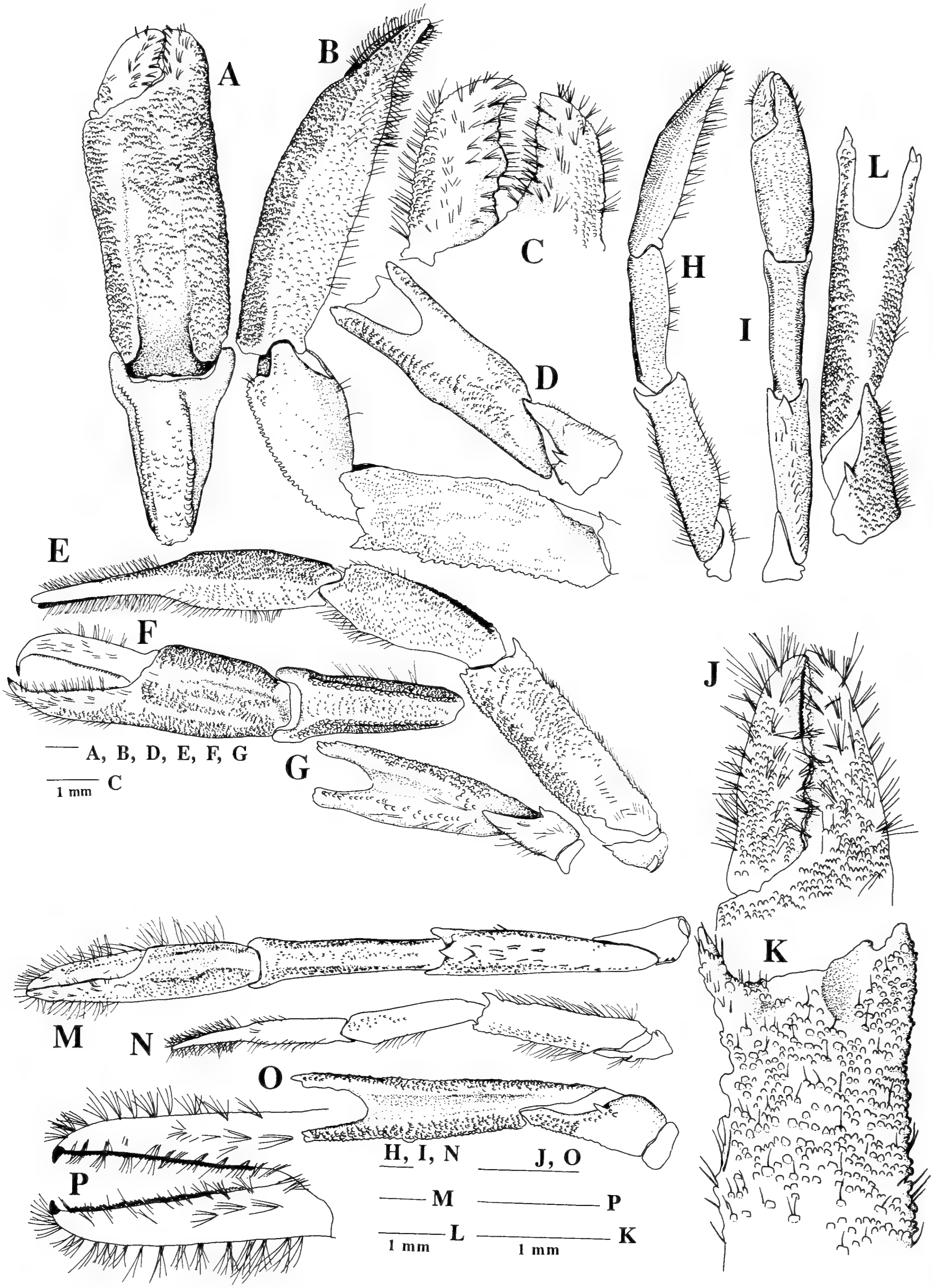

Fig. 3. *Icelopagurus tuberculosus*, new species. A–D, male right cheliped: A, whole (dorsal view); B, whole (lateral view); C, dactyl and fixed finger (dorsal view); D, merus and ischium (ventral view); E–G, male left cheliped: E, whole (lateral view); F, whole (dorsal view); G, merus and ischium (ventral view); H–L, female right cheliped: H, whole (lateral view); I, whole (dorsal view); J, dactyl and fixed finger (dorsal view); K, distal portion of merus (lateral view); L, merus and ischium (ventral view); M–P, female left cheliped: M, whole (dorsal view); N, whole (lateral view); O, merus and ischium (ventral view); P, dactyl and fixed finger (ventral

gle bearing very large spine, with distal angles each bearing blunt-tipped spine.

The size of the abdomen is subject to variation. The abdomen is small in the holotype male and comparatively reduced in male and female paratypes, although no distinct morphological variations are seen in the uropods and telson. Neither the number or shape of the pleopods differ between the holotype and paratype males.

Coloration.—Unknown.

Habitat.—10–20 m, sandy bottom. Housing unknown.

Distribution.—Known only from the type locality, Kumejima, Okinawa.

Etymology.—The name *tuberculosus* is from the Latin, *tuberculum*, diminutive of *tuber*, a swelling or lump, and the suffix, *-osus*, alluding to the tuberculate surfaces of the shield and pereopods characteristics of this new species.

Remarks.—Because the posterior portion of the abdomen of the paratype female is damaged, it cannot be confirmed whether or not it had a fourth pleopod.

Comparison with Icelopagurus crosnieri—The new species agrees with all of the diagnostic characters of *Icelopagurus* proposed by McLaughlin (1997) but is unique in having a large well-calcified, immovable plate that is partially fused with the posterior and posterolateral margins of the shield. This plate is most probably derived from the right and left accessory portions of the shield (sensu Lemaitre 1995) plus the linea transversalis (sensu Boas 1926, Pilgrim 1973). Generally in hermit crabs (excluding Pylochelidae and Lithodidae), the accessory portions of the shield consists of small, elongated movable, partially-calcified plates on either side of the posterolateral margin of the shield. The linea transversalis is a narrow, uncalcified hinge separating the gastric and cardiac regions of the carapace. However, as discussed below, well-developed and strongly-calcified accessory portions and linea transversalis occur in five genera which comprise a highly specialized group within pagurids (Poupin & McLaughlin 1996, McLaughlin 1997).

McLaughlin (1997) did not mention accessory portions of shield and linea transversalis in *Icelopagurus crosnieri*. Two paratype specimens of that species were examined (Fig. 1I, J, N), and no such structures were found; instead, there is a pair of broad, partially-calcified accessory portions of the shield and a narrow, uncalcified linea transversalis along the posterior margin of the shield. These structures are clearly separated from the shield by a soft membrane (Fig. 1I, J).

The morphology of the dorsal surface of the shield in the new species, *I. tuberculosus*, is also distinct. Anteriorly there is a transverse row of four prominent protuberances and a pair of similar protuberances on the anterolateral margins, all strongly armed with minute tubercles. The ocular peduncles are also distinct, armed with many tubercles. None of these characters occur in *I. crosnieri*.

The size of the abdomen of *I. tuberculosus* is small or somewhat reduced (Fig. 1K–M). The abdomen in *I. crosnieri* is normal, similar to that of typical pagurid crabs (Fig. 1N). Other morphological differences between the two species are given in Table 1.

Discussion

When establishing *Icelopagurus*, McLaughlin (1997) stated that it was superficially very similar to *Catapagurus*, both genera being characterized by a well-developed right sexual tube in males, females lacking specialized secondary sexual char-

←

view). A–G, holotype male, SL = 5.70 mm, Okinawa, Japan (CBM ZC 4700); H–P, paratype female (CBM ZC 4702), SL = 5.10 mm, Okinawa, Japan. Scales = 1 mm.

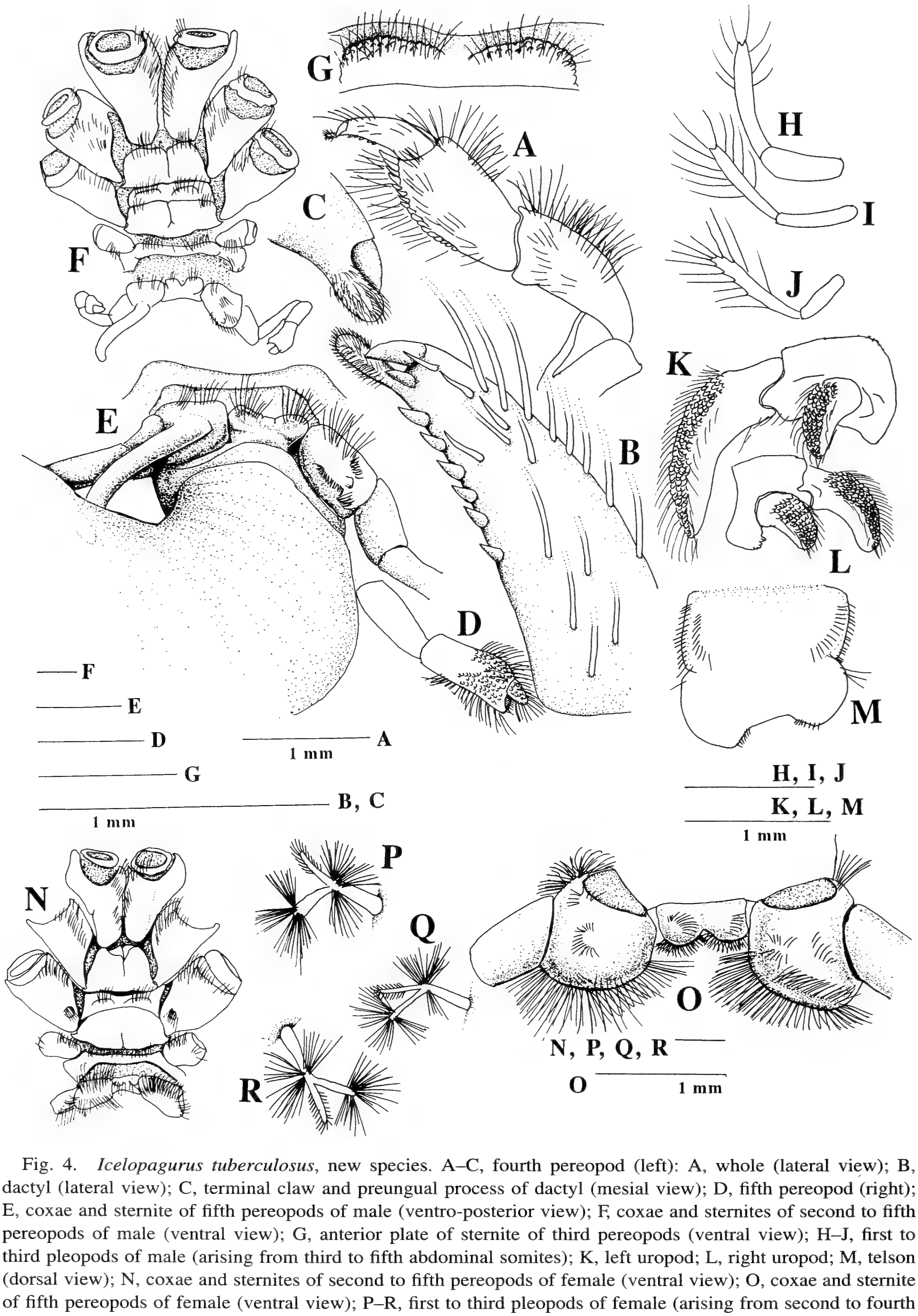

Fig. 4. *Icelopagurus tuberculosus*, new species. A–C, fourth pereopod (left): A, whole (lateral view); B, dactyl (lateral view); C, terminal claw and preungual process of dactyl (mesial view); D, fifth pereopod (right); E, coxae and sternite of fifth pereopods of male (ventro-posterior view); F, coxae and sternites of second to fifth pereopods of male (ventral view); G, anterior plate of sternite of third pereopods (ventral view); H–J, first to third pleopods of male (arising from third to fifth abdominal somites); K, left uropod; L, right uropod; M, telson (dorsal view); N, coxae and sternites of second to fifth pereopods of female (ventral view); O, coxae and sternite of fifth pereopods of female (ventral view); P–R, first to third pleopods of female (arising from second to fourth abdominal somites). A-M, holotype male, SL = 5.70 mm, Okinawa, Japan (CBM ZC 4700); N–R, paratype female, SL = 5.10 mm, Okinawa, Japan (CBM ZC 4702). Scales = 1 mm.

Table 1.—Comparison of morphology of ambulatory pereopods and telson in species of *Icelopagurus.*

	I. tuberculosus, new species	*I. crosnieri*
Second and third pereopods		
Dactyl: mesial face	concave	flat or slightly convex proximally
dorsomesial margin	row of numerous short corneous spines	row of short setae on proximal half and row of every long setae on distal half
ventromesial margin	row of numerous short corneous spines	very few setae
Propodus: dorsal face	granular spine-like setae on distal half	few irregular rows of spines spine-like setae entirely
Carpus: dorsal face	granular	few irregular rows of spines
Merus: dorsal face	1 or 2 very strong spines	rugose
ventrolateral face	granular	numerous spines
Posterior lobes of telson		
posterolateral margin	unarmed	4 long corneous spine-like setae
mesial margin	unarmed	few calcareous spines

acters, a rudimentary or vestigial external endopodal lobe on the maxillule, more or less reduced crista dentata with one accessory tooth, and a distinct tubular preungual process on the dactyl of the fourth pereopod. However, *Icelopagurus* is readily separated from *Catapagurus* by the shortness of the sexual tube and the distinct development of the telson.

Although the new species, *I. tuberculosus*, differs from both *I. crosnieri* and *Catapagurus* species in having short ocular acicles, the morphology of the ambulatory pereopods of *I. tuberculosis* is more similar to those of *Catapagurus* species which have dactyls shaped like sabre blades, such as *C. granulatus* Edmondson, 1951 and *C. ensifer* Henderson, 1893, than that of *I. crosnieri*. These characters include the ambulatory pereopods ending in sabre blade-shaped dactyls with dorsal and ventral rows of numerous corneous spine-like setae on the mesial face, and the meri having one or two very strong, subdistal dorsal spines. The ambulatory dactyls of *I. crosnieri* are not sabre blade-shaped, their mesial faces having a dorsal row of short setae on the proximal half, very long setae on the distal half, and ventrally only a few setae; the meri of the ambulatory pereopods of *I. crosnieri* lack a distinct dorsal spine.

During the course of this study, similar patterns of calcification were found in the posterior carapace in both *Icelopagurus* and *Catapagurus* species examined (*C. granulatus*, *C. ensifer*, *C. japonicus*, and three undescribed species collected). There are a pair of partially calcified bands in the areas between the cardiac sulci and sulci cardiobranchialis in *I. tuberculosus* (Fig. 1A) and in *I. crosnieri* (Fig. 1I). When McLaughlin & Lemaitre (1997) determined character states of calcification of the posterior carapace of hermit crabs, i.e., entirely calcified; posterolateral and/or posteromedial calcification; and entirely membranous or with only scattered small areas of calcification, they included *Icelopagurus* in the latter category. Although I agree with their classification because of small areas of those partially calcified bands, I think that future detailed studies on patterns of calcification of posterior carapace may provide useful information in hermit crab phylogeny.

McLaughlin (1997) also stated that *Icelopagurus* was ostensibly quite similar to *Pagurodes* Henderson, 1888 sensu stricto, which is currently represented only by *Pagurodes inarmatus* Henderson, 1888. However, *P. inarmatus* differs from both *I. crosnieri* and *I. tuberculosus* in having trichobranchiate gills, fourth pereopod dactyls without a preungual process, and telson with acutely triangular posterior lobes.

The new species, *I. tuberculosus*, shares several characters with taxa considered among the most highly specialized pagurid genera by Poupin & McLaughlin (1996) and McLaughlin (1997), namely, *Alainopagurus* Lemaitre & McLaughlin, 1995, *Alainopaguroides* McLaughlin, 1997, *Solitariopagurus* Türkay, 1986, *Porcellanopagurus* Filhol, 1885, and *Ostraconotus* A. Milne Edwards, 1880. These five genera are characterized by a well-calcified shield, distinct reduction of the abdomen, symmetrical uropods and telson, very broad sternites on the pereopods, absence of paired or unpaired pleopods in males, and lack of left fifth pleopod in females. Because of these morphological similarities, McLaughlin (1997) stated that these genera might conceivably be considered as sister taxa. Since *I. tuberculosus* also has a vaulted, well-calcified shield, a more or less reduced abdomen and elongated, slender chelipeds and ambulatory legs with very broad sternites, general impression of similarity is gained between *I. tuberculosus* and these genera.

As previously mentioned, the large, well-calcified and immovable plate on the carapace of *I. tuberculosus* is derived from the well-developed and calcified accessory portions of the shield and linea transversalis. The well-calcified condition of the linea transversalis is also seen in the five mentioned specialized genera (Table 2), and in at least two genera, *Solitariopagurus* and *Alainopagurus*, it is partially fused with the shield (Poupin & McLaughlin 1996, Lemaitre & McLaughlin 1995, McLaughlin 1997). The development and strong calcification of shield accessory portions are also known in these genera (Lemaitre & McLaughlin 1995, Poupin & McLaughlin 1996, McLaughlin 1997) (Table 2). In all of these genera, the linea transversalis and accessory portions are not completely fused together, being at best partially fused in *Solitariopagurus* and *Porcellanopagurus*.

In overall morphology, the two species of *Icelopagurus* are quite similar to *Alainopaguroides*, a monotypic genus represented by *A. lemaitrei* McLaughlin, 1997, in the morphology of the shield, cephalic appendages, mouthparts, pereopods and secondary sexual characters in the both sexes (Table 2). *Icelopagurus tuberculosus* is more similar to *Alainopaguroides* than *I. crosnieri* in the short ocular acicles, ambulatory legs with more or less blade-shaped dactyls bearing dorsal and ventral rows of regularly-spaced setae on the mesial face, and a more or less reduced abdomen. *Alainopaguroides* is distinguished from *Icelopagurus* in lacking unpaired or paired pleopods in males, having vestigial propodal rasps on the fourth pereopods, and symmetrical uropods and telson (Table 2). In addition, *I. tuberculosus* differs from *Alainopaguroides* in having large protuberances anteriorly on the shield.

Icelopagurus shares some characters with *Solitariopagurus*, currently recognized as having three representatives, *S. profundus* Türkay, 1986, *S. triprobolus* Poupin & McLaughlin, 1996, and *S. tuerkayi* McLaughlin, 1997. Both genera have a vaulted, well-calcified shield, obsolete or no external endopodal lobe of the maxillule, elongated, slender chelipeds and ambulatory legs, and a moderately long right sexual tube in males. Further characters shared between *I. tuberculosus* and *Solitariopagurus*, but not with *I. crosnieri*, include four large protrusions on the antero-dorsal portion of the shield (except *S. profundus*) with a well-developed, calcified accessory portion (but not fused as one in *Solitariopagurus*), and a more or less reduced abdomen. In *Solitariopagurus*, two or three wing-like expansions (except lateral projections of the shield) occur on each lateral margin of the shield. Also, *I. tuberculosus* has a projection on each anterolateral margin of the shield, and distinct anterolateral angles armed with tubercles. *Solitariopagurus* and *Icelopagurus* are immediately distinguished by a number of gills and shapes of a rostrum, lateral projections, oc-

Table 2.—Comparison of selected morphological characters between *Icelopagurus* and selected, specialized genera.

	Icelopagurus	*Porcellanopagurus*	*Alainopaguroides*	*Alainopagurus*	*Solitariopagurus*	*Ostraconotus*
Gill	11 phyllo.	11 phyllo.	11 phyllo.	11 phyllo.	10 phyllo.	10 phyllo.
Carapace						
Lateral projection development	weak	mod. well	weak	mod. well	mod. well to prominent	prominent
Accessory portion of shield	well calcified[a]/ partially calcified	mod. well calcified, broad[a]	well calcified	partially calcified, triangular[d]	well calcified, quadrate[e]	well calcified[f]
Linea transversalis	well calcified[a]/ uncalcified	partially calcified, broad, small	well calcified, rod-like	well calcified, very broad[a]	well calcified, very broad[a]	well calcified[f]
Ocular acicle	short, simple/ elongate, simple	reduced, simple	short, simple	elongate, multiple	reduced, simple	short, simple
2nd and 3rd pereopod dactyls	blade-shaped/ not blade-shaped	not blade-shaped	slightly blade-shaped	not blade-shaped	not blade-shaped	slightly blade-shaped
Female gonopore	paired	paired	paired	only left	only left	paired
4th pereopods						
Termination	semichelate	semichelate	semichelate	simple	subchelate	subchelate
Preungual process	prominent	absent	prominent	absent	absent	absent
Propodal rasp	1 row	1 row	rudimentary	1 row	1 row	absent
Male sexual tube						
Left	very short[b]	absent	very short	moderately long	short	moderately long
Right	long	absent[c]	long	moderately long	moderately long	moderately long
Abdomen	somewhat reduced /normal	reduced	reduced	reduced	reduced	reduced, folded beneath cephalothorax
Male pleopods	3rd–5th, unpaired left	absent	absent	absent	absent	absent
Female pleopods	2nd–4th?/2nd–5th unpaired, left	2nd–4th unpaired left	2nd–4th unpaired, left	2nd–4th unpaired, left	2nd–4th unpaired, left	2nd–4th, unpaired, left
Uropods	asymmetrical	symmetrical	symmetrical	symmetrical	symmetrical	symmetrical
Telson	asymmetrical	symmetrical	symmetrical	symmetrical	symmetrical	symmetrical
Median cleft	prominent	very small	small	absent	absent	?

In *Icelopagurus*, the character listed first is for *I. tuberculosus*, and the second for *I. crosnieri*. phyllo.: phyllobranchiate gills. a: partially fused with shield. b: a slight protrusion of vas deferens. c: but recently, existence of a protrusion of vas deferens was reported in *P. adelocercus* by McLaughlin & Hogarth (1998). d: described as posterolateral plates of carapace (Lemaitre & McLaughlin 1995). e: described as anterolateral plates of posterior carapace (Poupin & McLaughlin 1996). f: entire carapace is well calcified.

ular facicles and morphology of the abdomen and its appendages (Table 2).

Porcellanopagurus also has two or three wing-like expansions on each lateral margin of the shield (Borradaile 1916, Forest 1951, Takeda 1981, 1985; Suzuki & Takeda 1987, McLaughlin 1997, McLaughlin & Hogarth 1998). However, it differs from *Icelopagurus* in morphology of the abdomen and its appendages, and male sexual tube (Table 2). *Ostraconotus* (based on Türkay 1986, Poupin & McLaughlin 1996, McLaughlin 1997, McLaughlin & Lemaitre 1997) also has the shield with a transverse row of four somewhat large tubercles on the anterodorsal portion, and a right sexual tube in males, but differs from *Icelopagurus* in number of gills and structure of the abdomen and its appendages (Table 2). Furthermore, in the Paguridae, *Ostraconotus* is the only genus in which the posterior carapace is completely calcified (McLaughlin & Lemaitre 1997).

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A new species of crayfish of the genus *Procambarus* (Crustacea: Decapoda: Cambaridae) from Veracruz, Mexico

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Abstract.—*Procambarus* (*Austrocambarus*) *citlaltepetl*, new species, is described from Ciudad Mendoza, Veracruz, Mexico. The new species can be placed in the *mexicanus* Group, and is most similar to *P.* (*A.*) *mexicanus*, from which it can be distinguished by the absence of branchiostegal spines, gonopod with blade-like mesial process curved over the apex and thicker lateral portion, and annulus ventralis with complete preannular plate. SEM micrographs of the male and female genitalia of the new species, as well of those of *P.* (*A.*) *mexicanus*, are provided to facilitate comparisons, and to clarify the identity of the latter.

Confusion concerning the identity of the crayfish *Procambarus* (*Austrocambarus*) *mexicanus* (Erichson, 1846) has existed for more than a century, primarily because of the incomplete original description lacking figures, loss of the holotype, and the high degree of morphological variation found among the many populations assigned to this taxon (Villalobos 1954). Several efforts have been made to clarify the status of *P.* (*A.*) *mexicanus*. Villalobos (1954) described four new species, one subspecies, and redescribed six species of *Procambarus*, including *P.* (*A.*) *mexicanus*, most from central and southern Veracruz, and proposed the "*mexicanus*" Group for eight of these species. Hobbs (1987) synonymized *Cambarus aztecus* Saussure, 1857 with *P.* (*A.*) *mexicanus*, which he redescribed, listing 23 collection sites; he also described *P.* (*A.*) *olmecorum* Hobbs, 1987 an placed it in the "*mexicanus*" Group.

In spite of these efforts, the distribution range of *P.* (*A.*) *mexicanus* as reviewed by Hobbs (1987), still included a vast area in the states of Veracruz, Puebla, and Oaxaca (Fig. 1), and included a wide array of morphological forms. Presumably, the northern limit of the distribution range is in the environs of Jalapa, Veracruz; the southern limit occurs in Tuxtepec, Oaxaca; to the west it occurs along the slope of the Mexican central plateau; and to the east it reaches the Sierra de Los Tuxtlas, Veracruz (Fig. 1).

After a detailed examination of specimens from Rincón de la Doncella, Ciudad Mendoza, it became clear that they represented a new species, different but morphologically similar to *P.* (*A.*) *mexicanus*. In this study we describe this new species, *Procambarus* (*Austrocambarus*) *citlaltepetl*, and in order to clearly separate the new species from *P.* (*A.*) *mexicanus*, we provide scanning electron microscope (SEM) micrographs of the gonpod, annulus ventralis, and epistome of both species. The SEM micrographs of *P.* (*A.*) *mexicanus* were taken from specimens from the type locality in order to help in the recognition of other new forms which may exist within this Group.

All specimens used are deposited in the Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México (CNCR). Other abbrevia-

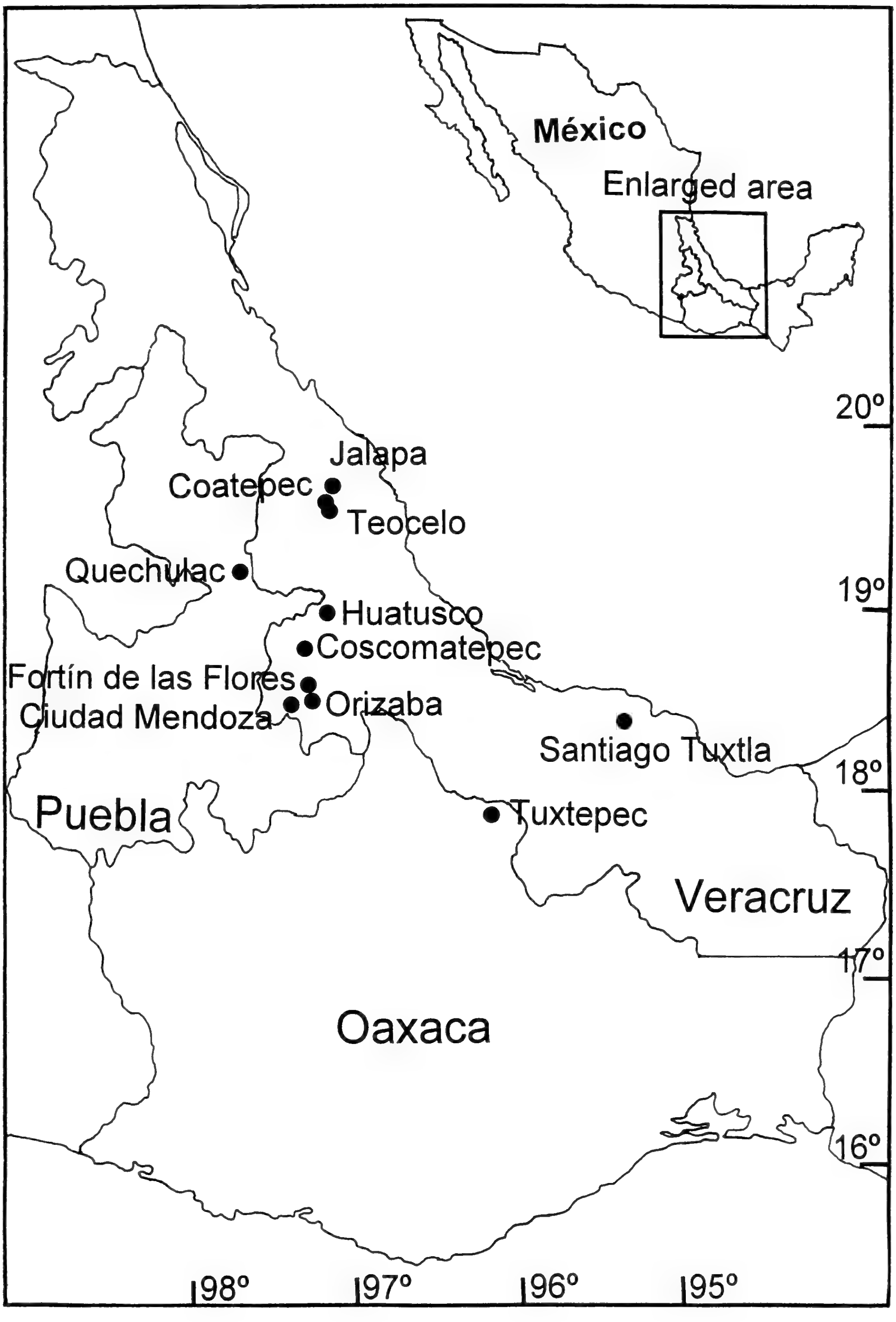

Fig. 1. Localities where *Procambarus* (*Austrocambarus*) *mexicanus* has been collected in the states of Puebla, Oaxaca, and Veracruz.

tions used are: coll, collector; RL, rostrum length; TCL, total carapace length; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Procambarus (*Austrocambarus*) *citlaltepetl*, new species

Figs. 2A–C, 3A–C, 4

Diagnosis.—Body pigmented, eyes normally developed. Rostrum devoid of marginal spines. Acumen length ranging from 0.07% to 0.14% of RL ($\bar{X}$ = 0.10%). Carapace with or without small cervical tubercle. Areola ranging from 7.1 to 16.8 ($\bar{X}$ = 10.9) times as long as wide, 30.8% to 39.5% ($\bar{X}$ = 34.9%) of TCL, with 1–3 punctations across narrowest part. Suborbital angle weak, infraorbital spine absent. Branchiostegal spine absent. Postorbital ridges well marked, slightly sinuous in dorsal view, converging anteriorly, ending in spine anteriorly. Antennal scale varying from 1.61 to 1.96 ($\bar{X}$ = 1.79) times as long as wide; maximum width at midlength. Chelipeds subequal, shorter than TCL, partially covered with squamous tubercles; chela moderately elongated, not pubescent, fingers shorter than palm, palm about twice as long as broad; movable finger with squamous tubercles along dorsal margin, opposable margin devoid of tubercles distally, finely serrate; fixed finger punctate, devoid of tubercles except for inferior margin, opposable margin finely serrate distally with 5 tubercles proximally. First pair of pereiopods shorter than total length of body, covered with small squamous tubercles from distal half of merus to proximal half of fingers. Ischium of third pereiopod armed with single, acute hook, reaching beyond articulation with basipodite. First pair of pleopods of male form I symmetrical, devoid of subterminal setae, reaching coxae of third pair of pereiopods; shoulder on cephalic surface slightly concave, forming rounded angle with cephalic border (Figs. 2A, 3A); mesial process blade-like, becoming narrower distally, laterodistally oriented (Fig. 2B), curved over apex in cephalic view (Fig. 2C); cephalic process absent; central projection triangular, cephalodistally oriented. Female with hinged annulus ventralis; preannular plate strong, complete, oriented perpendicular to longitudinal axis of body; annulus oval-shaped, divided by deep and narrow mesial groove, seminal receptacle opening on caudal portion as sinuous groove; postannular sclerite strong, oval-shaped, wider than annulus, cephalic margin subacute, caudal margin almost straight (Fig. 3B). Sternal plates adjacent to fifth pair of pereiopods wide, rounded, extending mesially, reaching postannular sclerite. Coxae of fourth and fifth pair of pereiopods separated.

Measurements of types.—See Table 1.

Holotypic male, form I.—Body pigmented. Cephalothorax subcylindrical, becoming thicker in branchial region, 0.91 times length of abdomen. Areola 15.6 times as long as wide, 34.9% of TCL (Fig. 4A). Dorsal surface of carapace densely punctate along branchial and cardiac regions. Lateral surfaces finely granulate along hepatic and branchial regions. Rostrum devoid of marginal spines; dorsal surface slightly concave, densely punctate posteriorly. Rostrum with lateral margins convergent, anterior width 2.1 mm, posterior width 3.6 mm, ending anteriorly in acute angle; subrostral ridges not evident in dorsal view, oriented ventrally. Acumen length 0.11% of RL, reaching anterior portion of third article of anntenular peduncle. Postorbital ridge moderately strong, ending anteriorly in triangular spine oriented laterally. Suborbital angle weak, infraorbital spine absent. Branchiostegal spine absent. Cervical groove with blunt tubercle in hepatic region (Fig. 4B).

Abdomen narrower than carapace. Somites with tergal region finely punctate, pleural region densely punctate. Dorsal surface of telson covered with short setae, cephalic section with 3 spines in posterolateral angles, caudal section with posterior margin rounded. Epistome triangular, ante-

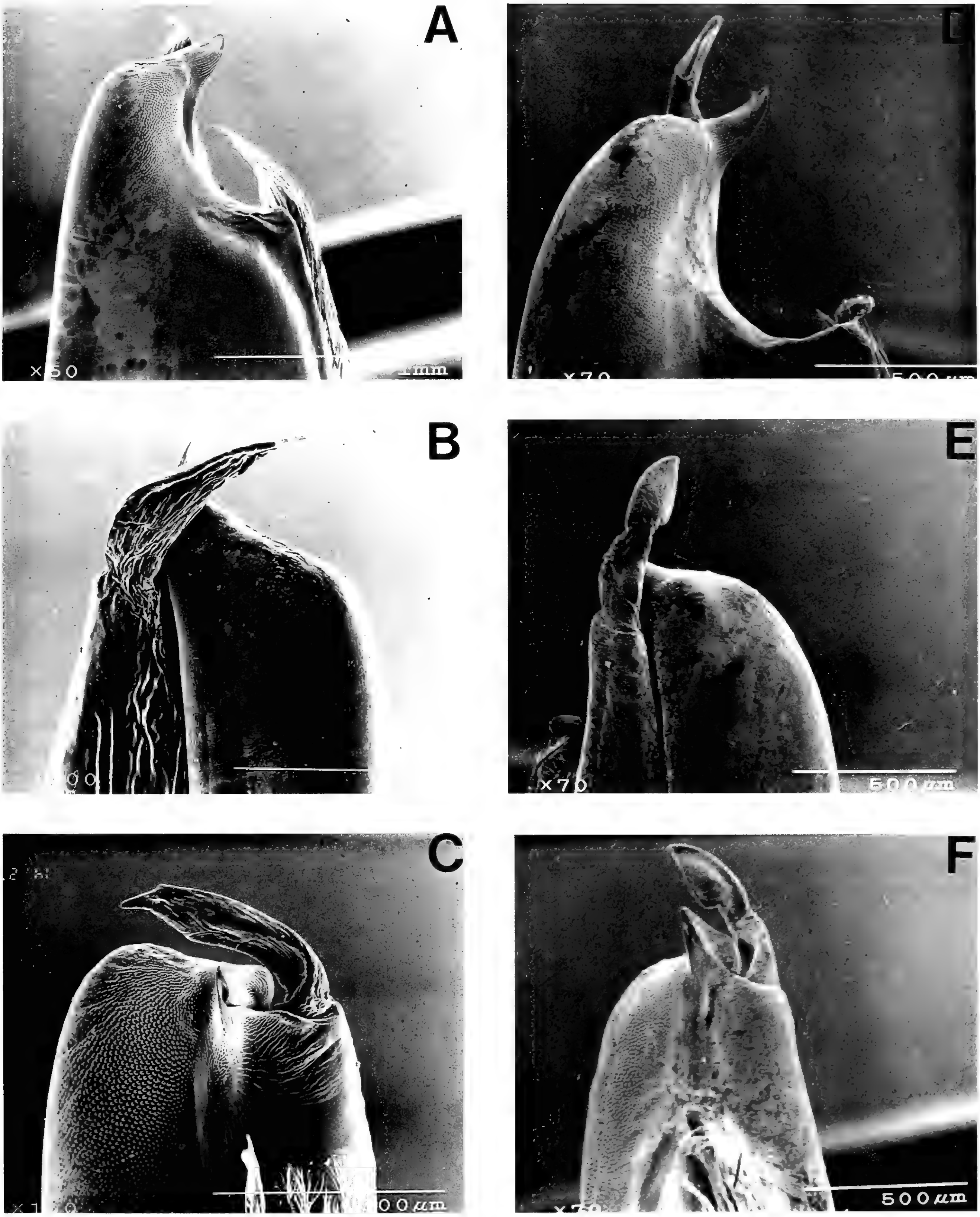

Fig. 2. Lateral (A, D), caudal (B, E), and cephalic views (C, F) of left gonopod. A–C, *Procambarus* (*Austrocambarus*) *citlaltepetl*, new species, holotype (CNCR 17317); D–F, *Procambarus* (*Austrocambarus*) *mexicanus* (CNCR 2339).

rior vertex triangular, posterior angles rounded, ventral surface slightly concave; cephalic lobe elongated, oval-shaped; main body with well defined fovea, anteriorly with second, larger depression (Fig. 3C). Antennal scale 1.72 times as long as wide, maximum width at midlength, lateral margin terminating in spine (Fig. 4C). Antennal

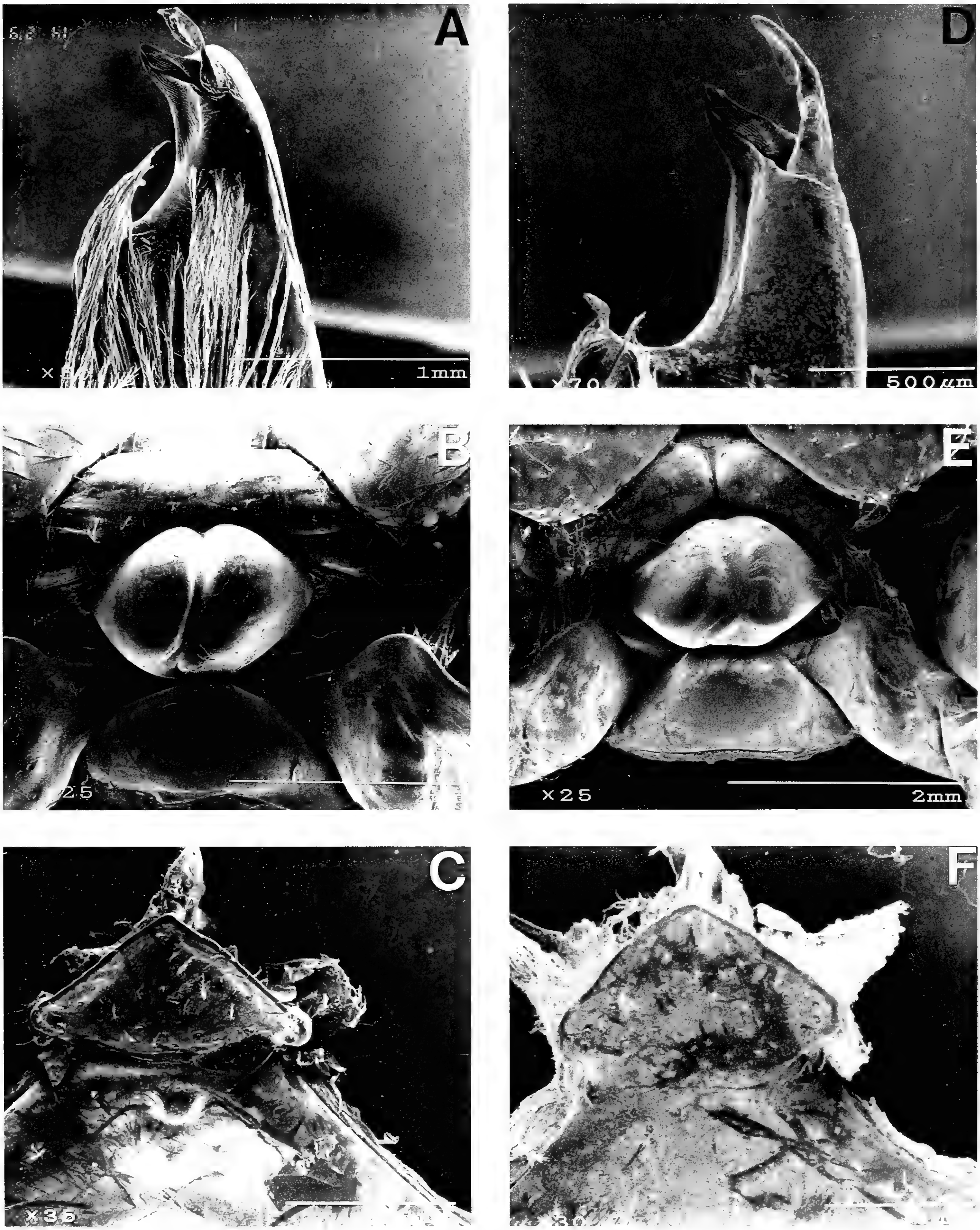

Fig. 3. Mesial view of left gonopod (A, D), annulus ventralis (B, E), and epistome (C, F). A–C, *Procambarus* (*Austrocambarus*) *citlaltepetl*, new species holotype (CNCR 17317); D–F, *Procambarus* (*Austrocambarus*) *mexicanus* (CNCR 2339).

peduncle with basis ending in short distolateral spine, ischium with lateral blunt tubercle. Third maxilliped reaching distal portion of third segment of antennal peduncle; midventral surface of ischium covered with fine, simple, plumose setae, laterally with tufts of short setae.

Chelipeds shorter than TCL, tuberculate

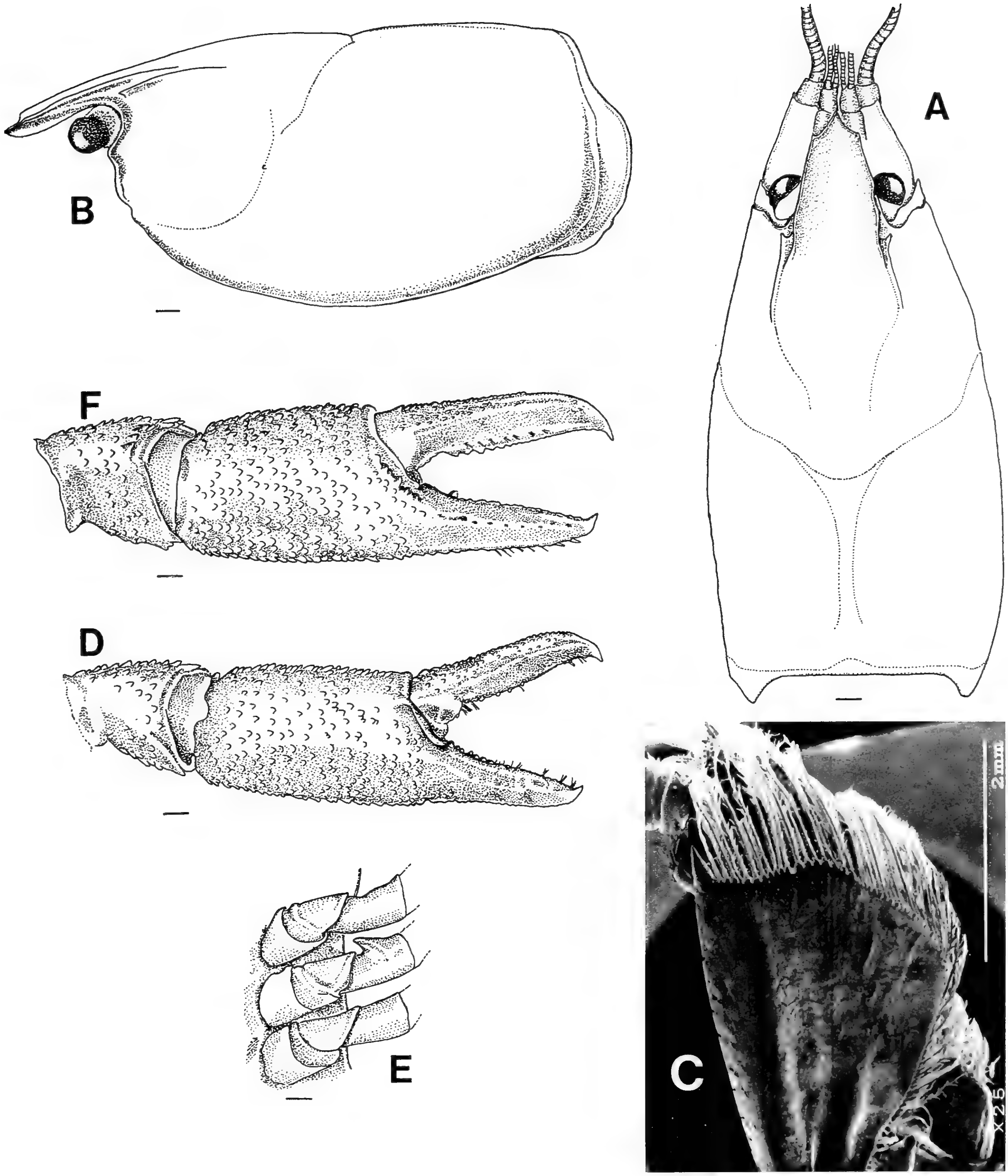

Fig. 4. *Procambarus* (*Austrocambarus*) *citlaltepetl*, new species (all figures of holotype (CNCR 17317), except F of female allotype (CNCR 17318)): A, carapace, dorsal view; B, carapace, lateral view; C, antennal scale; D, distal podomeres of cheliped; E, basal podomeres of left second, third, and fourth pereiopods; F, distal podomeres of cheliped. Scale bars represent 1 mm.

from distal half of merus to midlength of fingers. Right chela moderately elongated, 2.9 times as long as broad, not pubescent, fingers slightly shorter than palm; uniformly covered with squamous tubercles except on fingers. Palm about 1.8 times long as broad. Movable finger with squamous tubercles along dorsal margin, lateral surfaces punctate, covered with regularly spaced tufts of setae, opposable margin finely serrate, devoid of tubercles distally, with 4–5 small tubercles proximally. Surface of fixed

Table 1.—Measurements (mm) of type specimens of *Procambarus* (*Austrocambarus*) *citlaltepetl*, new species.

	Holotypic male, form I	Allotypic female	Morphotypic male, form II
Total length	52.6	67.5	61.8
Carapace			
Total length	25.2	32.7	30.5
Postorbital length	20.6	26.4	24.5
Width	12.6	16.0	14.4
Areola			
Length	8.8	12.2	10.5
Width	0.7	1.0	0.7
Rostrum			
Length	6.8	7.8	7.8
Anterior width	2.1	2.5	2.4
Posterior width	3.6	5.0	4.7
Acumen length	0.7	1.0	1.0
Cheliped			
Length of mesial margin of palm	9.2	6.6	8.7
Width of palm	6.2	6.2	6.5
Length of lateral margin	16.7	16.3	18.6
Length of dactyl	8.7	8.7	10.5
Abdomen			
Width	10.8	14.3	10.4
Length	27.5	34.9	31.9

finger punctate, devoid of tubercles except for difuse row along inferior margin; lateral surfaces covered with regularly spaced tufts of setae; opposable margin finely serrate with 5 well defined tubercles proximally (Fig. 4D).

Carpus short, approximately conical in shape, dorsal and lateral surfaces covered with subsquamous tubercles, lateral surface with shallow longitudinal groove, inferior surface with small, scattered subsquamous tubercles. Distal third of merus with minute tubercles along mesial and lateral surfaces; inferior border with 2 rows of blunt tubercles, inner row with small tubercles increasing in size distally, outer row with larger tubercles ending distally in large spiny tubercle.

Ischium of third pair of pereiopods with simple acute hook, overreaching basioischial articulation (Fig. 4E).

First pleopods as described in Diagnosis.

Proximal lobes of uropods with short, acute spines. Endopodite with distomedial spine located premarginally, and well developed distolateral spine. Exopodite with 3 spines on distolateral angle, external and internal ones fixed, medial one largest, articulated.

Allotypic female.—Similar to holotype, differing in following characters: acumen length 0.12% of RL; areola 12.2 times as long as wide, 37.3% of TCL; chelae more robust, 2.7 times as long as broad, fingers longer than palm, palm about 1.5 times as long as broad (Fig. 4F); sternal thoracic plate tapering anteriorly, wide between third pair of pereiopods, becoming ridge-like by third maxillipeds. Annulus ventralis as described in Diagnosis.

Paratypic male, form II.—Differing from holotype in following characters: cardiac and gastric regions of carapace less densely punctate, acumen length 0.12% of RL, areola 15 times as long as wide; rostrum with scattered punctations, rostral borders converging anteriorly; ischium of third pair of pereiopods with small blunt projection, not reaching basioischial articulation.

Apical structures of first pair of pleopods poorly developed, non corneous; mesial process strong and rounded apically, anterior margin of central projection rounded, central projection divided into cephalic and caudal portions by groove.

Type locality.—Rincón de la Doncella Park (altitude 1400 m), Ciudad Mendoza, Municipio de Camerino Z. Mendoza, Veracruz (18°48′N, 97°10′W). Rincón de la Doncella is a spring fed lake that carries water all year.

Disposition of types.—Holotypic male form I CNCR 17317, allotypic female CNCR 17318, and morphotypic male form II CNCR 17319. Paratypic males form I (8) CNCR 2326.

Material examined.—All from Rincón de la Doncella Park, Ciudad Mendoza, 1400 m of altitude, Veracruz, México: 23 ♂ form I, 17 ♂ form II, 25 ♀ (CNCR 500), 18 May 1956, coll. A. Villalobos; 3 ♂ form I, II ♂ form II, 21 ♀ (CNCR 508), 1 ♂ form I (CNCR 17317), 1 ♀ (CNCR 17318), 1 ♂ form II (CNCR 17319), 28 Aug 1948, coll. A. Villalobos; 2 ♂ form I, 2 ♂ form II, 11 ♀, 20 juv. (CNCR 17021), 1 Nov 1995, colls. J. L. Villalobos, F. Alvarez, R. Robles, J. Calderón.

Etymology.—The specific epithet *citlaltepetl* is taken from "Citlaltepetl", in nahuatl "mountain of the star", or "Pico de Orizaba", the highest mountain in Mexico, from which the springs feeding Rincón de la Doncella originate. The name is treated as a noun in apposition.

Remarks.—*Procambarus* (*Austrocambarus*) *citlaltepetl*, new species, is morphologically similar to *P.* (*A.*) *mexicanus*. The new species can be separated from *P.* (*A.*) *mexicanus* through the following characters: branchiostegal spine absent; gonopod with mesial process blade-like, curved over lateral portion of apex; in cephalic view, lateral portion of gonopod thicker than mesial portion; preannular plate of annulus ventralis straight, undivided, perpendicular to longitudinal axis of body; annulus ventralis more rounded, mesial groove narrower and deeper, seminal receptacle opening shorter, postannular sclerite of annulus ventralis oval-shaped; and epistome with well defined fovea and an anterior excavation, anterior lobe triangular, cephalic lobe elongated.

The new species is also similar to *P.* (*A.*) *veracruzanus* Villalobos, 1954, *P.* (*A.*) *ruthveni* (Pearse, 1911), and *P.* (*A.*) *zapoapensis* Villalobos, 1954, in the general shape of the gonopod and annulus ventralis. However, marked differences exist in the carapace and chelipeds among these species.

Procambarus (*Austrocambarus*) *mexicanus*, as defined by Hobbs (1987), still represents a variety of closely related forms distributed over a distance of more than 185 km from Jalapa, Veracruz to Tuxtepec, Oaxaca, from the rim of the central plateau at an altitude of 1440 m to areas in the coastal plains near the Gulf of Mexico. A detailed study of the populations assigned to this species will probably result in the discovery of additional new species. Rojas (1998) described the high degree of morphological variation found among these populations.

Acknowledgments

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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A new species of freshwater crab of the genus *Strengeriana* Pretzmann, 1971, from Colombia (Crustacea: Decapoda: Pseudothelphusidae)

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Abstract.—A new species of the genus *Strengeriana* Pretzmann, 1971, is described. With the addition of the new species, this genus now includes 15 species, distributed in the Sierra Nevada de Santa Marta, and the Western, Central and Eastern Cordilleras of the Colombian Andes, at altitudes ranging from 700 to 1800 m above sea level. The species are distinguished by morphological characteristics of the first male gonopod.

The genus *Strengeriana* Pretzmann, 1971, comprises a group of small pseudothelphusid crabs that inhabit mountain streams. The discovery of a new species of *Strengeriana*, described herein, raises the number of species in the genus to 15, all of which are distributed in the Sierra Nevada de Santa Marta, and the Western, Central and Eastern Cordilleras of the Colombian Andes, at altitudes ranging from 700 to 1800 m above sea level. The systematics and biogeography of the genus were reviewed by Rodríguez & Campos (1989), Campos & Rodríguez (1993), and Campos (1995). The new species was discovered in the collections of Museo La Salle, Santa Fé de Bogotá, Colombia (MLS). The abbreviations cb and cl stand for carapace breadth and carapace length, respectively.

Family Pseudothelphusidae Rathbun, 1893
Tribe Strengerianini Rodríguez, 1982
Genus *Strengeriana* Pretzmann, 1971
Strengeriana casallasi new species
Figs. 1–3

Holotype.—Vereda San Jerónimo, Municipio Casabianca, Tolima Department, Colombia, 1500 m alt., 1 Jun 1997, leg. R. Casallas: 1 male cl 14.6 mm, cb 23.5 mm (MSL 278).

Paratypes.—Same locality data as holotype: 1 male, cl 13.0 mm, cb 19.7 mm (ICN-MHN-CR 1711), 2 males, cl 12.3, 11.8 mm, cb 18.5, 17.6 mm, 3 females, cl range 11.2–12.0 mm, cb range 17.4–18.0 mm (MLS 279).

Diagnosis.—First male gonopod short, stout; mesial lobe forming crest, with 2 spines adjacent to mesial process; mesial process wide, lanceolate, with 4 strong spines on mesial border, bearing 5 less prominent spines on lateral border, and 1 bifid spine distally; cephalic lobe bearing strong conical process, a subtriangular, almost rounded, process, directed latero-caudally; with proximal, cephalic acute spine fused to mesial process, but with free tip.

Description of holotype.—Carapace (Fig. 1a) with wide, deep cervical groove curving posteriorly and not reaching lateral margin. Anterolateral margin with deep depression behind anteroexternal orbital angle, followed by papillae, and second shallow depression at level of cervical groove; rest of margin with papillae. Postfrontal lobes small, oval, delimited anteriorly by transverse depression; median groove absent. Surface of carapace in front of postfrontal lobes flat, inclined anteriorly. Upper border of front convex in dorsal view, marked with

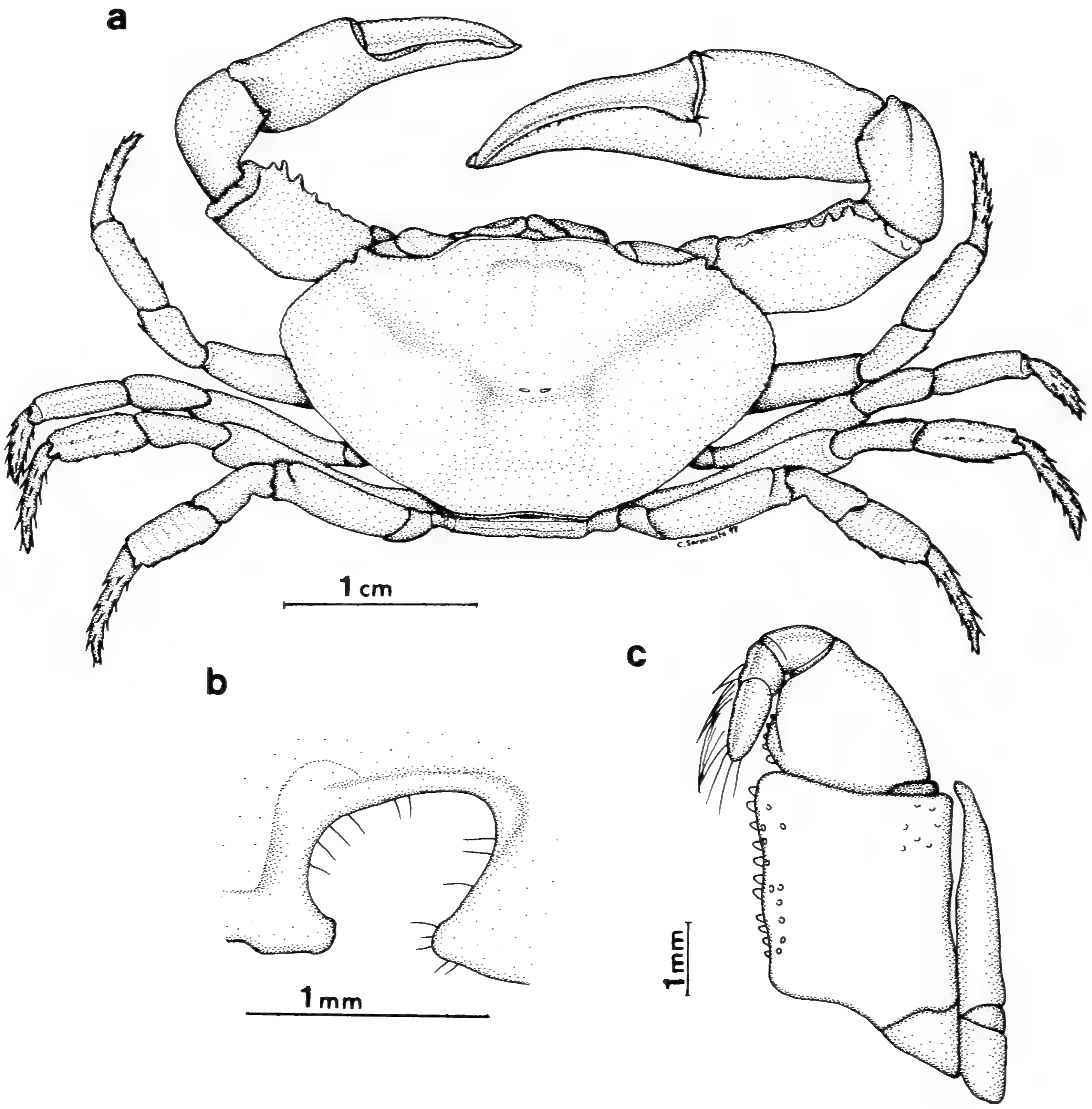

Fig. 1. *Strengeriana casallasi*, new species, holotype (MLS 278), a, dorsal view of carapace and pereiopods; b, aperture of efferent channel; c, left third maxilliped external view.

row of tubercles; lower margin visible in dorsal view, strongly sinuous in frontal view, and with tubercles. Surface of front between upper and lower borders high and vertical. Upper and lower orbital margins each with row of tubercles. Dorsal surface of carapace covered with small papillae; limits between regions well demarcated. Merus of endognath of third maxilliped regularly recurved, with shallow depression on distal part of external margin; exognath overreaching lateral margin of ischium of third maxilliped (Fig. 1c). Orifice of efferent branchial channel partially closed by spine at jugal angle and by extension of lateral lobe of epistome (Fig. 1b).

First pereiopods heterochelous, right cheliped larger than left. Merus with 3 crests: upper crest with rows of tubercles, internal lower crest with rows of teeth, and external lower crest with few tubercles. Carpus with blunt distal spine. Palms of both chelipeds smooth, swollen. Fingers of chelae gaping when closed, tips crossing, and with rows of tubercles (Fig. 1a) Walking legs (second to fifth pereiopods) slender, but not unusu-

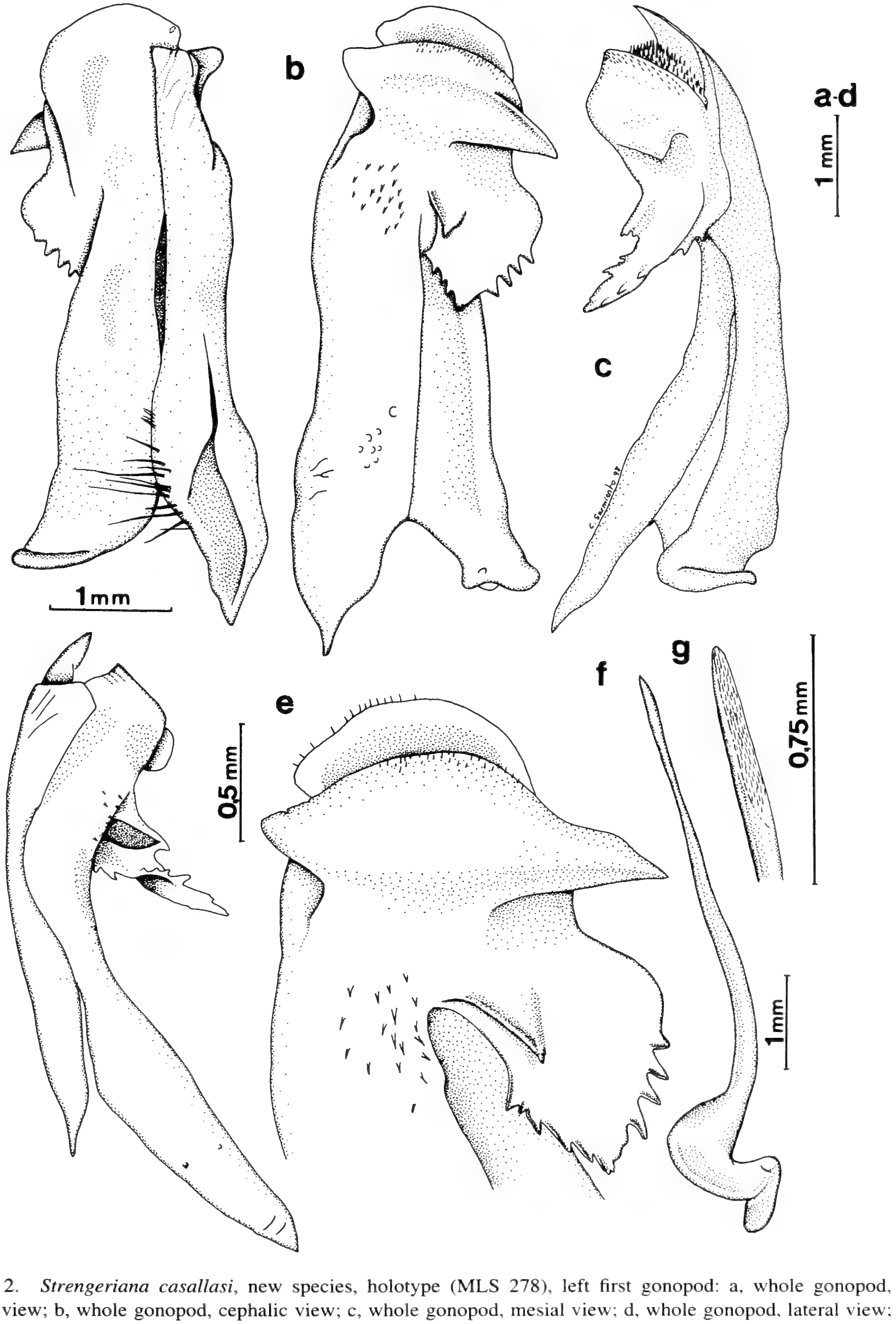

Fig. 2. *Strengeriana casallasi*, new species, holotype (MLS 278), left first gonopod: a, whole gonopod, caudal view; b, whole gonopod, cephalic view; c, whole gonopod, mesial view; d, whole gonopod, lateral view; e, apex, distal view. Left second gonopod: f, whole gonopod, caudal view; g, apex distal view.

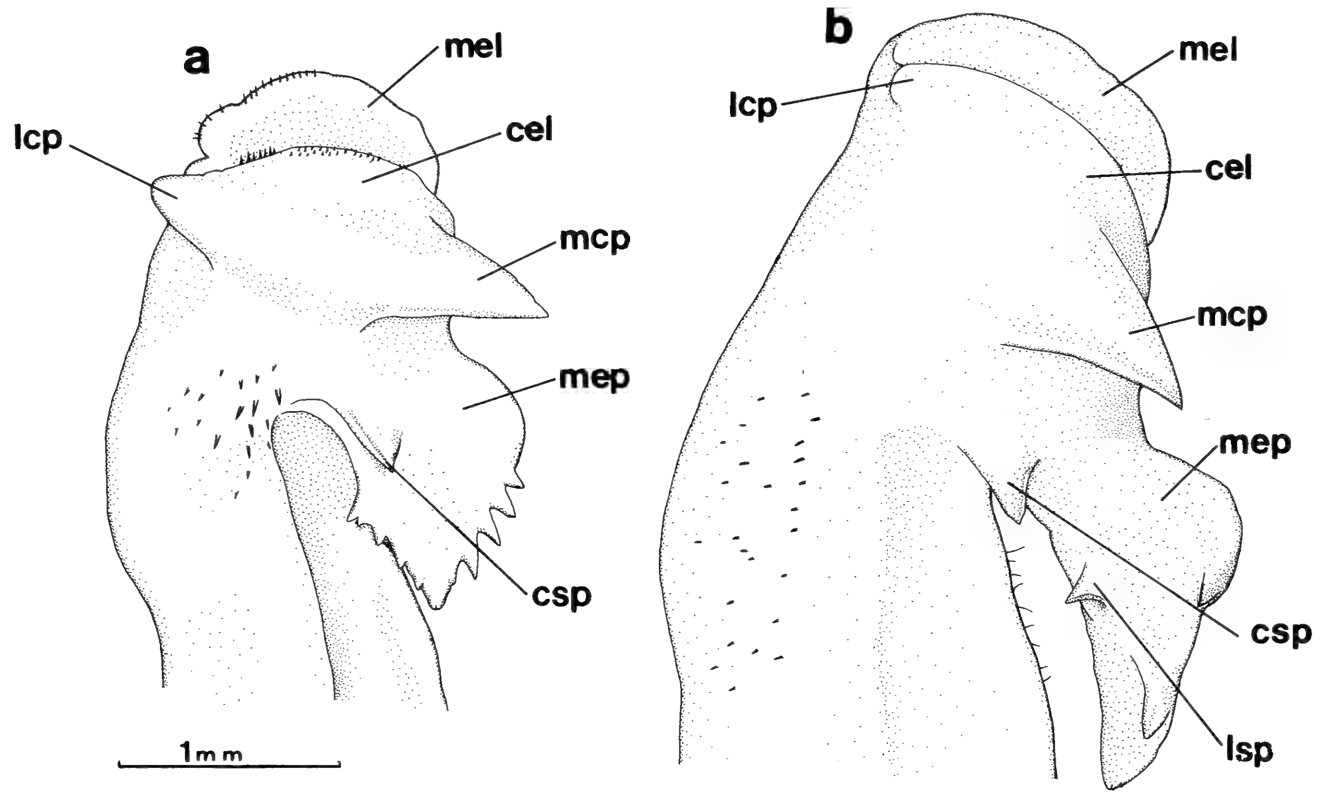

Fig. 3. *Strengeriana casallasi*, new species, holotype (MLS 278), left first gonopod: A, apex distal view; *Strengeriana maniformis* Campos and Rodríguez, 1993, holotype (ICN-MHN-CR 0938), left first gonopod: B, apex distal view. Abbreviations: cel, cephalic lobe; csp, cephalic spine; lcp, lateral-cephalic process; lsp, lateral spine; mcp, mesial-cephalic process; mel, mesial lobe; mep, mesial process.

ally elongated, those of second to fifth pereiopods each with 5 rows of large spines diminishing in size proximally, arrangement of spines on dactylus of left third pereiopod as follows: anterolateral and anteroventral rows with 5 spines plus 3 intercalated papillae, external row with 5 spines plus 2 proximal papillae, posteroventral and posterolateral rows with 4 spines.

First male gonopod short, stout; mesial lobe forming crest, with 2 spines adjacent to mesial process (Fig. 2c, d); mesial process wide, lanceolate, with 4 strong spines on mesial border, bearing 5 less prominent spines on lateral border, and 1 bifid spine distally (Fig. 2a, b, c, d, e); marginal lobe simple, with long ridge on lateral surface; mesial lobe forming long slit with cephalic lobe where spermatic channel is located; cephalic lobe bearing strong conical process, (Fig. 2a, b, c, e), a subtriangular, almost rounded process directed latero-caudally (Fig. 2a, b, e), and proximal cephalic acute spine fused to mesial process, but with free tip (Fig. 2b, c, d, e). Spermatic channel with rows of dark spines, and spinules on distal border of cephalic lobe. Caudal setae strong. Cephalic distal surface with rows of strong dark spines. Second male gonopod with spinules on distal portion, tip cup-shape (Fig. 2f, g).

Color (nomenclature after Smithe 1975).—Specimens preserved in alcohol are dark brown (near 223A, Mars Brown), with olive-brown specks on the dorsal side of carapace. The walking legs are paler brown (Verona Brown, 223B) dorsally, and reddish-brown (Tawny, 38) ventrally. The chelae are paler brown (Verona Brown, 223B) dorsally, and buffy-brown (Sayal Brown, 223C) ventrally. The ventral surface of the carapace is buffy-brown (Sayal Brown, 223C).

Etymology.—The species is named in honor of Hermano Roque Casallas, who collected the specimens.

Remarks.—This species is similar to *Strengeriana maniformis* Campos & Rodríguez, 1993. The two can be distinguished by features of the first male gonopod. The mesial process (Fig. 3a, mep) in *S. casallasi* is wide, lanceolate, with four strong spines on the mesial border, five less prominent spines on the lateral border, one bifid spine distally, and shows a torsion of 90° relative to *S. maniformis*. The mesial process (Fig. 3b, mep) in *S. maniformis* is longer, oblong, with a strong distal spine, followed proximally by a series of spines, diminishing in size, and a slender spine (Fig. 3b, 1sp) located near the middle of the lateral surface of the process (the last absent in *S. casallasi*). The cephalic lobe (Fig. 3a, cel) in *S. casallasi* shows a subtriangular, almost rounded process (Fig. 3a, 1cp) directed latero-caudally, and a proximal acute cephalic spine (Fig. 3a, csp) fused to the mesial process. In *S. maniformis*, the subtriangular process (Fig. 3b, 1cp) on the lateral side of the gonopod is vestigial, and the proximal cephalic spine (Fig. 3b, csp) is well separated from the mesial process.

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A new genus and species of South American fishes (Teleostei: Characidae: Cheirodontinae) with a derived caudal fin, including comments about inseminating cheirodontines

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Abstract.—*Acinocheirodon melanogramma* from tributaries of the rio São Francisco and the rio Jequitinhonha, Minas Gerais, Brazil, is described as a new genus and species of inseminating cheirodontines. The adult males are distinguished by possession of modified thirteenth to fifteenth, ventral caudal-fin rays bearing dorsally directed hooks surrounded by fleshy, possibly glandular, structures. These structures appear similar to, but are here hypothesized as convergent with some of the derived caudal glandular organs of certain glandulocaudine characids and the species of the incertae sedis characid genus *Brittanichthys*. Putative relationships of these taxa to the new genus are explored and rejected. The new species is referred to the Cheirodontinae on the basis of a cladistic diagnosis of this subfamily. Hypotheses of relationships with other inseminating cheirodontines bearing modified caudal fins are explored.

Resumo.—*Acinocheirodon melanogramma*, dos afluentes do rio São Francisco e rio Jequitinhonha, Minas Gerais, Brasil, é descrito como um novo gênero e nova espécie de Cheirodontinae com inseminação. Os machos adultos são caracterizados por possuirem o décimo terceiro ao décimo quinto raios da nadadeira caudal modificados, curvados ventralmente, portando ganchos e tecidos hipertrofiados semelhantes, mas consideradas convergentes com os órgãos caudais glandulares de certos Glandulocaudinae e de *Brittanichthys*, um gênero incertae sedis em Characidae. Relações hipotéticas entre estes táxons e o novo gênero são exploradas e rejeitadas. A nova espécie é referida a Cheirodontinae com base em uma nova diagnose cladistica da subfamília. São discutidas as hipóteses de relações com outros Cheirodontinae inseminados e portando nadadeiras caudais modificadas.

While searching for cheirodontine characids in the collections of the Museu Nacional de Rio de Janeiro, one of us (LRM) found seven specimens of an undescribed small characid species from the rio Jequitaí, rio São Francisco drainage, Minas Gerais, Brazil. Another specimen from the middle portion of the rio Jequitinhonha, Minas Gerais, Brazil was found (by SHW) in the Museu de Zoologia da Universidade de São Paulo while searching for glandulocaudine characids. The rio Jequitinhonha is independent of the rio São Francisco basin, but is an adjacent coastal plain river of eastern Brazil. Subsequent joint collections of Museu de Ciências e Tecnologia, Pontificia

Universidade Católica do Rio Grande do Sul, Porto Alegre, the Academy of Natural Sciences, Philadelphia, and the Universidade Federal de São Carlos, São Paulo resulted in additional specimens from both rivers.

Some of the caudal-fin structures of this species appear convergent with those of certain of the glandulocaudine characids, especially those of the tribe Corynopomini of eastern Brazil and the rio Paraguay basin. Also, males in the new genus bear decurved caudal-fin rays in the ventral caudal-fin lobe, suggesting some of the caudal-fin modifications present in the glandulocaudine tribe Glandulocaudini. Our collaboration regarding the description of the new species grew out of our respective and joint interests in the cheirodontine and glandulocaudine characids and the primary and secondary sexual features found in both groups such as their gonad modifications associated with insemination and their caudal-fin modifications associated with courtship.

The new species has hooks on some of the caudal-fin rays and hypertrophied caudal-skin tissue surrounding the hooks that may be glandular. The caudal-fin hooks in males of the new genus (Figs. 3–6) are derived compared to other inseminating cheirodontines that have caudal-fin hooks in that not only are they directed dorsoanteriorly, but the hooks are longer and more slender and are borne by thickened ray segments. Compare these hooks with those shown for "*Odontostilbe*" *mitoptera* (Fink & Weitzman, 1974:fig. 3). Note that Malabarba et al. in Malabarba (1998) included "*O.*" *mitoptera* in their new tribe Compsurini, but so far the genera of this group have not been fully analyzed cladistically and a meaningful generic assignment for this species is not available. We therefore use the most recent generic allocation from Malabarba (1998). Because the new genus and species is included in the cheirodontine tribe Compsurini by several synapomorphies at several nodes and is therefore excluded from the Glandulocaudinae as well as other characid groups bearing caudal-fin hooks, its caudal hooks may be considered derived independently from those excluded taxa. The posteriorly placed caudal-fin hooks of the new genus and species might suggest a relationship to the species in the characid genus *Brittanichthys* Géry, 1965b: 13, but this is rejected in more detail below.

Four synapomorphies were provided by Malabarba (1994, 1998), also briefly discussed by Weitzman & Malabarba (1999), to diagnose a monophyletic Cheirodontinae in a more restricted and rigorous sense than that defined by Eigenmann (1915) and discussed by Géry (1977). The new genus and species shares all four of these synapomorphies and we do not consider it to be closely related to the glandulocaudines, or to *Brittanichthys*.

After initiating our study of this new species, it was discovered that those cheirodontine characids bearing modified hypertrophied caudal tissue and/or hooks on some of the caudal-fin rays are inseminating (Burns et al. 1997) as are all glandulocaudines (Burns et al. 1995), and *Brittanichthys* (see Weitzman et al. 1994, Weitzman & Menezes 1998). However, Burns et al. (1998) found that the testis morphology and the fine structure of the sperm cell nuclei of the glandulocaudines are uniquely derived. Inseminating cheirodontines also have derived sperm nuclei, but these are differently modified from those of the glandulocaudines as well as those of certain other inseminating characids (Burns et al. 1998). This suggest a hypothesis of independent acquisition of insemination of cheirodontines and glandulocaudines, but the two subfamilies could be sister taxa, simply having their sperm cell bodies derived in different directions from an inseminating common ancestor. However, Malabarba (1988) offered evidence that the Compsurini which includes the new genus, is a sister group to a taxon derived from within the non-inseminating cheirodontine groups and therefore the tribe is not a sister taxon to the Glandulocaudinae or other inseminating characid groups. The possible relationships of the new genus to other inseminating cheirodontines are briefly explored below.

Methods

Our comments on the phylogeny of the Cheirodontinae and other characids are based on the concepts of phylogenetic systematics as reviewed and discussed by Wiley (1981). The term diagnostic character is used to designate one or a series of synapomorphies or autapomorphies that are characteristic of a particular taxon. The term distinguishing character is used for one or a series of characters that help to distinguish one taxon from others, but no phylogenetic information is implied; see also Weitzman et al. (1994:48). Distinguishing characters may or may not be apomorphic. No phylogenetic information is implied because the potential comparative derived nature of distinguishing characters are not analyzed. The two terms, diagnostic character(s) and distinguishing character(s), are so defined in order to differentiate phylogenetic (cladistic) treatments from those bearing no phylogenetic information.

Counts and measurements are the same as those described by Fink & Weitzman (1974:1–2) and Menezes & Weitzman (1990:382–383). For counts recorded in the descriptions of the new species, the holotype is listed separately and first. This is followed in parentheses by the range, mean ($\bar{X}$) and total number of specimens having that count. When the condition of the specimens were such that certain characters could be taken from only a few specimens and reasonable descriptive statistics were impossible, only the extremes and a statement of the modal count are given, but there will be no mode when all counts are the same. In the Table nearly all measurements other than standard length (SL) are expressed as a percentage of SL, except subunits of the head that are recorded as a percentage of the head length (HL). Vertebral counts include the Weberian apparatus. The terminal half centrum, hypural bones and associated vertebral elements, together usually designated as $PU_1 + U_1$, but not necessarily consisting only of those vertebral elements, were counted as one vertebra. Vertebral counts and usually fin-ray counts were taken from radiographs and from C&S (cleared and stained) preparations prepared according to Taylor & van Dyke (1985).

As in Menezes & Weitzman (1990:383), geographic entities (such as rivers) and place names (except those of countries) are in the language of the country of origin. Countries are in English because English names are available for these. The word rio (rio in Portuguese, río in Spanish) is not capitalized when referring to a river (thus, for example, río Baria in Venezuela and rio Itá in Brazil). However, rio would be capitalized when referring a place name such as a town or city. We do this in an attempt to avoid the transferal of English style and grammar onto foreign place names and geographical entities. Coordinates are used whenever possible, but are used only when we have confidence in their approximate accuracy.

The following acronyms are used for institutions and collections: FMNH, Field Museum of Natural History, Chicago; MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MNRJ, Museu Nacional do Rio de Janeiro, Rio de Janeiro; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; UFSCar, Universidade Federal de São Carlos, São Carlos; USNM, former United States National Museum, now the National Museum of Natural History, Smithsonian Institution, Washington D.C.

In addition to HL and SL the following abbreviations are used in the text or figures: C&S = alizarin red s and alcian blue stained specimens cleared with trypsin; spm(s) = specimen(s).

Acinocheirodon, new genus

Type species.—Acinocheirodon melanogramma, new species.

Diagnosis.—The penultimate and antepenultimate ventral procurrent caudal-fin rays of males have their tips ventrally expanded, forming a small keel in the ventral profile of the caudal fin (Figs. 1, 3–4). The cheirodontines *Serrapinnus piaba* (Lütken, 1874), *S. calliura* (Boulenger, 1900), *S. kriegi* (Schindler, 1937), and *S. notomelas* (Eigenmann, 1915) also bear three ventrally expanded posteriormost ventral procurrent caudal-fin rays, forming a small keel in the ventral profile of the caudal fin. Although the same procurrent rays are involved in the keels of those cheirodontine species referred to *Serrapinnus* Malabarba (1998), and *Acinocheirodon*, these differ in shape and involve different portions of the fin rays in the two genera. The four *Serrapinnus* species have an expansion along the posterior half of the ray rather than at the tip of the last three ventral procurrent caudal-fin rays and are more closely related to *Cheirodon* Girard (1855) with which they share several synapomorphies involving the anteriormost ventral procurrent caudal-fin rays, and specifically to *Spintherobolus* Eigenmann (1911) by sharing several synapomorphies associated with the anal fin of males, (Malabarba 1998, Weitzman & Malabarba, 1999).

The thirteenth, through the fifteenth principal caudal-fin rays of males are ventrally bowed, leaving wider spaces between principal caudal-fin rays twelve to fifteen than found between the other caudal-fin rays of this species (Figs. 1, 3–6).

The thirteenth and fourteenth principal caudal-fin rays of fully mature males bear thickened ventrally expanded segments.

The fourteenth principal caudal-fin ray of males has a dorsally extending flap along the proximal two thirds of its length. This does not overlap the thirteenth principal caudal-fin ray. The tissue between the fourteenth and fifteenth principal caudal-fin rays of males has a large dorsally extending flap that overlaps the fourteenth ray along almost its entire length. There is a ventral smaller skin flap along the posterior half of this structure that does not overlap the fifteenth principal caudal-fin ray ventrally (Figs. 3, 6). Hypertropied soft tissue surrounds the caudal-fin ray hooks and extends anteriorly in diminishing amounts along fin rays thirteen to fourteen to their bases (Figs. 3, 6). This tissue may be glandular, but this needs histological confirmation.

The presence of anal-fin hooks positioned along the posterolateral border of the anal-fin rays and directed to the anal-fin base; the anal fin not pigmented along its distal margin; the five cusped dentary teeth, with three central cusps larger and nearly equal in size (Fig. 7B); and the complete lateral line; were all found ambiguous regarding relationships, but also distinguished *Acinocheirodon* from the other members of the Compsurini in a global parsimony analysis (Malabarba 1998).

Etymology.—The first component of the name *Acinocheirodon* is from the Greek, *akaina* = thorn or spike and refers to the spines on the caudal-fin rays. The remainder of the word refers to the characid genus *Cheirodon* in reference to our referral of the new genus to the Cheirodontinae.

Acinocheirodon melanogramma, new species
Figs. 1–7

Note: This species and genus equals "undescribed genus and species B" in Burns et al. (1997) and "new genus and species B" in Malabarba (1998).

Type specimens.–Brazil, Minas Gerais, rio São Francisco drainage.

Holotype–MNRJ 16455, male, 31.8 mm SL, município de Bocaiúva, córrego Cachoeira, tributary to rio Jequitaí, km 413 of highway BR 135, approximately 17°28′S, 44°02′W (Reference map: WAC—Carta Aeronáutica Mundial 3190, Goiânia, 1976), 24–30 Sep 1990, D. F. Moraes Jr.

Fig. 1. *Acinocheirodon melanogramma*, new species, holotype, MNRJ 16455, male, 31.8 mm SL; Brazil, Minas Gerais, município Bocaiúva, córrego Cachoeira, tributary to rio Jequitai, rio São Francisco basin, 24–30 September 1990.

Paratypes—MNRJ 13435, 4 spms., 2 males, 27.4–28.0 mm SL, 1 female, 27.4 mm SL, 1 male C&S, 28.6 mm SL; MCP 18596, 1 male, 27.6 mm SL (listed as undescribed genus and species B in Burns et al. 1997); MCP 18598, 1 female, 26.3 mm SL (listed as undescribed genus and species B in Burns et al. 1997), all collected with

Fig. 2. *Acinocheirodon melanogramma*, new species, paratype, MNRJ 13435, female, 27.4 mm SL; Same locality data as in Fig. 1.

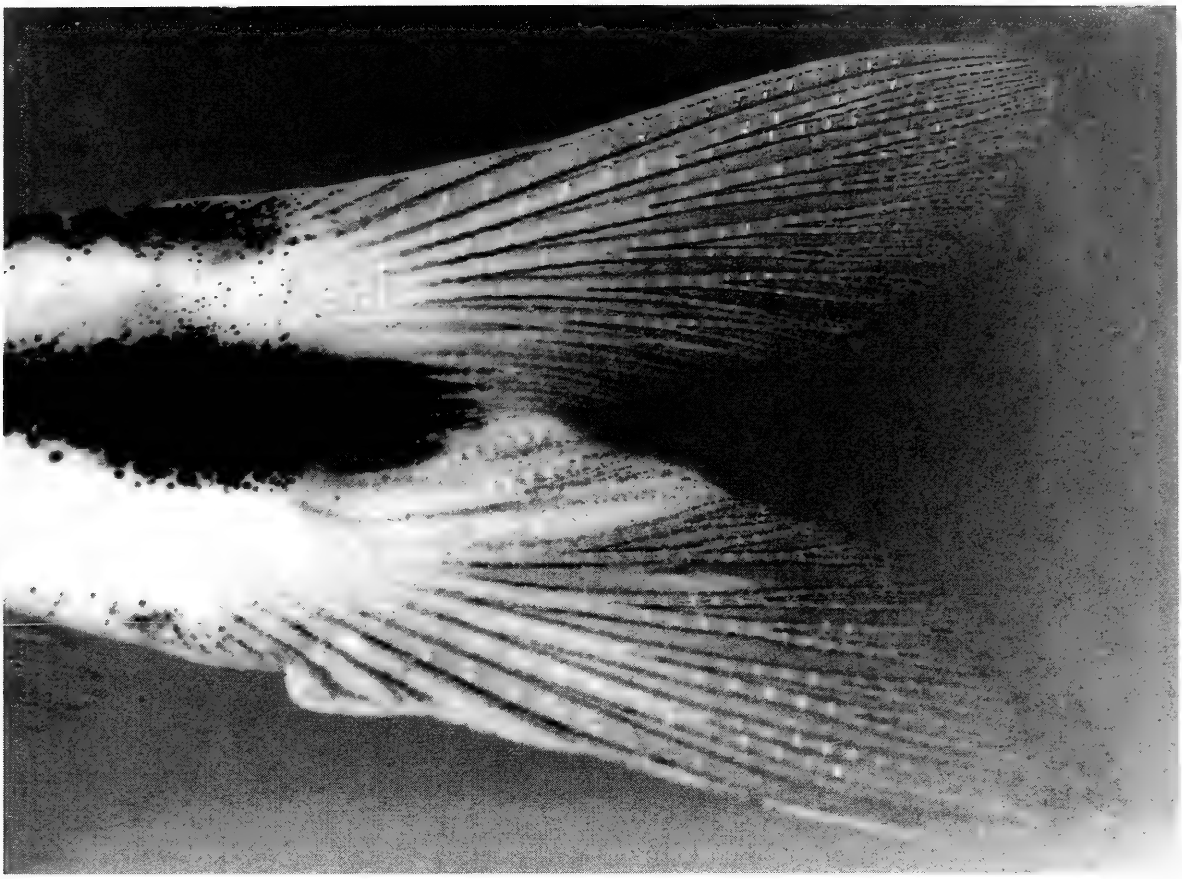

Fig. 3. *Acinocheirodon melanogramma*, new species, paratype, MNRJ 13435, male, 28.0 mm SL; same locality data as in Fig. 1. Caudal peduncle and fin (lateral view, left side, rays 13 and 14 bear fin hooks).

the holotype. MCP 16472, 6 spms, 2 males, 27.0–28.1 mm SL, 4 females, 26.2–30.0 mm SL; ANSP 176238, 7 spms, 3 males, 24.5–26.2 mm SL, 4 females, 21.9–25.6 mm SL, both lots collected from highway BR 153, S of Montes Claros, município de Bocaiúva, approximately 17°65′31″S, 43°49′48″W, 20 Jul 1993, R. E. Reis, S. A. Schaefer, J. P. Silva, & E. L. Pereira.

Non-type specimens from rio Jequitinhonha drainage:—MCP 19142, 16 spms, 9 males, 31.6–34.4 mm SL, 7 females, 29.1–37.3 mm SL; ANSP 173799, 16 spms, 14 males, 31.4–36.5 mm SL, 2 females, 29.6–31.4 mm SL, both lots from rio Jequitinhonha at São Pedro do Jequitinhonha, Itaobim, approximately 16°30′35″S, 41°20′02″W, 20 Jan 1995, R. E. Reis, W. G. Saul, S. Schaefer, & J. F. P. da Silva. MZUSP 5132, 1 spm., C&S, male, 34.4 mm SL, municipio de Medina, rio Jequitinhonha at Itaobim, approximately 16°33′S, 041°30′W (Reference map: WAC—Carta Aeronáutica Mundial 3189, Belo Horizonte, 1976), 25 Jun 1966, H. Britski and N. Menezes. USNM 318486, 59 spms, 4 young males, 23.3–29.7 mm SL, 55 juveniles and females, 17.3–24.9 mm SL, tributary of rio Jequitinhonha known as rio ribeirão, approximately 4–5 km ESE of município de Jordânic, about 15°54′S, 40°10′W, 12 Jul 1991, R. M. C. Castro & S. Jewett. MCP 18597, 2 spms, females, 30.5–37.7 mm SL (listed as undescribed genus and species B in Burns et al. 1997); MCP 19238, 8 spms, 4 males, 28.4–32.2 mm SL, 1 male, C&S, 33.3 mm SL, 3 females, 26.4–35.1 mm SL; MZUSP 52434, 8 spms, 4 males, 28.3–35.7 mm SL, 4 females, 29.9–30.6 mm SL, all three lots from rio Jequitinhonha below mouth of rio Araçuai, município de Itira, 10 Jan 1989, J. C. Garavello, A. S. Soares, A. I. Alves, & J. C. Soares.

Diagnosis.—The same as for the genus. All unambiguous characters listed in the diagnosis above are secondary sexual features

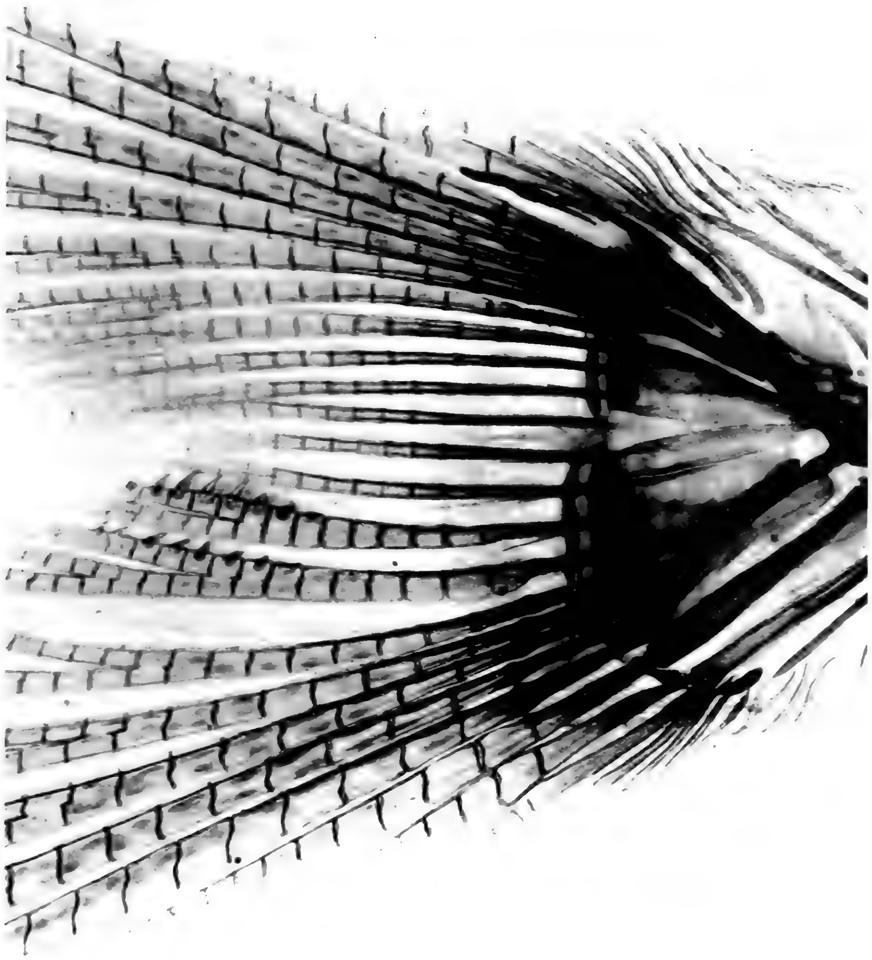

Fig. 4. *Acinocheirodon melanogramma*, new species, paratype, MNRJ 13435, cleared and stained male, 28.6 mm SL; same locality data as in Fig. 1. Caudal fin base, procurrent caudal-fin rays and hook-bearing portion of caudal fin.

that allow only the identification of males of *A. melanogramma* among cheirodontines.

Distinguishing characters.—The following distinguishing characters allow the recognition of both male and female specimens: A small, but distinctive black band occurs along the distal tip of the first unbranched dorsal-fin ray (Figs. 1–2) and distinguishes *A. melanogramma* from other cheirodontines, except *Macropsobrycon uruguayanae* Eigenmann (1915) and *Compsura heterura* Eigenmann (1915). The absence of modified caudal-fin scales and the presence of multicuspid instead of conical teeth, respectively distinguish *A. melanogramma* from *C. heterura* and *M. uruguayanae.*

Description.—Morphometrics given in Table 1. Body moderately elongate and compressed, greatest depth at dorsal-fin origin or somewhat anterior to this position if intestinal canal full of food or female gravid. Predorsal profile convex to snout tip. Profile of body from base of posterior dorsal-fin ray to adipose-fin origin straight or slightly convex, slightly concave posterior to adipose-fin origin. Ventral profile of body convex from tip of lower jaw to pelvic-fin origin and moderately concave to straight from there to anal-fin origin. Profile along male's anal-fin base somewhat convex in anterior half and slightly concave posteriorly. In female entire anal-fin base relatively straight. Dorsal and ventral profiles of caudal peduncle somewhat concave in both sexes. Caudal peduncle slightly longer than deep. Head small, snout short and rounded. Mouth terminal, maxilla short and positioned at an angle of approximately 45

Fig. 5. *Acinocheirodon melanogramma*, new species, paratype, MNRJ 13435, cleared and stained male, 28.6 mm SL; same locality data as in Fig. 1. Caudal-fin portion bearing hooks, right side, anterior is to right.

degrees relative to long axis of body. Posterior end of maxilla reaching a vertical passing through anterior border of iris.

Premaxilla (see Fig. 7A) with 6–7 large more or less symmetrical teeth bearing 3–5 cusps. Center cusp largest, producing an arched tooth profile. Three main cusps are always large. When more than three cusps present, lateral cusps very small. Small cusps usually absent on most medial tooth and on fifth or sixth large tooth posteriorly. Teeth of premaxilla somewhat compressed with teeth and all cusps in a single row. Premaxillary teeth not compressed as much as those of dentaries or maxillae. Maxilla with 2, rarely 1 or 3 teeth, each usually bearing 5 cusps. Lateral cusps, when present, always smaller than central ones. Maxillary teeth compressed, bearing 3 major more or less flattened conical cusps of approximately equal size; these form a single row on tooth's cutting edge. Dentary teeth 7–9 in a single row, each tooth with 5 cusps. Each tooth with 3 large central cusps: each of these compressed, in a single row and forming sharp cutting edge. One

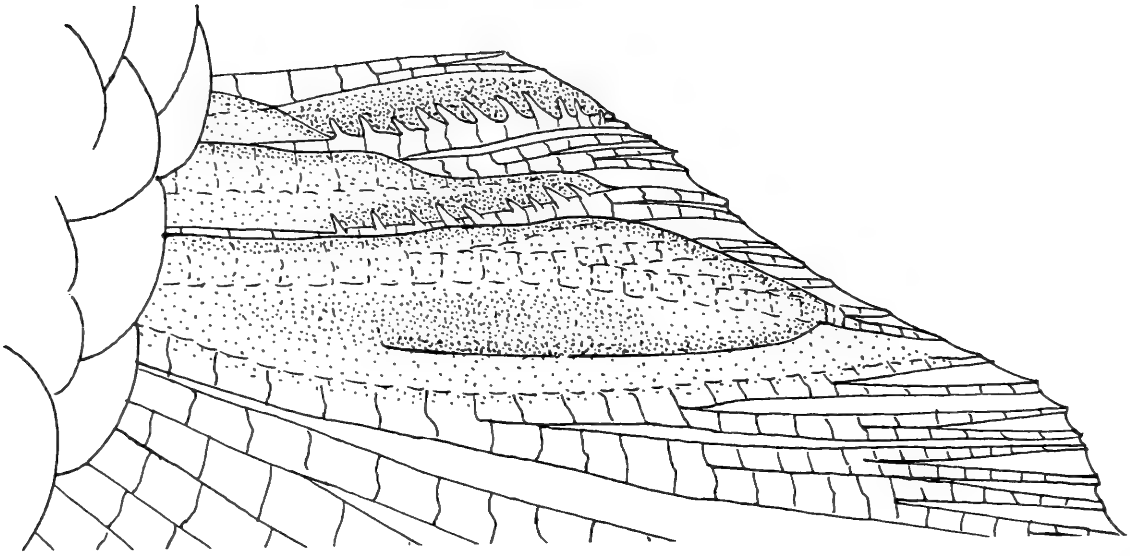

Fig. 6. *Acinocheirodon* cf. *melanogramma*, new species, MCP 19142, male, 34.2 mm SL, Brazil, Minas Gerais, Itaobim, rio Jequitinhonha at São Pedro do Jequitinhonha, 20 January 1995. Caudal-fin rays twelve (up) through fifteen (below), other lower caudal-fin rays partially drawn. Figure shows the distribution of the hypertrophied soft tissue (also present in some specimens from the rio São Francisco) surrounding the hooks and extended anteriorly in diminishing amounts along fin rays thirteen to fourteen to their bases (darkened areas); the large dorsally directed slightly recurved hooks dorsal to the thirteenth and fourteenth principal caudal-fin ray; and the large dorsally extending flap from the fourteenth and fifteenth principal caudal-fin rays of males.

very small cusp at base of larger lateral cusps on each side of each tooth. Median tooth largest and next 3–4 teeth gradually diminish in size, fifth or sixth tooth abruptly smaller and with only 3 cusps. Next posterior teeth much smaller, bearing 2 cusps and last tooth small, unicuspid and conical.

Dorsal-fin rays ii, 9 in all specimens ($n = 19$). First unbranched ray about half length of second. Dorsal-fin origin approximately at midlength of body. Adipose-fin origin a little anterior to posterior anal-fin insertion.

Anal-fin rays iv, 19 (iii–v, 16–19, $\bar{X} = 17.7$, $n = 19$; mostly 17–18; 1 specimen 16, and 3 specimen 19). Female anal fin with anterior 6–7 branched rays very long, forming prominent anterior lobe. Rays posterior to anterior lobe abruptly short. Distal border of anal fin concave and then straight posterior to anterior lobe. Distal border of male anal fin decreasing in length more gradually than in females so that lobe not as sharply distinct from remainder of fin as in females, but anterior anal-fin lobe of adult males proportionally longer than in females or juveniles. Anal-fin rays of males with small, elongate, retrorse hooks present on longest unbranched ray, and on first 7–13 (usually 8–10) branched rays. Hooks present only on posterior branches of rays and on distal parts of main ray, never on its proximal portion. One pair of bony hooks per ray segment, two pairs rarely occur on first branched ray and posterior unbranched ray-bearing hooks.

Pectoral-fin rays i, 10 (i, 10–12, = 10.8, $n = 20$). Distal ends of longest rays not extending to pelvic-fin origin. Pelvic-fin rays i, 7 ($n = 20$). Pelvic-fin origin anterior to a vertical passing through dorsal-fin origin. In females longest ray does not reach anal-fin origin; in males longest ray reaches just to anal-fin origin. Pelvic fins with unilateral, ventromedian antrorse bony hooks; unbranched and branched rays bearing 1, 2, or rarely 3 slender hooks per segment along most of their lengths. Number of segments bearing hooks varies among males, those males bearing more hooks appearing more mature.

Principal caudal-fin rays 10/9. Dorsal procurrent caudal-fin rays 13 (7–13, $\bar{X} = 10.1$, $n = 20$; 7 in one specimen). Ventral

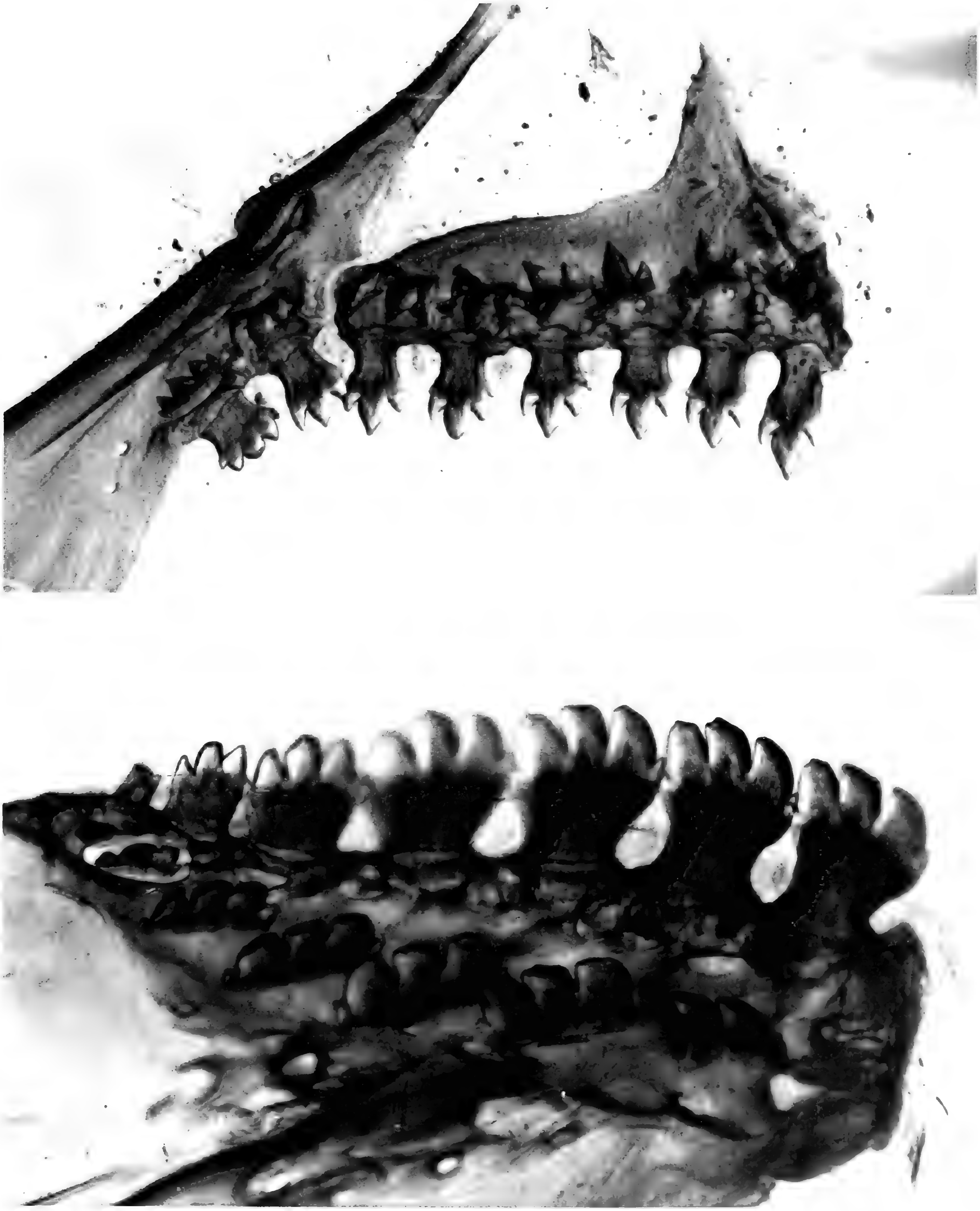

Fig. 7. *Acinocheirodon melanogramma*, new species, paratype, MNRJ 13435, cleared and stained male, 28.6 mm SL; same locality data as in Fig. 1. Jaws and teeth of right side. Anterior is to right. Top = maxilla and premaxilla. Bottom = mandible. Note: replacement teeth visible because bone is translucent.

procurrent caudal-fin rays 11 (7–11, $\bar{X}$ = 8.8, n = 20). Distal tip of penultimate and antepenultimate ventral procurrent caudal-fin rays of males ventrally expanded and forming small ventral keel seen in ventral profile of caudal fin; Figs. 1, 3–4. Other ventral procurrent caudal-fin rays not modified. Males with modified 13th through

Table 1.—Morphometrics of *Acinocheirodon melanogramma,* new species from the rio São Francisco basin and *Acinocheirodon* cf. *melanogramma* from the rio Jequitinhonha basin. Standard length is expressed in mm; measurements through head length are percentages of standard length; the last four entries are percentages of head length. All specimens are from Brazil, Minas Gerais. Described ranges for type specimens (rio São Francisco basin) include measurements of the holotype MNRJ 16455, male, and following paratypes: MCP 18596, 1 male, MCP 18598, 1 female, MNRJ 13435, 2 males and 1 female (measurements of one C&S specimen not taken), MCP 16472, 2 males and 4 females, ANSP 176238, 2 males and 3 females (two specimens not measured). Other specimens (not types—rio Jequitinhonha): ANSP 173799, 4 males and 1 female (11 specimens not measured), USNM 318486, 4 males (55 specimens not measured), MCP 19142, 4 males and 5 females (7 specimens not measured), MCP 19238, 3 males (5 specimens not measured), MZUSP 52434, 1 male (7 specimens not measured).

		TYPE specimens—rio São Francisco basin						NOT TYPES—rio Jequitinhonha basin					
		males			females			males			females		
Character	holo-type	*n*	low–high	$\bar{X}$	*n*	low–high	$\bar{X}$	*n*	low–high	$\bar{X}$	*n*	low–high	$\bar{X}$
Standard length (mm)	31.8	8	24.3–31.8	27.4	9	24.0–29.3	26.5	12	30.9–35.7	32.7	6	29.1–33.9	32.1
Snout to anal-fin origin	61.6	8	59.1–65.3	61.9	9	60.5–64.6	63.1	12	60.2–64.4	62.1	6	61.2–64.9	63.2
Snout to dorsal-fin origin	51.3	8	47.5–52.2	50.3	9	48.3–53.7	51.2	12	49.5–51.5	50.4	6	49.7–52.8	50.9
Snout to pelvic-fin origin	45.0	8	44.5–49.6	46.3	9	45.9–47.9	46.9	12	42.6–47.7	45.4	6	42.6–48.1	45.5
Dorsal-fin base length	12.3	8	11.7–13.7	12.9	9	12.4–14.2	13.0	12	10.9–14.1	12.9	6	12.2–13.3	12.9
Anal-fin base length	26.4	8	24.7–27.9	26.2	8	23.2–26.2	24.5	12	24.6–30.0	27.4	6	24.4–26.9	25.9
Caudal peduncle length	14.8	8	13.0–14.8	13.8	8	12.0–15.7	13.8	12	10.5–13.7	12.1	6	10.8–13.2	12.2
Caudal peduncle depth	11.9	8	10.6–12.0	11.4	9	9.8–11.3	10.8	12	11.6–13.4	12.4	6	11.3–12.1	11.7
Depth at dorsal-fin origin	27.0	8	25.7–31.3	28.2	9	26.6–29.6	28.4	12	26.4–29.6	27.9	6	26.7–29.1	28.1
Dorsal-fin height	26.1	7	25.0–28.5	26.4	7	23.1–25.7	24.5	12	23.7–27.8	25.9	6	24.5–26.7	26.0
Pelvic-fin length	18.6	8	16.7–18.6	17.7	9	15.4–17.5	16.7	12	17.1–20.0	18.5	6	15.8–18.2	17.4
Pectoral-fin length	20.8	8	20.3–21.7	20.8	7	18.6–21.4	20.0	10	18.6–21.6	20.4	6	20.0–22.5	20.9
Bony head length	25.2	8	25.0–27.6	26.1	9	24.7–27.8	26.1	12	23.5–25.3	24.6	6	23.0–25.3	24.3
Snout length	22.5	8	20.5–22.9	21.7	9	20.6–26.2	22.7	12	20.5–24.1	22.6	6	20.5–24.1	22.3
Upper jaw length	28.8	8	28.6–30.6	29.4	9	29.4–32.9	30.4	12	28.4–36.8	31.5	6	31.3–34.2	32.6
Horizontal eye diameter	33.8	8	31.3–34.3	32.6	9	30.0–35.3	32.7	12	32.1–36.8	33.4	6	33.3–35.6	34.7
Least interorbital width	31.3	8	28.6–31.3	29.7	9	26.8–30.8	29.3	12	28.0–32.1	30.0	6	29.5–31.6	30.4

15th principal caudal-fin rays curved, having dorsally concave profile; rays 13th and 14th thickened and bearing dorsally (on each side) 8 to 11 elongated and strong hooks in 1 row; Figs. 4–6. Young or immature males have 1 to 8 hooks on each of these rays; number of hooks increases according to size of specimen.

Scales cycloid. Lateral line usually not complete, with perforated scales 37 (31–37, $\bar{X} = 34.9$, $n = 4$; 31 in one specimen, other specimens 34–37), last one to three scales of this longitudinal row of scales not perforated. Total number of scales in lateral line row 37 (34–37, $\bar{X} = 36.5$, $n = 14$). Scale rows between dorsal-fin origin and lateral line 6 (5–6, $\bar{X} = 5.8$, $n = 18$), scale rows between lateral line and pelvic-fin origin 4 (3–4, $\bar{X} = 3.9$, $n = 18$). Predorsal scales 12 (11–13, $\bar{X} = 11.7$, $n = 18$), usually in 1 regular series. Scale rows around caudal peduncle 14. Males and females with a scale sheath on anal-fin base consisting of one row with 4 or 5 small scales covering bases of unbranched rays and first 4–5 branched rays.

Supraneurals 5 (4 or 5). Precaudal vertebrae, including Weberian apparatus, 17 (17–18, $\bar{X} = 17.1$, $n = 12$); caudal vertebrae, including posterior half centrum, 17 (17–19, $\bar{X} = 17.8$, $n = 12$); counts taken from x-ray negatives and one cleared and stained specimen.

Color in alcohol.—Both sexes with approximately same preserved color pattern; Figs. 1–2. Body pale brownish yellow in specimens preserved in formalin long enough to destroy guanine pigment. Lateral body stripe broad and black posteriorly, becoming pale and narrow anteriorly and disappearing anterior to dorsal-fin origin. Humeral spot absent. What appears to be a humeral spot in Figs. 1–2 is black interior wall of swim bladder seen through membranous tympanum plus a few extra dark chromatophores on borders of scales just anterior to tympanum. Dark body stripe continues broadly onto middle caudal-fin rays, but not extending to termination of these rays. Otherwise caudal fin white or pale brownish yellow. Exposed borders of scales delineated by dark chromatophores, especially on dorsal body surface where the pigment is darker. Midline of dorsal body surface from nape to caudal-fin origin very dark. All fins hyaline except dorsal fin with 1 small dark bar between first and second rays from about distal tip of first unbranched ray and to about midpoint of second unbranched ray; Figs. 1–2. Head black to gray dorsally, especially dark near nape. Sides of head and opercles silvery where guanine pigment not destroyed by formalin, sides of head otherwise whitish yellow. Some dark chromatophores surround nares and border of upper jaw bones. Lower jaw white, without dark pigment except at symphisis where few dark chromatophores border its contours.

Sexual dimorphism.—The females lack hooks in the pelvic, anal, and caudal fins, while the mature, sexually active males bear numerous hooks on these fins. Caudal-fin rays thirteen and fourteen (rarely fifteen) of males bearing hooks and hypertrophied tissue. Large dorsal skin flaps occur along the connective tissue between the fourteenth and fifteenth caudal-fin rays and along thirteenth caudal-fin ray. Females have dorsal skin flaps along the proximal length of fourteenth and fifteenth caudal-fin rays, but these are small and almost imperceptible. The penultimate and antepenultimate ventral procurrent caudal-fin rays of males are ventrally expanded forming a small ventral keel on the caudal fin. These keels are absent in females.

Distribution.—Known from the basin of the rio São Francisco in Minas Gerais, Brazil. A second population found in the basin of the rio Jequitinhonha, Minas Gerais, Brazil is tentatively assigned to *A. melanogramma* (see Remarks below).

Etymology.—The name *melanogramma* is from the Greek, *melas*, = black + *gramme* = line. The name refers to the distinctive black bar on the large anterior unbranched dorsal-fin ray.

Remarks.—Besides the type specimens from the rio São Francisco basin, on which we based the above description, we obtained additional lots of what appear to be *A. melanogramma* from four localities along the rio Jequitinhonha. Although these specimens have the same counts and most other characters as those from the rio São Francisco, mature males of the population samples from these two river systems can be differentiated by their caudal peduncle depth relative to caudal peduncle length. Figure 8 illustrates these differences. Specimens available from the rio São Francisco basin seem to be fully mature, even though they are of smaller size than the fully mature specimens from the rio Jequitinhonha, but the sample sizes are small. We suggest that the differences we found in caudal peduncle length versus its depth might possibly be due to small sample size of fully mature adult males and prefer to not assign a new name for the rio Jequitinhonha population until further comparative material is available. However, it seems best to refer to the rio Jequitinhonha population sample as *Acinocheirodon* cf. *melanogramma.* Other data from rio Jequitinhonha samples are: Anal-fin rays iii–v, 16–21, $\bar{X}$ = 18.4, n = 49; mostly 17–19; 1 specimen 16, 2 specimens 20, and 1 specimen 21. Pectoral-fin rays i, 9–11, $\bar{X}$ = 10.4, n = 33. Pelvic-fins i, 7–8, $\bar{X}$ = 7, n = 33; i, 8 in one specimen. Dorsal procurrent caudal-fin rays 8–13, $\bar{X}$ = 10.4, n = 46. Ventral procurrent caudal-fin rays 7–11, $\bar{X}$ = 9.6, n = 46. Lateral line with 34–36 perforated scales, $\bar{X}$ = 35.5, n = 13. Total number of scales in lateral line row 35–38, $\bar{X}$ = 36.8, n = 13. Scale rows between dorsal-fin origin and lateral line 5–6, $\bar{X}$ = 5.8, n = 16, scale rows between lateral line and pelvic-fin origin 3–4, $\bar{X}$ = 3.9, n = 16. Predorsal scales 11–13, $\bar{X}$ = 11.8, n = 16, usually in regular series. Scale rows around caudal peduncle 14. Supraneurals 4 or 5. Precaudal vertebrae, including Weberian apparatus, 16–18, $\bar{X}$ = 17, n = 66; caudal vertebrae, including posterior half centrum, 16–19, $\bar{X}$ = 17.5, n = 66); counts taken from x-ray negatives and two cleared and stained specimens. For body and head ratios expressed as percentages; see Table 1. One male (MCP 19238, 31.9 mm SL) unusual in that 15th principal caudal-fin ray has two hooks dorsally.

Discussion of possible relationships.—The new species is placed in the Cheirodontinae on the basis of a new diagnosis of this characid subfamily provided by Malabarba (1994, 1998) and briefly discussed in Weitzman & Malabarba (1999). The new species shares all four synapomorphies proposed to diagnose cheirodontines: Presence of a large, nearly triangular hiatus of muscles covering the anterior swimbladder between the first and second pleural ribs (pseudotympanum), 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; Humeral spot absent (Fig. 1–2); Teeth pedunculate, greatly expanded and compressed distally (Fig. 7); Only one tooth series present in the premaxilla (Fig. 7).

The new species also displays some, we suggest convergent, similarities with certain members of the characid subfamily Glandulocaudinae and the characid genus *Brittanichthys.* Burns et al. (1997) found that some cheirodontines are inseminating, as is the case for all examined glandulocaudines (Burns et al. 1995). We hypothesize, however, that the similarities of *A. melanogramma* to the species of *Brittanichthys* and glandulocaudines are homoplastic because *Brittanichtys* lacks the synapomorphies diagnosing the Cheirodontinae.

Mimagoniates microlepis (Steindachner, 1876) and *Mimagoniates rheocharis* Menezes & Weitzman (1990:389 fig. 5, and p. 401, fig. 24, p. 408 + pp. 419) also have hook-bearing, ventrally bowed caudal-fin rays. Menezes & Weitzman (1990) hypothesized a phylogeny of the glandulocaudine tribe Glandulocaudini that would exclude *A. melanogramma* from close relationship

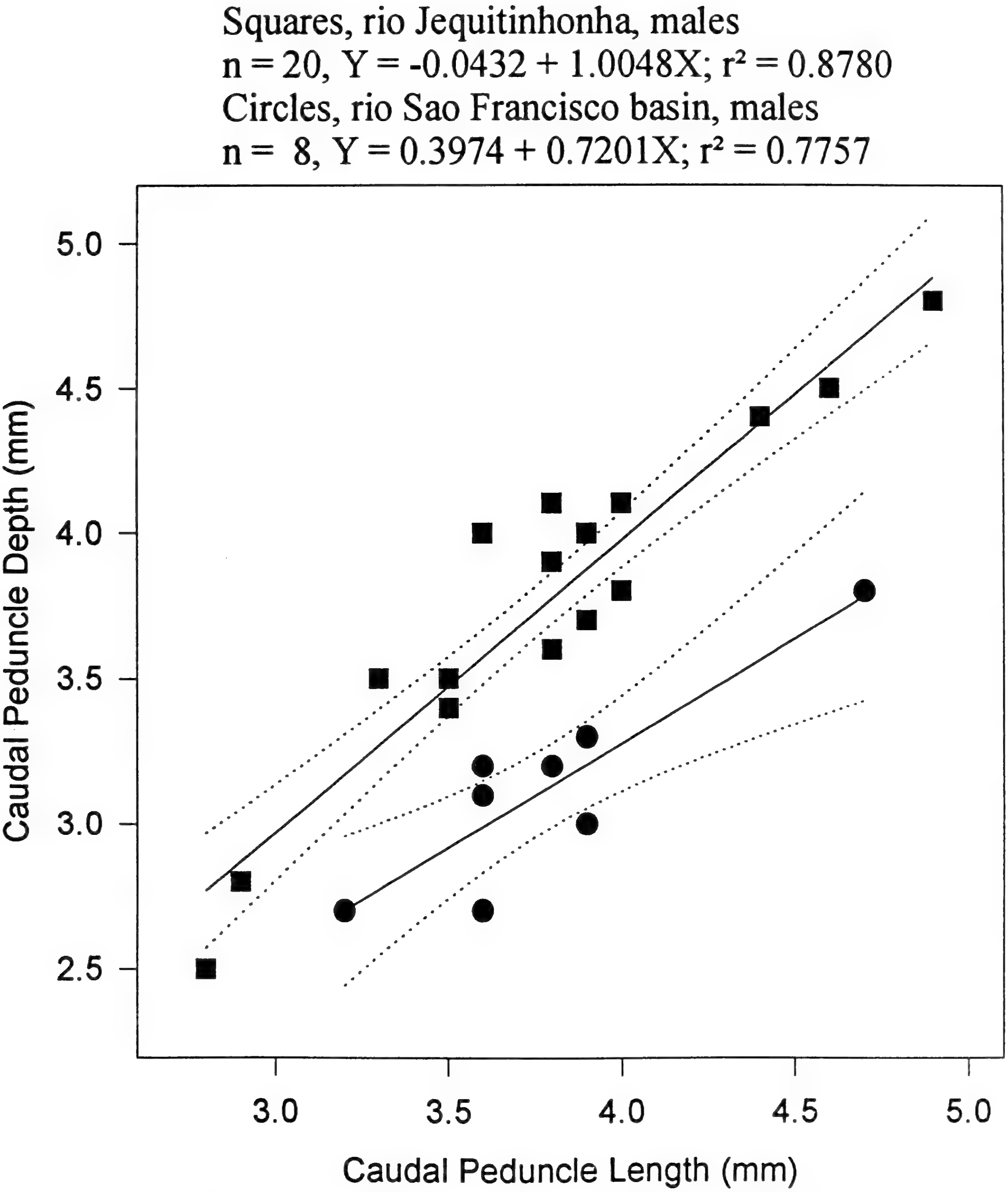

Fig. 8. Graph of caudal peduncle depth as a function of its length for *Acinocheirodon melanogramma* from rio São Francisco basin (circles) and of *Acinocheirodon* cf. *melanogramma* from the rio Jequitinhonha (squares). Note that the 95% confidence intervals do not overlap with the means of the compared population samples indicating a statistically significant difference. These differences are discussed in the text.

with the Glandulocaudini and especially with the derived glandulocaudin species, *M. microlepis* and *M. rheocharis*. *Acinocheirodon melanogramma* lacks a hypertrophied caudal scale or scales associated with glandular tissue at the base of the tail that is apparently present in all glandulocaudines except *Landonia latidens* Eigenmann

& Henn *in* Eigenmann et al. (1914). *Acinocheirodon melanogramma* also lacks the synapomorphies of the tribe Glandulocaudini and of the subfamily Glandulocaudinae (Weitzman & Menezes 1998). There are some soft structures associated with the base of the caudal fin in *A. melanogramma* that might be assumed to be an indication of glandulocaudine relationships. These are described as skin flaps and hypertrophied tissues between the thirteenth to fifteenth principal caudal-fin rays. *Acinocheirodon melanogramma* apparently acquired its derived caudal tissues independently of those of the glandulocaudines because it lacks most of the features diagnosing the Glandulocaudinae and has those diagnosing the Cheirodontinae of Malabarba (1994, 1998).

Acinocheirodon melanogramma, as well as certain other cheirodontines (see Burns et al. 1997), are inseminating characids as are glandulocaudines (Burns et al. 1995). We note, however, that glandulocaudines have a large area of the posterior testis modified for sperm storage, but this was not observed among examined inseminating cheirodontines, tribe Compsurini, including *Acinocheirodon*, see Malabarba (1998). This further suggests, among other characters respectively diagnosing the glandulocaudine tribes and the Cheirodontinae, that insemination arose independently within the Cheirodontinae and in the Glandulocaudinae.

The male specimens of *A. melanogramma* have ventrally bowed caudal-fin rays bearing dorsoposteriorly recurved hooks in the ventral caudal-fin lobe as do males of *Brittanichthys axelrodi* Géry (1965b:fig. 9–10). The question of a relationship among *A. melanogramma* and the species of *Brittanichthys* is as problematic as the suggestion of a relationship of *A. melanogramma* to members of the Glandulocaudinae. Unfortunately the relationships of *Brittanichthys* with other characids remain uncertain. *Brittanichthys* was referred to a subtribe, the Aphyoditeini, of his tribe Cheirodontidi by Géry (1965a:14, 18, 20–22) and to a tentative subgroup of the Cheirodontinae named the Aphyoditeina by Géry (1977:543) who spent a considerable effort in a precladistic attempt to discern the relationships of *Brittanichthys* based on certain of its anatomical resemblance's to other characid genera. Géry justifiably had many reservations about his results, but suggested that *Brittanichthys* might be related to *Leptobrycon* Eigenmann (1915) and *Thrissobrycon* Böhlke (1953). We do not argue with that opinion and suggest that the preliminary osteological evidence we have seen may confirm this, but, as Géry, we believe that the matter needs much further investigation. Géry (1977:591, 594) essentially did not alter his estimate of the relationships of *Brittanichthys*. Géry's Aphyoditeina has never been phylogenetically diagnosed but its included genera (*Paracheirodon* Géry (1960a), *Atopomesus* Myers (1927), *Oligobrycon* Eigenmann (1915), *Aphyocharacidium* Géry (1960b), *Oxybrycon* Géry (1964), *Axelrodia* Géry (1965a), *Prodontocharax* Eigenmann & Pearson in Pearson (1924), *Microschemobrycon* Eigenmann (1915), *Parecbasis* Eigenmann (1914), *Macropsobrycon* Eigenmann (1915), *Aphyodite* Eigenmann (1912), *Brittanichthys*, *Leptobrycon* and *Thrissobrycon*) were placed in the Cheirodontinae by Géry (1977:586–587, 590–591, 594–595) apparently because its species have a single row of premaxillary teeth. We note here that *Paracheirodon simulans* Géry (1963) is an exception and has two rows of premaxillary teeth; see Weitzman & Fink (1983). We cannot treat the putative Aphyoditeini or Aphyoditeina here except to note that only two of the genera (*Macropsobrycon* and *Prodontocharax*) placed in this subtribe by Géry were considered Cheirodontinae in the more restrictive sense of Malabarba (1994). See Malabarba (1998) for further comments on the Aphyoditeini and the Aphyoditeina and a historical review of the various treatments by Géry of the genera he ultimately included in his Cheirodontinae, Géry (1977).

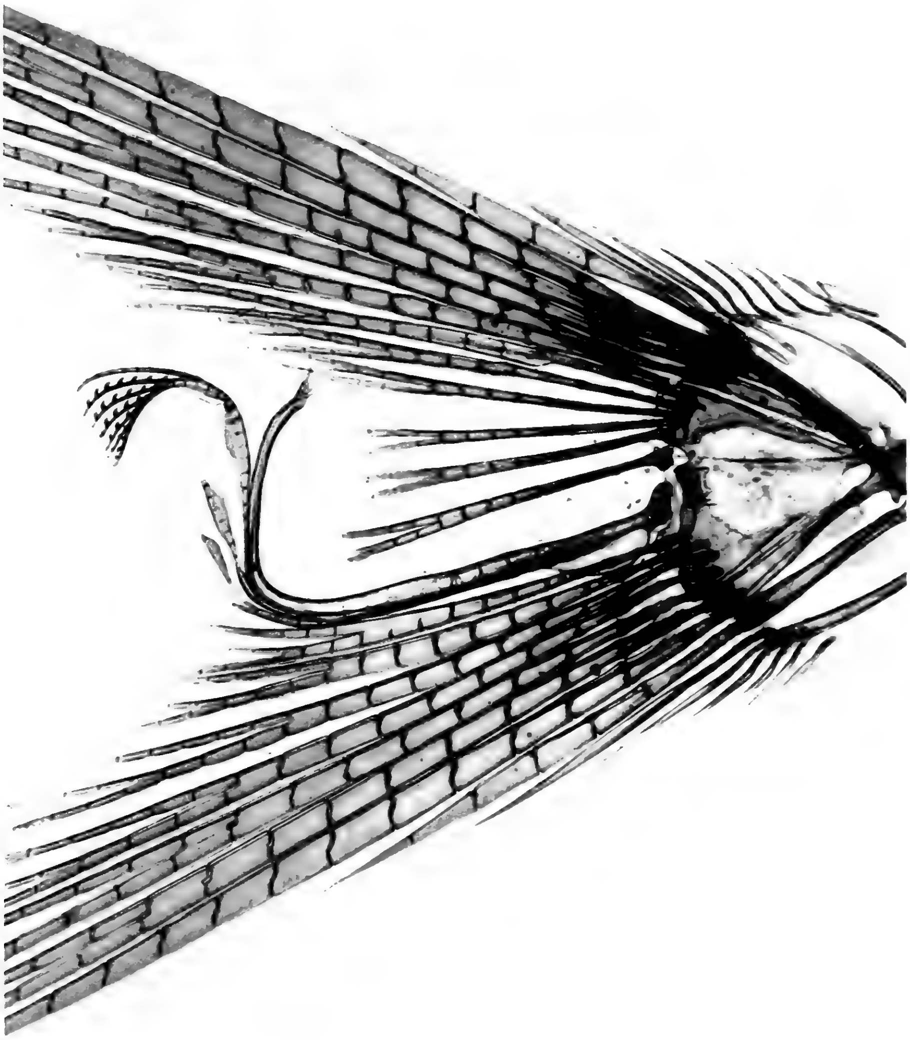

Fig. 9. *Brittanichthys axelrodi*, USNM 221992, cleared and stained male, 22.7 mm SL; Brazil, Amazonas, rio Negro, near mouth of rio Urubaxi. Caudal-fin base, procurrent caudal-fin rays and hook-bearing portion of caudal fin. Anterior to right.

Géry (1965:14) also considered the possibility that *Brittanichthys* might be a glandulocaudine. His opinion was that if it does belong among that group (which he suggested is polyphyletic) its relationships could be remotely with the Xenurobryconini. Weitzman & Fink (1985:13, 21) noted that although *Brittanichthys* shared fused hypurals and parhypural with the xenurobryconin glandulocaudines, its lack of both a caudal gland and the modified xenurobryconin arrangement of the caudal squamation excluded any relationship based on a cladistic analysis of the character distributions of the taxa they studied. According to Weitzman et al. (1994:53), however, the fact that *Brittanichthys* is an inseminating characin with a sperm storage area in the testis raises the question again. See also Weitzman & Menezes (1998).

Although *A. melanogramma* and *Brittanichthys axelrodi* share recurved hooks on the caudal fin and share curved ventral caudal-fin rays, these structures are derived in different ways in these two genera (compare Figs. 3–6 and 9–10). *Acinocheirodon melanogramma* has several soft caudal structures that are derived states apparently absent in *Brittanichthys*. The derived curved fin ray of *Brittanichthys* is the twelfth principal caudal-fin ray (Fig. 9–10) while in *A. melanogramma* it is the thir-

Fig. 10. *Brittanichthys axelrodi*, USNM 221992, cleared and stained male, 22.7 mm SL; same locality data as in Fig. 9. Hook-bearing portion of caudal fin, right side, anterior to right.

teenth through the fifteenth principal caudal-fin rays (Figs. 4–6). As noted in Weitzman & Fink (1985:13, 21) and Weitzman et al. (1994) the parhypural and hypural are fused in *Brittanichthys*. In our cleared and stained specimens of *Acinocheirodon* these bones are separate (one C&S specimen of *A. melanogramma* has them so closely placed that we can only distinguish the two isolated elements by pressing them with a needle where they are in contact). This removes a source of possible synapomorphic support for a relationship between these taxa. The fact that *A. melanogramma* has the cheirodontine synapomorphies and that these are absent in *Brittanichthys* corroborates a hypothesis that *A. melanogramma* is not closely related to *Brittanichthys axelrodi*.

Among cheirodontine genera, in the more restricted sense of Malabarba (1994), *A. melanogramma* (called "undescribed genus and species B"—MCP 18596, MCP 18597 and MCP 18598—by Burns et al. 1997 and "new genus and species B" by Malabarba, 1998), *Saccoderma melanostig-*

ma Schultz (1944), *Compsura heterura* Eigenmann, *Compsura gorgonae* (Evermann & Goldsborough, 1909), *Macropsobrycon uruguayanae*, some species currently referred to the polyphyletic "*Odontostilbe*," "*O.*" *dialeptura* (Fink & Weitzman, 1974) and "*O.*" *mitoptera*, and an undescribed species (called "undescribed genus and species A" by Burns et al., 1997 and "new genus and species A" by Malabarba, 1998) were found to be inseminating. Also, all these species have hypertrophied caudal tissues and/or hooks on the caudal-fin rays, suggesting they may represent a monophyletic group and were united in the cheirodontine subtribe Compsurini by Malabarba et al. in Malabarba (1998).

Homologies of the specialized structures and putative apomorphies in the caudal fin among inseminating cheirodontines, need further investigation. Each of the three genera listed above have apomorphies that allow their recognition as natural assemblages among the Cheirodontinae, but possible hypotheses of possible relationships among them and with *A. melanogramma* need phylogenetic study.

Acinocheirodon melanogramma has hooks in the ventral lobe caudal-fin rays as do certain other inseminating cheirodontines. *Acinocheirodon melanogramma* has large recurved hooks along the dorsolateral surface of the dorsal branches of caudal-fin rays 13–14, and rarely and less-developed hooks also on ray 15. Caudal-fin hooks are also present in *Saccoderma hastata* (Eigenmann, 1913) and are distributed on the thirteenth to eighteenth (usually the fourteenth to the seventeenth) principal caudal-fin rays. In "*Odontostilbe*" *dialeptura* caudal-fin hooks occur on the twelfth to sixteenth, and in *Macropsobrycon uruguayanae* from the twelfth to fourteenth caudal-fin rays (plus several spinelets along the proximal half of the caudal-fin rays 14 to 18). See Fink & Weitzman (1974:8, fig. 3 and 34, fig. 26) respectively for figures of the caudal fins of "*O.*" *dialeptura* and *S. hastata.* These two species have one hook for each ray segment except at the distal end of each ray where the hooks are small and there may be as many as three hooks per segment, especially in *S. hastata*. *Macropsobrycon uruguayanae* has one hook for each ray segment along the distal one-third of caudal-fin rays twelve to fourteen. The hooks on the caudal-fin rays of all these species are on the dorsolateral surfaces of the rays. In *Saccoderma hastata* and *O. dialeptura* the hooks occur on at least two of the branches of the larger rays (13–15). The hooks are not large and organized like those of *A. melanogramma* on thickened rays. Instead the rays of all examined cheirodontine species except *A. melanogramma* remain slender in their hook-bearing areas. Further, the hooks of the other inseminating cheirodontines are relatively small compared to the hooks on the anal fin of *A. melanogramma* whose caudal-fin hooks are considerably enlarged. Although the hooks are present on the ventral lobe of the caudal fin in all the species discussed, they do not all occur on the same caudal-fin rays and are of different shapes. Caudal-fin ray hooks may be informative regarding relationships among inseminating cheirodontines and deserve further investigation, but the presence of hooks in the lower lobe of the caudal fin itself as a synapomorphy uniting *A. melanogramma* to those other inseminating cheirodontines bearing hooks is not congruent with a cladogram (Malabarba 1998) of inseminating cheirodontines that results from other characters discussed below.

Species of *Saccoderma*, have an enlarged caudal-pouch scale in the ventral lobe of the caudal fin, mainly represented by the posterior ultimate scale of the scale row immediately ventral to the lateral-line scale row. This scale has a free posterior border and covers a pouch open to the surrounding water. While bearing hooks on the lower lobe of the caudal fin, neither *A. melanogramma* nor *Macropsobrycon uruguayanae* have modified caudal-fin scales, as described for *Saccoderma*. A pouch scale, not as well-developed as in species of *Saccod-*

erma, is also found in the lower caudal-fin lobe of *Compsura heterura*. This species bears no caudal-fin hooks, but is inseminating. *Compsura gorgonae* is like *Compsura heterura*, but has a less modified caudal scale. *Compsura heterura*, *Compsura gorgonae*, and *Saccoderma* species have the enlarged scale 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. This suggests that the derived caudal fin, its scales, and its ligaments are homologous among these cheirodontines. *Odontostilbe dialeptura* also has some enlarged scales on the ventral caudal-fin lobe, but these are not as developed as those found in the species of *Compsura* and *Saccoderma* and are attached to the fourteenth and nineteenth principal caudal-fin rays.

Males of *A. melanogramma* have a large dermal flap or fold that extends posteriorly from between the interradialis muscles. This flap originates between the fourteenth and fifteenth principal caudal-fin rays and mostly overlaps the fourteenth ray along almost its entire length (Fig. 6). This flap forms the ventrolateral wall of a shallow, elongate dorsally open pocket or trough that lies between the flap and the body of the fourteenth ray. There is a smaller ventral flap, along the posterior half of this structure that does not overlap the fifteenth principal caudal-fin ray ventrally. The fourteenth principal caudal-fin ray also has a dorsally directed skin flap along the proximal two-thirds of its length. This flap does not overlap the thirteenth principal caudal-fin ray. On the dorsal caudal-fin lobe there are two additional flaps. These are folded or directed ventrally. These flaps extend about half the proximal length of the sixth and seventh rays. Females also have dermal flaps extending ventrally from the sixth and seventh caudal-fin rays and dorsally from the fourteenth and fifteenth rays, but these are always smaller than that flaps described for the males. These flaps do not show in Fig. 2, being obscured by other caudal-fin tissues. These flaps are very similar in appearance to lateral ray skin flaps sometimes found on the dorsal, anal and also caudal-fin rays of fishes that live in fast water streams and fold their fins to reduce friction of the fin while swimming. Many characids, as for example *Brycon pesu* Müller and Troschel, have such flaps, although they are smaller in relative size than those of *A. melanogramma*. The large, derived flaps present in males of *Acinocheirodon* constitute one of the apomorphies of the genus (see the Diagnosis of *Acinocheirodon*). None of the other inseminating cheirodontines has derived skin flaps as described for *A. melanogramma*. Species of *Saccoderma* and *Compsura heterura* also have small, slightly circular skin flaps along the midlength of the dorsal border of the principal caudal-fin rays 16–19 and 15–19, respectively. These flaps occur near the opening of the caudal pouch medial to the enlarged pouch scale. These flaps are found on different caudal-fin rays than in *Acinocheirodon*, and have distinctly different shapes. They are putatively considered non homologous with the similar structures in *Acinocheirodon* because they occur on different rays.

In addition, *A. melanogramma* has hypertrophied soft tissue, especially around the hooks of the thirteenth and fourteenth fin rays (Fig. 3). This hypertrophied tissue extends anteriorly in continuously reduced amounts along these fin rays to their proximal ends and also occurs distributed along the fifteenth principal caudal-fin ray that has no hooks.

Weitzman & Fink (1985:96–99) rather extensively discussed caudal-fin structures and their possible function among glandulocaudines, and proposed that many of the modified structures of the male xenurobryconin caudal fin and the pouch scales of other glandulocaudines may serve as a pumping mechanism increasing the rate of dissemination of a pheromone or pheromones into the surrounding water from glandular tissue situated in and around the opening of the pouch or sac. Almost all glandulocaudines have a caudal pumping mechanism, but most have a "passive pump" in that there is no derived direct caudal muscle involvement. In the Xenurobryconini there is direct, derived muscle involvement, especially in *Xenurobrycon* Myers & Miranda-Ribeiro (1945), *Tyttocharax* Fowler (1913), and *Scopaeocharax* Weitzman & Fink (1985). Although considered non homologous structures with regard to those in glandulocaudines, the relatively large scale structure and flaps of the inseminating cheirodontines could have a similar function to that in the species of the glandulocaudines. This could be true for the various species of *Saccoderma* and for *C. heterura*, which have developed skin flaps near the opening of the caudal pouch scales. However, *A. 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, just ventral to and surrounding the hypertrophied soft tissue found around the hooks of the thirteenth and fourteenth fin rays. This tissue may be glandular in nature, but we have no histological preparations of it at this time. The courtship behavior of this species has not been observed, but we suggest that the large and specialized skin flaps of the caudal fin in *A. melanogramma* males may also be part of a mechanism for increasing the rate of pheromone dissemination in the surrounding water during courtship. Mechanisms for the dissemination of pheromones may be important for inseminating characids, both cheirodontines and glandulocaudines.

Caudal fin structures aside, tooth morphology suggests that *A. melanogramma* could be related to the genera *Aphyocheirodon* Eigenmann (1915) and *Cheirodontops* Schultz (1944). The teeth of *Acinocheirodon* usually have five cusps and are differentiated according to their distribution on the jaws (Fig. 7). The five-cuspid premaxillary teeth are symmetrical and elongate with the central cusp the largest. The anteromedial dentary teeth are the largest in the lower jaw and are usually five-cuspid. Each of the dentary teeth has the central three cusps largest and of equal size. The lateral cusps of each tooth are tiny and are situated more ventrally than the three medial cusps. The remaining more laterally-placed dentary teeth, are posteriorly graded and reduced in size, robustness, and cusp number with the most posterior tooth often unicuspid. These teeth are similar to those found in *Aphyocheirodon hemigrammus* Eigenmann (1915) and *Cheirodontops geayi* Schultz (1944), but similar teeth are also found in *Serrapinnus microdon* (Eigenmann, 1915), *Serrapinnus heterodon* (Eigenmann, 1915), and *Holoshesthes pequira* (Steindachner, 1882).

Serrapinnus microdon and *Serrapinnus heterodon* share several synapomorphies with *Cheirodon* and *Spintherobolus* as briefly discussed by Malabarba (1998). Species in these genera are not inseminating and thus are not considered as closely related to *Acinocheirodon melanogramma* or the other inseminating cheirodontines. See Malabarba (1998) for a more complete discussion. *Holoshesthes pequira* appears more closely related to *Odontostilbe fugitiva* Cope than to any other described Cheirodontinae (as hypothesized by Malabarba, 1994, 1998), and is also not inseminating (Burns et al. 1997).

Although tooth morphology suggests *Acinocheirodon* may be related to the genera *Aphyocheirodon* and *Cheirodontops*, insemination is unknown for both later genera. However, no mature specimens of these last two species were available for examination. We are not confident about a hypothesis of close relationship between *Acinocheirodon* and the genera *Aphyocheirodon* and *Cheirodontops* because tooth morphology is highly variable among other characids and also among cheirodontines. The specialized dentary teeth, with the three central cusps about equally developed and forming the cutting edge may have evolved several times in the Cheirodontinae, for example in *H. pequira*, *S. microdon* plus *S. heterodon*, *Acinocheirodon*, *Aphyocheirodon* and *Cheirodontops*, as supported by Malabarba's (1998) hypothesis of relationships among cheirodontines. Histological studies of gonads and morphological studies of the caudal fin of adult and mature specimens of both genera may provide new and better insights about the relationships of these cheirodontine genera.

Comparative material.—Brittanichthys axelrodi: USNM 221992, 1 C&S spm, male, 22.7 mm SL, Brazil, Amazonas, rio Negro, near mouth of rio Urubaxi, Amazonas, Brazil. *Compsura gorgonae*: MCP 11988, 3 C&S spms, MCP 11989, 7 spms, rio Caimito at Chorrera falls, in backwater above dam, Panama Prov., Panama. *Compsura heterura*: MZUSP 39177, 9 spms, ribeirão do Gado, tributary of rio São Francisco, Minas Gerais, Brazil. *Macropsobrycon uruguayanae*: MCP 11996, 2 C&S spms, arroio Dom Marcos, on the road BR 290, Rio Grande do Sul, Brazil and MCP 16169, 13 spms, Antioquia, Uraba, tributary of rio Guap, rio Leon drainage, Colombia. *Odontostilbe dialeptura*: MCP 11992, 5 C&S spms and MCP 11989, 15 spms, creek about 4 mi up Pese Road from junction with Chitre–Divisa Road, Herrera Province, Panamá. *Odontostilbe mitoptera*: MCP 14713, 2 C&S spms, rio Claro-Golfito road, just east of Bar Roded, Costa Rica. *Saccoderma hastata*: FMNH 56383 (holotype), Soplaviento, Colombia. *Saccoderma melanostigma*: USNM 228325, 7 specimens, Zulia, rio Yasa MCPO. Libertad, Estado Zulia, Venezuela. *Saccoderma robusta*: USNM 175308, 16 spms, Chibogado, Sinu Cordoba, Colombia.

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Psilotris amblyrhynchus, a new seven-spined goby (Teleostei: Gobiidae) from Belize, with notes on settlement-stage larvae

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Abstract.—*Psilotris amblyrhynchus* is described from one adult and one juvenile collected in shallow waters in the vicinity of Carrie Bow Cay, Belize, Central America. Settlement-stage larvae of the new species were collected in a stationary plankton net and are used to augment the description; two of these were reared through metamorphosis. *Psilotris amblyrhynchus* is distinguished from other western Atlantic seven-spined gobies on the basis of meristic features and pigment pattern. *Psilotris* is one of 15 genera assigned by Birdsong et al. (1988) to the "*Gobiosoma* group," but the genus is not defined on the basis of derived characters. Assignment of the new species to *Psilotris* is based on its having separate pelvic fins, seven spines in the first dorsal fin, no scales, and no head pores. None of these characters by itself is unique within the *Gobiosoma* group to *Psilotris*, and the configuration of the pelvic fins is highly variable among gobies. Our inability to diagnose *Psilotris* cladistically, along with our discovery of resemblances between larvae of *Psilotris amblyrhynchus* and those of another western Atlantic member of the *Gobiosoma* group, *Nes longus*, suggest that generic concepts within the *Gobiosoma* group should be reassessed.

The gobiid genus *Psilotris* is distinguished from all other western Atlantic genera by the following combination of characters: seven spines in the first dorsal fin; pelvic fins separate; scales absent; head pores absent. These characters, while of questionable phylogenetic significance, conveniently characterize the included species. Five species are currently recognized: the type species, *Psilotris alepis* Ginsburg, 1953; *P. batrachodes* Böhlke, 1963; *P. celsus* Böhlke, 1963; *P. kaufmani* Greenfield et al., 1993; and *P. boehlkei* Greenfield, 1993. They are distinguished from one another by color pattern, fin-ray counts (Table 2), and a few proportional measurements. The specimens described here possess the four distinguishing features of *Psilotris*, but they cannot be assigned to any of the five recognized species.

Methods

Counts and measurements follow Hubbs & Lagler (1958). Institutional abbreviations follow Leviton et al. (1985). The dorsal-fin formula was proposed by Birdsong et al. (1988) to describe the relationship between the dorsal-fin pterygiophores and the neural interspaces of the vertebral column. The first digit represents the neural interspace into which the anteriormost pterygiophore inserts. The digits following the hyphen denote the number of pterygiophores that insert into each subsequent interspace. The holotype was x-rayed to obtain vertebral

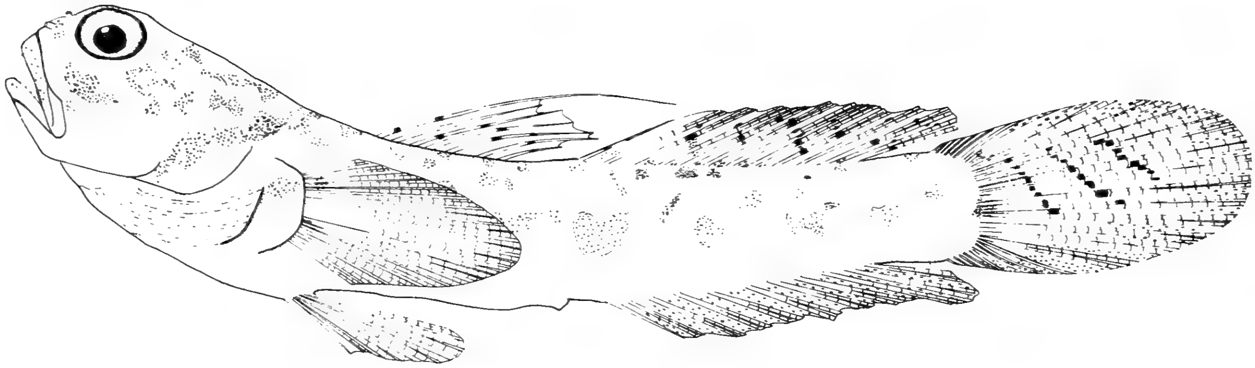

Fig. 1. *Psilotris amblyrhynchus*, holotype, USNM 321019, 34.0 mm SL.

and fin-ray counts. For larvae, these counts were obtained by clearing several specimens in trypsin and counterstaining them with alizarin red and alcian blue. Adult and juvenile specimens of the new species were collected with rotenone or quinaldine. Larvae were collected in a 1.0 by 0.5-m rectangular plankton net with 505 μm mesh, fished passively over the reef flat by suspending it from a pier on the seaward side of Carrie Bow Cay, Belize. Selected captured larvae were anesthetized with MS-222, examined under a dissecting microscope, then reared in small, nylon-mesh breeder traps set in a raceway in a flow-through seawater system. Reared larvae were fed cultured brine shrimp.

Psilotris amblyrhynchus new species
Figs. 1, 2, 3A, B

Holotype.—USNM 321019 (34.0 mm SL), Belize, western Caribbean, between Carrie Bow Cay and Twin Cays, lagoon—"shot hole," 15–20 ft (4.6–6.1 m), 17 Sep 1990, G. D. Johnson, et al.

Other specimens.—USNM 347250 (1, 14.2), Caribbean, Belize, shallow spur and groove just east of Carrie Bow Cay, ca. 20 ft (6.1 m), 9 Sep 1997, C. C. Baldwin and D. G. Smith. Larvae: all collected in a stationary plankton net on seaward side of Carrie Bow Cay, Belize; USNM 350086 (1, 11.5), 10 Jun 1993, 2130 hr; USNM 350087 (2, 11.5), 13 Jun 1193, 2130 hr, cleared and stained; USNM 350088 (1, 13.0), 14 Jun 1993, 2330 hr; USNM 350089 (1, 12.5), 20 Jun 1993, 2100–2330 hr; USNM 350090 (1, 11.5), 20 Jun 1993, 2130 hr; USNM 350091 (1, 11.0), 21 Jun 1993, 2300 hr; USNM 350092 (1, 14.0), 19–22 Jun 1993, reared; USNM 350093 (1, 16.8), 28 Jul 1994, reared; USNM 350094 (2, 10.5–11.5), 8 Aug 1994, cleared and stained.

Comparative material.—Larvae of *Nes longus*, all collected in a stationary plankton net on seaward side of Carrie Bow Cay, Belize: USNM 350189 (1, 11.0), 23 Jul 1992, 2230–2300 hr; USNM 350190 (2, 10.0), 27 Jul 1992, 2000–2030 hr; USNM 350191 (1, 11.0), 27 Jul 1992, 2230n2300 hr; USNM 350192 (3, 9.5), 16 Jun 1993,

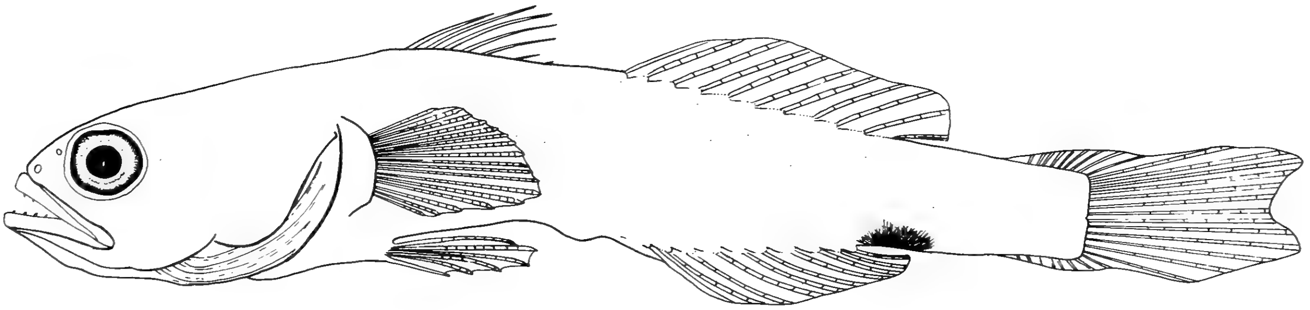

Fig. 2. *Psilotris amblyrhynchus*, larva, USNM 350088, 13.0 mm SL.

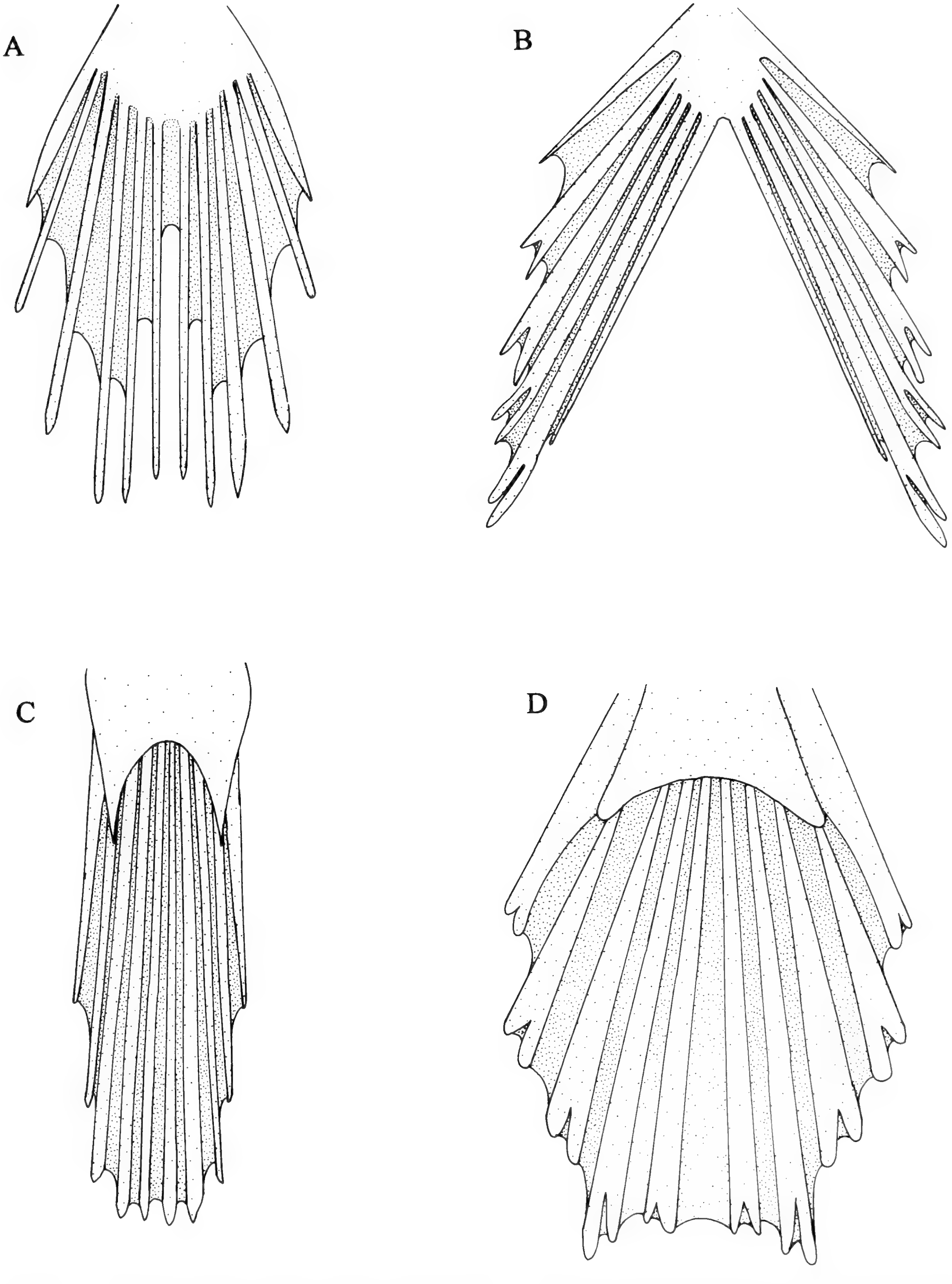

Fig. 3. Pelvic fins: development from larva to juvenile. A. *Psilotris amblyrhynchus*, USNM 350088, larva, 13.0 mm SL. B. *Psilotris amblyrhynchus*, USNM 347250, juvenile, 14.2 mm SL. C. *Nes longus*, USNM 350194, larva, 10.5 mm SL. D. *Nes longus*, USNM 350197, reared juvenile, 16.5 mm SL.

2030 hr; USNM 350193 (4, 9.0–11.0), 20 Jun 1993, 2000–2030 hr, three specimens cleared and stained; USNM 350194 (1, 10.5), 2 Sep 1996; USNM 350195 (1, 10.5), 5 Sep 1996; USNM 350196 (7, 9.5–17.0), 28 Jul 1994, reared; USNM 350197 (5, 15.0–19.3), Sep 1997, reared; USNM 350198 (1, 9.5), 12 Jun 1993, 2100 hr, cleared and stained. *Psilotris alepis*: USNM 123231 (holotype, 13 mm SL), St. Croix, Virgin Islands, 8 Apr 1937. *Psilotris batrachodes*: USNM 274946 (1, 13.0), Carrie Bow Cay, Belize, depth 12–25 ft (6–8 m), 10 Jun 1981; USNM 317025 (1, 17.8), Caribbean, Tobago, Sisters Rocks, depth to 60 ft (18 m), 14 Sep 1990; USNM 317026 (3, 7.0–8.5), Caribbean, Tobago, windward side of Little Tobago Is., depth 60 ft (18 m), 7 Sep 1990; USNM 317480 (1, 15.5), patch reef south of Carrie Bow Cay, Belize, depth 20–30 ft (6–9 m), 26 Mar 1987. *Psilotris boehlkei*: ANSP 124619 (3 paratypes, 17.5–18.2), St. Barthelmy, West Indies, Port de Gustavia, off rocky cliffs just S. of Anse Galet, depth 60–65 ft (10.3–19.8 m), 14 Jul 1965. *Psilotris celsus*: ANSP 133274 (4, 20.0–26.0), Bermuda, between Sinky and Cross Bays, off Sonesta Beach, 9.1–10.6 m, 30 Jul 1975. *Psilotris kaufmani*: ANSP 131712 (2 paratypes, 15.0–16.5), Jamaica, Discovery Bay, depth 130 ft (40 m), 16 Jun 1974. *Gobulus myersi*: USNM 347348 (3, 22–25), Belize, Pelican Cays, Manatee Cay, depth 1–3 ft (0.3–1 m), 19 Oct 1997).

Diagnosis.—A species of *Psilotris*, as currently construed, with 11–12 elements in the second dorsal fin; 9–11 anal-fin rays; pale ground color with a series of dusky blotches on side of body; small, distinct, dark spots on dorsal-fin rays; three narrow, oblique bars on caudal fin; first dorsal spine elongate in adults.

Description of holotype (Fig. 1).—A moderately elongate goby without scales or head pores. Snout short and blunt, anterior profile of head steep, no rostral frenum. Eye large, its diameter greater than snout length; interorbital space very narrow. Both nostrils tubular, the anterior one longer. Posterior end of jaw below posterior half of eye. Teeth slender, conical, slightly recurved, widely spaced, uniserial. Gill opening restricted, not extending past base of pectoral fin. Second dorsal and anal fins relatively long, the base of each longer than caudal peduncle. Anteriormost spine of first dorsal fin greatly elongate, reaching middle of base of second dorsal fin when appressed. Caudal fin elliptical, middle rays much longer than those above and below. Pelvic fins almost completely separate, only a small basal membrane connecting the inner rays of the two sides (Fig. 3B).

Measurements in mm, with proportions in parentheses: SL 34.0, preanal length 19.7 (58% SL), head length 10.0 (29% SL), snout length 2.2 (22% head length), eye diameter 2.5 (25% head length), interorbital width 0.3 (3% SL), upper-jaw length 4.8 (48% head length), depth at dorsal-fin origin 5.1 (15% SL), depth at anus 4.5 (13% SL), least depth of caudal peduncle 3.5 (10% SL), length of base of second dorsal fin 8.6 (15% SL), posterior end of dorsal fin to origin of caudal fin 3.4% 10% SL, base of anal fin 6.7 (20% SL), pectoral-fin length 8.6 (25% SL), caudal-fin length 9.7 (29% SL), pelvic-fin length 5.8 (17% SL). Meristic features: dorsal-fin rays VII+12, anal-fin rays 11, pectoral-fin rays 17, branchiostegal rays 5, vertebrae 11 + 16 = 27, dorsal-fin formula 3-221110.

Color in alcohol: Ground color pale yellowish brown, with dusky markings as follows: diffuse dark spot on cheek below eye; dark oblique streak from just behind opercle to dorsum directly above pectoral base and before dorsal origin; a diffuse spot on pectoral base; approximately 16 diffuse dark saddles, irregular and uneven in intensity, from nape to base of caudal fin; approximately seven diffuse midlateral blotches on body between pectoral fin and base of caudal fin, with smaller blotches in between; discrete, small, dark spots on dorsal-fin spines and rays; three oblique dark bars on caudal fin, oriented anterodorsal to posteroventral.

Table 1.—Meristic characters for specimens of *Psilotris amblyrhynchus*. ^{c} = cleared and stained. ^{x} = x-rayed.

USNM	SL in mm	Dorsal rays	Anal rays	Pectoral rays	Vertebrae
321019^x	34.0	VII + 12	11	17	11 + 16 = 27
347250	14.2	VII + 11	10	—	—
350092	14.0	VII + 11	9	17	—
350093	16.8	VII + 11	10	—	—
350087^c	11.5	VII + 12	11	19	11 + 16 = 27
350087^c	11.5	VII + 12	11	19	11 + 16 = 27
350094^c	11.0	VII + 11[1]	11	18	11 + 16 = 27
350094^c	11.5	VII + 12	10	18	11 + 16 = 27

[1] Eleven rays but 12 pterygiophores.

Other specimens.—Only one adult specimen, the holotype, is known, and the description is based on it. We have also collected 12 immature specimens, including a small, field-caught juvenile and 11 larvae, two of which were reared through transformation. None of these specimens has the full complement of adult characters, and we therefore do not designate them as paratypes. Nevertheless, they do provide additional meristic data that help characterize the species. Four of the larvae were cleared and stained, and their counts are presented in Table 1, along with counts from the field-caught juvenile and the two transformed larvae. Of the eight specimens for which counts are available, all have seven spines in the first dorsal fin. Four specimens have 12 elements in the second dorsal fin, and four have 11. In one of the latter, however, the penultimate pterygiophore does not support a ray; the specimen thus has 12 pterygiophores but only 11 rays. Fin rays can be difficult to count in small specimens, especially when the fin is depressed, as it is in most of the specimens. The only way to obtain unambiguous counts is to x-ray the specimen (if it is large enough) or to clear and stain it. Of the five specimens subjected to one of these techniques, four have 12 second-dorsal elements, and the fifth has 11 rays but 12 pterygiophores. Four of these five also have 11 anal-fin rays. The three specimens that were simply counted by gross examination have 11 second dorsal-fin elements and 9–10 anal rays. The pectoral-ray counts obtained were also higher in the cleared and stained specimens (18–19) than in the alcohol specimens (17), suggesting to us that we may be undercounting the fin rays in gross examination.

The field-caught juvenile (USNM 347250, 14.2 mm SL) was photographed shortly after capture and had the following color pattern: a few melanophores on side of opercle and on base of pectoral fin; one melanophore immediately above opercle on right side; one or two melanophores behind eye and on top of head above brain; a single small melanophore on ventral midline just behind anal fin; a small melanophore on fifth dorsal spine; a few small melanophores on snout and upper jaw; three indistinct yellow stripes on head, originating from upper, middle, and lower margin of eye and extending approximately to posterior end of opercle; a few indistinct yellow spots along base of dorsal fin.

Development.—The settlement-stage larvae (Fig. 2) are characterized by a large, very conspicuous, expanded melanophore midventrally over the posterior end of the anal fin. There is very little other pigment, only some internal melanophores on the dorsal surface of the gas bladder and at the posterior end of the intestine, and a dark midventral streak immediately before the pelvic fin. The caudal fin is truncate rather than elliptical. The pelvic fins are largely united, the rays of the two sides nearly parallel rather than sharply diverging (Fig. 3A). The membrane connecting the inner-

Table 2.—Meristic characters in species of *Psilotris*.

Species	Dorsal rays	Anal rays	Pectoral rays
P. alepis	VII + 10	9	15
P. batrachodes	VII + 9–10	7–8	16
P. boehlkei	VII + 10–11	10	16–18
P. celsus	VII + 10–11	9–11	16–17
P. kaufmani	VII + 10–11	10–11	16–19
P. amblyrhynchus	VII + 11–12	9–11	17–19

most rays of the two sides extends approximately ⅓ to ½ of the way from the base to the tip. There is no frenum connecting the spines, however. The largest of the larvae collected in the plankton net are about 11.5 mm SL. The 14.0-mm reared specimen still has the conspicuous ventral melanophore, but it is smaller relative to the size of the body. The pelvic fins appear more divergent, and the membrane connecting the medial rays is greatly reduced, extending not more than about an eighth of the distance from the base of the rays to their tips. The caudal fin is more elongate, but the middle rays are not greatly prolonged. The 16.8-mm reared specimen retains the midventral melanophore, but it is even less conspicuous than in the 14.0-mm specimen. A few melanophores are present along the base of the dorsal fin, but no other pigment is visible. The pelvic fins are almost completely separate, and they diverge strongly. The membrane connecting the medial rays is restricted to the base of the rays. The caudal fin is rounded, although the elongation of the middle rays is still not extreme. The first dorsal spine is not elongate. The field-caught juvenile, although smaller (14.2 mm SL) than the larger of the two reared specimens, is slightly more developed. The ventral melanophore is still present but is small and contracted. Definitive pigment as described above is beginning to appear. The pelvic fins are separate and diverge strongly (Fig. 3B). The caudal fin has still not attained the elongation seen in the holotype, and the first dorsal spine is not elongate.

Distribution and habitat.—*Psilotris amblyrhynchus* is currently known only from the vicinity of Carrie Bow Cay on the barrier reef in Belize, western Caribbean (16°48′N, 88°05′W). The holotype was collected between Carrie Bow Cay and Twin Cays in one of a series of "shot holes" created by seismic sounding. The habitat was described as an open sand patch in beds of turtle grass (*Thalassia testudineum*) at a depth of 15–20 feet (4.5–6.1 m). The field-caught juvenile was taken from the shallow spur and groove reef complex just seaward of Carrie Bow Cay at a depth of approximately 20 feet (6.1 m).

Etymology.—From the Greek *amblys*, blunt, obtuse; and *rhynchos*, snout, muzzle. In reference to the blunt anterior profile of the head. To be treated as a noun in apposition.

Key to the species of *Psilotris* (modified from Greenfield, 1993)

1a. Pectoral fin with dark brown to black bar running dorsoventrally at a posterior angle across fin; dorsal and caudal fins also with dark bars; anal-fin elements 7 or 8 (usually 7); second dorsal-fin elements 9–10 (nearly always 9) .... *P. batrachodes*

1b. Pectoral fins lacking bar running dorsoventrally at a posterior angle across fin, fin is bicolored (upper half black) or unpigmented; anal-fin elements 8–11 2

2a. Pectoral-fin rays 15; anal-fin elements 8–9 .... *P. alepis*

2b. Pectoral-fin rays 16–19; anal-fin elements 9–11 3

3a. Caudal fin with 3 oblique, dark

bars; snout very short and blunt, with steep anterior profile; second dorsal-fin elements 11–12 .... *P. amblyrhynchus*

3b. Caudal fin without 3 oblique, dark bars; snout more acute, with flatter anterior profile; second dorsal-fin elements 10–11 4

4a. Pectoral fin bicolored, dark brown to black on upper 9–11 rays and membranes and white below; anal-fin elements 10–11 (usually 11) .... *P. kaufmani*

4b. Pectoral fin not bicolored; anal-fin elements 9–11 (usually 10) 5

5a. Posterior end of jaw extending past posterior margin of pupil; caudal peduncle slender (80–89 thousandths of SL); snout short (44–55 thousandths of SL) ..... *P. boehlkei*

5b. Posterior end of jaw not extending past posterior margin of pupil; caudal peduncle deeper (greater than 92 thousandths of SL); snout longer (greater than 55 thousandths of SL) .... *P. celsus*

Comparison and Relationships

"Anyone who has attempted to identify the naked or partially scaled Atlantic gobies in and around the genera *Gobiosoma* and *Garmannia* will appreciate the difficulty experienced in placing even generically any specimen." With those words, Böhlke & Robins (1968:47) began their study of New World seven-spined gobies, which remains the most comprehensive treatment of the group. They included 17 genera in their key (Böhlke & Robins 1968:51): *Psilotris*, *Varicus*, *Chriolepis*, *Gobulus*, *Nes*, *Pycnomma*, *Gymneleotris*, *Eleotricus*, *Risor*, *Parrella*, *Barbulifer*, *Enypnias*, *Bollmannia*, *Aruma*, *Microgobius*, *Ginsburgellus*, and *Gobiosoma*. Four other genera were subsumed as subgenera under an expanded concept of *Gobiosoma*: *Austrogobius*, *Elacatinus*, *Garmannia*, and *Tigrigobius*. Böhlke & Robins (1969) added two more genera, *Evermannichthys* and *Pariah*. They excluded *Parrella*, *Microgobius*, and *Bollmannia* from their analysis of relationships because "*Parrella* is a composite and the other two are only distantly related" (Böhlke & Robins 1968:146). The resulting diagram (Fig. 4) expressed Böhlke & Robins's concept of relationships among the 16 genera and five subgenera. This is not a classification based on cladistic methods, which had not yet come into wide use, and the genus *Gobiosoma* as construed by Böhlke & Robins is a classic paraphyletic group. Nevertheless, by resurrecting *Austrogobius*, *Elacatinus*, *Garmannia*, and *Tigrigobius*, one can extract a generic phylogeny from the diagram, even though the characters on which it is based are not shown, and this phylogeny can serve as a testable hypothesis.

Birdsong (1975:180), although still not using phylogenetic methods, considered the American seven-spined gobies to be a "natural assemblage," based largely on vertebral number (11 + 16–17) and dorsal-fin formula (3-221110), characters that he observed to be "extremely stable". . . with many groups of gobioids." He placed the 17 genera from Böhlke & Robins's (1968: 51) key, plus *Evermannichthys*, *Pariah*, and *Palatogobius*, in the tribe Gobiosomini (Birdsong 1975:182, properly spelled Gobiosomatini). He noted that the "*Gobiosoma* group" is united by a distinctive character, the fusion of hypurals 1–2 with hypurals 3–4 and the urostyle, but he did not provide a list of genera in that group. Birdsong stated only that he found this character state in four subgenera of *Gobiosoma* as well as in nine genera presumably derived from *Gobiosoma*. He further noted that *Microgobius*, *Bollmannia*, *Parrella*, and *Palatogobius* do not show this fused caudal condition and thus are excluded from the *Gobiosoma* lineage. Birdsong et al. (1988: 189) treated the "*Gobiosoma* group" as comprising 17 genera: Birdsong's (1975: 182) Gobiosomatini minus the "*Microgobius* group," and with the questionable ad-

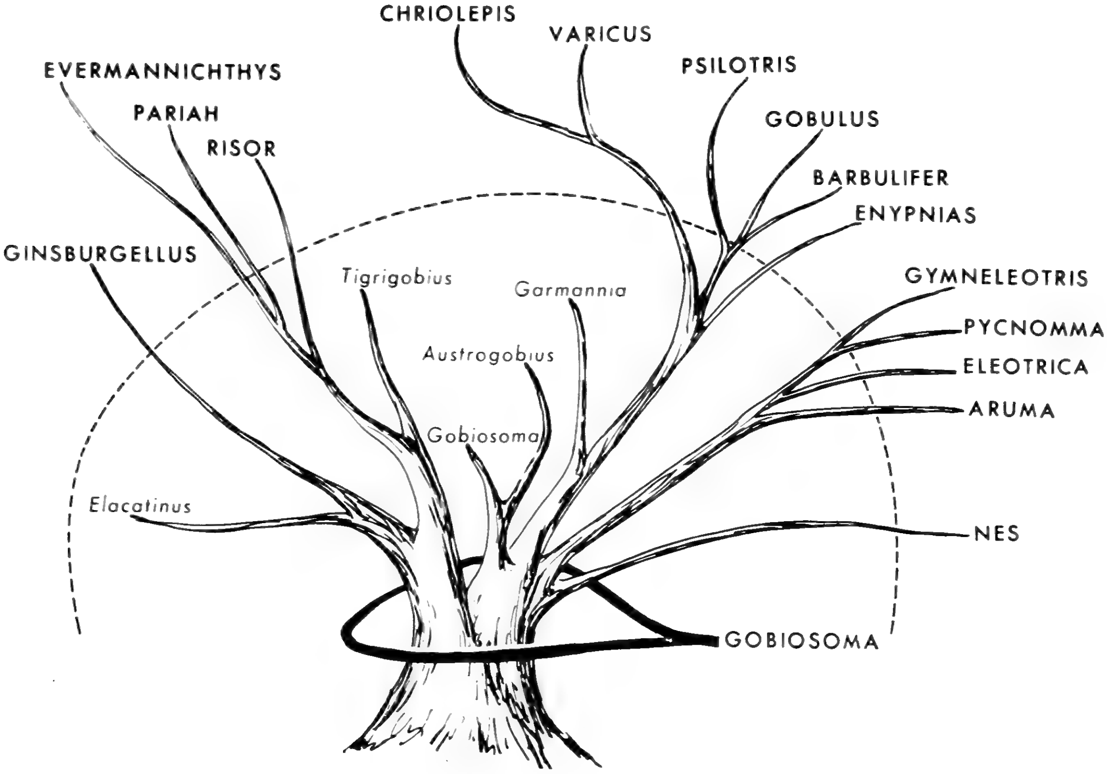

Fig. 4. Diagram of relationships (from Böhlke & Robins 1969).

dition of *Ophiogobius*, an eastern Pacific genus.

Psilotris is a member of the Gobiosomatini of Birdsong (1975) based on the presence of seven dorsal spines, 11 + 16–17 vertebrae, and a dorsal-fin formula of 3-221110. It further belongs to the "*Gobiosoma* group" by virtue of its fused hypural elements. In Böhlke & Robins's (1968:51) key to genera, *Psilotris* falls out in the first couplet along with *Varicus*, *Chriolepis*, *Gobulus*, and *Nes*, all characterized by the absence of head pores. Within this group, the genera are separated by the presence or absence of scales and by the form of the pelvic fins, either united or separate. Böhlke & Robins made no claim that their key is anything more than a convenient way to identify specimens. Nevertheless, it is intriguing that four of the five genera are adjacent on Böhlke & Robins's tree (Fig. 4). The lone outlier is *Nes*, which arises from near the base of another branch. *Nes*, however, is of special interest to us, as we have collected larvae of *Nes longus* and reared them through transformation. Larvae of *Nes longus* and *Psilotris amblyrhynchus* are strikingly similar, both having a very large melanophore on the ventral midline at the posterior base of the anal fin. Indeed, at first we did not separate larvae of the two species. It was only after our reared specimens transformed into two distinct species that we reexamined the larvae and recognized the difference. Larvae of *Nes longus* have a second midventral melanophore at the anterior base of the anal fin, in addition to the large one at the posterior end.

The most obvious difference between adults of *Nes longus* and *Psilotris amblyrhynchus* is the form of the pelvic fins. Throughout the ontogeny of *Nes*, the pelvic fins of the two sides are completely fused, and there is a well developed frenum between the spines (Fig. 3C, D). In juvenile and adult *Psilotris amblyrhynchus* the pelvic fins are almost entirely separate, with only a rudimentary membrane between the bases of the inner rays (Fig. 3B). As distinctive as this character may seem, it is subject to great variation among gobies, even among closely related species. Within the genus *Coryphopterus*, for example, the pelvic-fin condition spans the complete spectrum from fully fused to separate. In larvae of *Psilotris amblyrhynchus*, the pelvic fins are largely united (Fig. 3A), the interradial membrane retreating during transformation (Fig. 3B); this suggests that the separate pelvic fins are secondarily derived. Although the character is often treated dichotomously (united vs. separate) in keys such as Böhlke & Robins's, the condition is not so clear-cut. *Gobulus*, for instance, is keyed out by choosing "ventral fin united," yet *Gobulus* has no interspinal frenum, and the membrane between the inner rays of the two sides extends no more than a third of the way from the base of the ray to its tip. This condition is actually closer to that in *Psilotris* than in *Nes*. With only a slightly greater reduction of the interradial membrane in *Gobulus*, the distinction between it and *Psilotris* would disappear.

The other distinctions between *Nes longus* and *Psilotris amblyrhynchus* are the greater elongation of the body with age in *Nes* and the presence of an extra vertebra (28 rather than 27). Resemblances between the two species are the steep anterior profile of the head, with its large eye and short snout, and the elongate first dorsal spine in adults.

There is no unique feature that distinguishes *Psilotris* from the other members of the "*Gobiosoma* group." It is characterized only by the combination of three character states: no scales, no head pores, and separate pelvic fins. Each of these characters shows a wide range of conditions. For example, some genera are completely scaled from head to tail, some are partially scaled, some have only two small scales at the base of the caudal fin, and some have no scales at all. The number of pores also varies; sometimes within a single species certain pores can be present or absent. The variability in pelvic-fin condition has already been discussed. The trends within the evolution of these characters cut in different ways across genera. Greenfield (1993:773) correctly pointed out that *Psilotris* is not defined by any shared derived characters, and the species are not very similar in general appearance. *Psilotris alepis* (the type species) and *P. batrachodes* seem most different from *P. amblyrhynchus*. They are both small, relatively stubby gobies with low fin-ray counts. Neither has an elongate dorsal spine, and the anterior head profile is different. *Psilotris celsus* has two elongate dorsal spines rather than one as in *P. amblyrhynchus*. This species is also relatively stubby, and the eye and mouth are smaller than those of *P. amblyrhynchus*. The teeth of *P. alepis*, *P. batrachodes*, and *P. celsus* are described as being in several to many rows on the jaws, as opposed to the widely spaced, uniserial pattern found in *P. amblyrhynchus*. *Psilotris kaufmani* also has the first two dorsal spines elongate (based on fig. 1 in Greenfield et al. 1993, though it was not mentioned in the text). The color pattern of *P. kaufmani* is quite different from that of *P. amblyrhynchus*, it has a much shallower snout profile, it has fewer second-dorsal-fin elements (10–11 vs. 11–12), and it inhabits deeper areas of reefs and dropoffs. *Psilotris boehlkei* lacks elongate dorsal spines (again based on the figure in Greenfield, 1993, as the character was not mentioned in the text), and it has fewer second dorsal-fin elements (10–11).

Our assignment of the new species to *Psilotris* must be considered tentative pending further study of generic concepts among seven-spined gobies. Although larval morphology suggests a possible relationship between *Psilotris amblyrhynchus* and *Nes longus*, little comparative information is available on larval morphology of other species of the "*Gobiosoma* group."

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Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 7. Probable parentage of *Calliphlox iridescens* Gould, 1860

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Abstract.—*Calliphlox iridescens* Gould, 1860 is hypothesized to be a hybrid between *Calliphlox amethystina* and *Chlorostilbon aureoventris*. The hybrid, collected at Nova Friburgo, Rio de Janeiro, Brazil, exhibits a blended mosaic of plumage characters of the presumed parental species. External measurements of the hybrid fall between the character means of the parental species and approach the values expected from least squares regression of parental measurements.

The miniature woodstar, *Calliphlox iridescens* Gould, 1860, was described from a unique specimen collected at Nova Friburgo, about 100 km northeast of Rio de Janeiro, Brazil. Gould (1860:310) observed.

> "If, as I believe, I am right in referring this little bird to the genus *Calliphlox*, it is one of the most remarkable Humming-birds that it has fallen to my lot to describe. In its size and form it is very similar to *C. amethystina*, but in colouring it is like a *Chlorostilbon*."

The singular appearance of the specimen prompted Gould (1861:plate 359) to make it the type of a new genus, *Smaragdochrysis*, which was adopted by Elliot (1878) and Salvin (1892). The taxonomic validity of *iridescens* was not questioned until Butler (1931:347) remarked in a brief note:

> "May I regard my belief that the little Humming-bird which Gould described (P.Z.S. 1860, p. 310) as *Calliphlox*? *iridescens* . . . is really a hybrid between *Calliphlox amethystina* (Gm.) and *Chlorostilbon* [*aureoventris*] *prasinus* (Less.)? . . . I have examined it repeatedly, and to my eye its external characters are entirely a mixture of those of these two species."

Subsequent authorities listed *Calliphlox iridescens* as a hybrid (e.g., Berlioz 1932, 1938; Peters 1945; Gray 1958; Wolters 1976) or omitted it altogether (e.g., Morony et al. 1975, Sibley & Monroe 1990). The taxonomic status of *C. iridescens* is still uncertain, however, because the accounts of Butler (1931) and Berlioz (1932, 1938) did not adequately review the morphological characters of the specimen in question and those of its putative parental species. In this paper, I confirm the hybrid origin of *Calliphlox iridescens* employing the methods outlined in Graves (1990) and Graves & Zusi (1990).

Material and Methods

The type of *Calliphlox iridescens* (BMNH 1888.7.25.102 in The Natural History Museum, formerly British Museum of Natural History) appears to be an adult male in definitive plumage. This opinion is based upon the absence of striations on the maxillary ramphotheca (Ortiz-Crespo 1972), the presence of an iridescent gorget, and moderately elongated outer rectrices which lack terminal spots or markings.

I compared the specimen with series of all species in the subfamily Trochilinae, the typical hummingbirds (Zusi & Bentz 1982, Sibley & Monroe 1990, Bleiweiss et al. 1997), in the collection of The Natural History Museum. Color transparencies and videotape of the specimen were also compared with the collections of the National

Museum of Natural History, Smithsonian Institution. A second specimen of *Calliphlox iridescens*, reported by Ruschi (1951) and deposited in the Museu Nacional, Rio de Janeiro (M. N. 18275; "Brasil), was not examined. For the purposes of hybrid diagnosis (Graves 1990), I considered all hummingbirds (Trochilinae) that occur in the state of Rio de Janeiro as potential parental species (Appendix 1).

Measurements of wing chord, bill length (from anterior extension of feathers), and rectrix length (from point of insertion of the central rectrices to the tip of each rectrix) were taken with digital calipers and rounded to the nearest 0.1 mm (Table 1). Color descriptions were made under natural light.

I considered four alternatives—the specimen represents an unrecognized color morph of a species listed in Appendix 1, a chemically-altered artifact, a hybrid, or a valid species. Because *Calliphlox iridescens* differs significantly in size and shape from all species in the subfamily Trochilinae, it does not represent a previously undiscovered color morph or chemically-altered artifact. As hybrids have no standing in zoological nomenclature, the burden of proof rests on the systematist to refute the possibility of hybridization before bestowing species status on a unique specimen. I was unable to reject the hypothesis of hybridity and thus refer to the specimen as a hybrid in the remainder of the paper.

The diagnosis was approached hierarchically. The pool of potential parental species (a maximum of $\binom{27}{2}$ = 351 pairwise combinations, Appendix 1) was narrowed by the comparative analysis of plumage and soft part colors and feather shape. The restrictive hypothesis then was tested with an analysis of size and external proportions. In previous papers I used bivariate plots of mensural characters and least squares regression lines (Wilkinson 1989) projected through parental measurements to illustrate the relationship of hybrids to their hypothesized parental species (e.g., Graves & Newfield 1996, Graves 1998a, 1998b).

Table 1.—Ranges and means (± one standard deviation) of measurements (mm) of representative specimens (adult male) of *Chlorostilbon aureoventris*, *Calliphlox amethystina*, and their probable hybrid, *C. aureoventris* × *C. amethystina* (=*Calliphlox iridescens* Gould, 1860; BMNH 1888.7.25.102). Measurements of male *Chlorestes notatus* are included for comparison.

	aureoventris (*n* = 12–14[a])	*amethystina* (*n* = 10–11[b])	*notatus* (*n* = 11[c])	Hybrid BMNH 1888.7.25.102
Wing chord	43.3–50.7 (46.6 ± 2.3)	30.4–33.1 (32.0 ± 0.9)	47.3–50.5 (48.8 ± 1.1)	39.1
Bill length	13.4–17.2 (14.9 ± 1.2)	11.4–13.6 (12.5 ± 0.8)	14.9–16.8 (15.8 ± 0.7)	14.2
Rectrix 1 (R1)	18.6–23.7 (21.2 ± 1.8)	13.3–15.1 (14.2 ± 0.6)	27.3–30.1 (28.8 ± 1.0)	17.3
Rectrix 2 (R2)	20.4–25.0 (22.5 ± 1.8)	16.1–17.4 (16.9 ± 0.5)	27.5–31.3 (29.4 ± 1.0)	21.0
Rectrix 3 (R3)	22.1–27.3 (24.4 ± 2.0)	20.8–25.0 (23.0 ± 1.1)	26.9–31.4 (29.2 ± 1.2)	23.9
Rectrix 4 (R4)	24.5–30.4 (27.0 ± 1.9)	28.0–31.1 (29.7 ± 0.9)	26.2–31.2 (28.6 ± 1.3)	28.6
Rectrix 5 (R5)	26.3–32.7 (28.8 ± 2.0)	32.2–36.9 (33.8 ± 1.4)	25.6–29.5 (27.3 ± 1.1)	30.3[d]

[a] Bahia (*n* = 8); Rio de Janeiro (*n* = 3); São Paulo (*n* = 3).

[b] Bahia (*n* = 1); "Brazil" (*n* = 3); Minas Gerais (*n* = 3); Rio de Janeiro (*n* = 4).

[c] Bahia (*n* = 2); "British Guiana" (*n* = 1); Pará (*n* = 8).

[d] Rectrix tip frayed.

Fig. 1. Ventral and dorsal views of adult male *Chlorostilbon aureoventris* (top), *Calliphlox amethystina* (bottom), and their putative hybrid, *C. aureoventris* × *C. amethystina*, (=*Calliphlox iridescens* Gould, 1860; BMNH 1888.7.25.102).

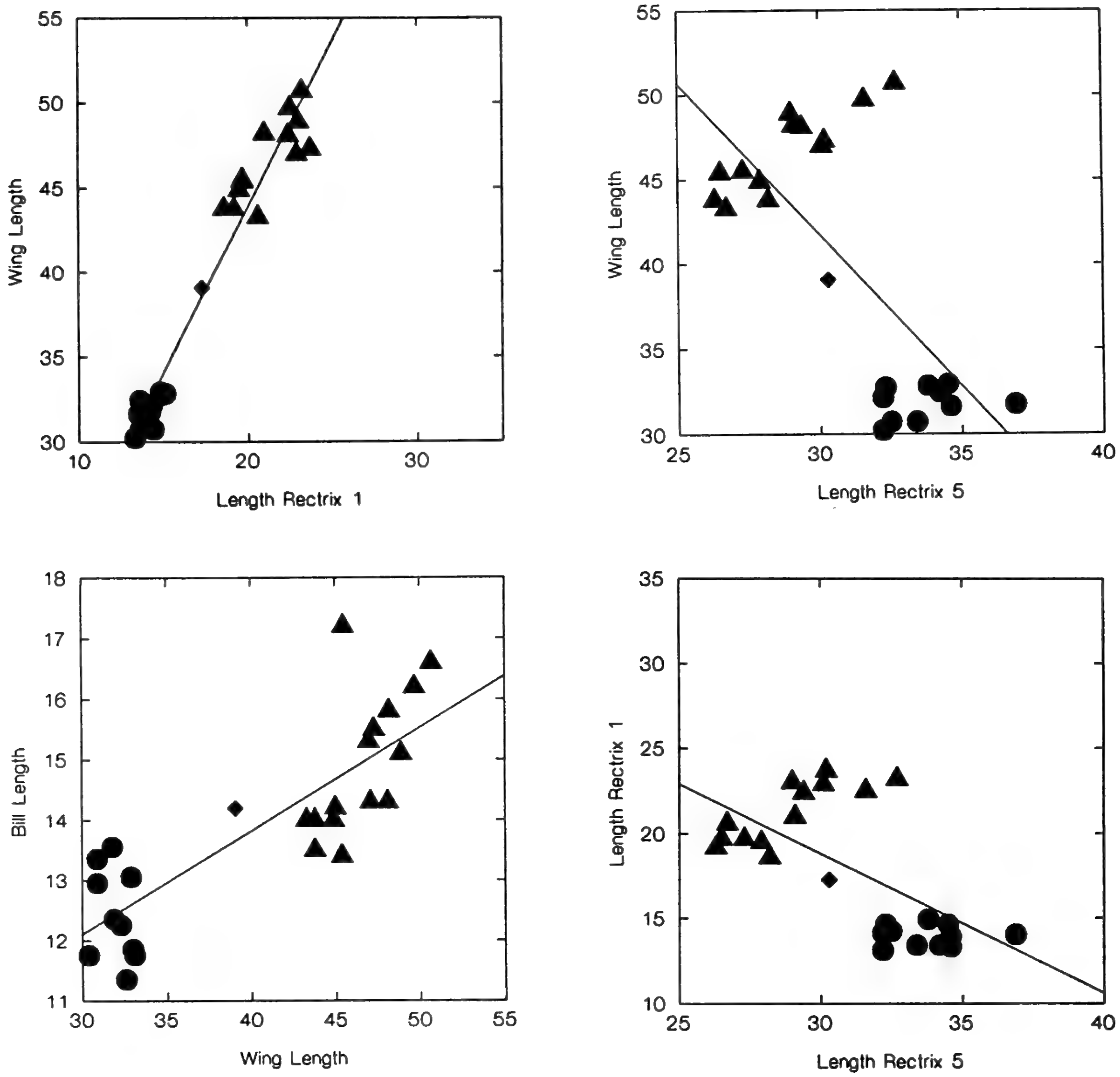

Fig. 2. Bivariate plots of selected measurements (see Table 1) of adult male *Chlorostilbon aureoventris* (▲), *Calliphlox amethystina* (●), and their putative hybrid (♦), *C. aureoventris* × *C. amethystina*, (=*Calliphlox iridescens* Gould, 1860; BMNH 1888.7.25.102). Least squares regression lines are illustrated for comparison.

Table 2.—The percent difference between measurements (mm) of the hybrid (=*Calliphlox iridescens* Gould, 1860; BMNH 1888.7.25.102) and the mensural midpoints (average of character means from Table 1) of species combinations.

	Chlorestes notatus & *Calliphlox amethystina*	Hybrid	*Chlorostilbon aureoventris* & *Calliphlox amethystina*	Hybrid
	Parental Midpoint	Percent Difference	Parental Midpoint	Percent Difference
Wing chord	40.4	3.2	39.3	0.4
Bill Length	14.4	0.5	13.7	3.8
R1	21.5	24.0	17.7	2.3
R2	23.2	10.2	19.7	6.7
R3	26.1	9.2	23.7	0.9
R4	29.2	2.0	28.3	1.0
R5	30.5	0.8	31.3	3.3

Close proximity of hybrids and regression lines (for all pairwise combinations of variables) was interpreted as evidence consistent with the specified hybrid hypothesis, assuming polygenic inheritance of external morphology. Concordance of results from plumage and size analyses is regarded as strong support for the hypothesis (Graves 1990, Graves & Zusi 1990).

Results and Discussion

Plumage characters.—The hybrid possesses several characters that facilitate the identification of its parental species: (a) brilliant silvery-green gorget; (b) moderately forked tail (fork depth = 43% of tail length); and (c) mandibular ramphotheca yellowish-brown (Fig. 1). Perhaps as informative, the hybrid *lacks* several conspicuous traits that are present among source pool species (Appendix 1): (a) contrasting rump band; (b) brilliant frontlet or coronal patch; (c) rufous or chestnut pigmentation on rectrices; (d) pronounced blue or violet iridescence on body plumage; (e) white rectricial spots; (f) white bases or margins of gorget feathers; (g) thickened primary rachises; and (h) racket-tipped or attenuated rectrix tips.

This association of characters can be derived from only two of the possible pairwise combinations of species (Appendix 1): *Chlorestes notatus* × *Calliphlox amethystina* and *Chlorostilbon aureoventris* × *Calliphlox amethystina*. Other combinations of species can be eliminated from consideration because they either lack characters exhibited by the hybrid, or possess one or more distinctive characters that are not expressed, even subtly, in the hybrid. The geographic ranges of *C. aureoventris* and *C. amethystina* overlap extensively in Brazil, and both are found in the vicinity of Nova Friburgo. *C. notatus* appears to reach its southern limit on the Atlantic coastal plain near the city of Rio de Janeiro and is not known to occur in the uplands near Nova Friburgo. However, 19th century collections of birds from Nova Friburgo often contained species from nearby lowlands (fide J. F. Pacheco, pers. comm.). *C. notatus* and *C. aureoventris* are similar in size and plumage color, differing most noticeably in tail shape—square or slightly rounded in *C. notatus*, shallowly forked in *C. aureoventris* (Table 1).

External measurements.—I evaluated the two parental hypotheses by inspecting raw data, bivariate plots, and least squares regressions of measurements. Measurements of the hybrid fell within the character means of both possible parental combinations, *Chlorestes notatus* × *Calliphlox amethystina* and *Chlorostilbon aureoventris* × *Calliphlox amethystina*. External measurements of the hybrid most closely approximate the values expected from least squares regression of measurements of *Chlorostilbon aureoventris* × *Calliphlox amethystina* (Fig. 2, Appendix 2). Hybrid characters differ from the parental midpoints (average of parental character means, Table 2) of *C. aureoventris* × *C. amethystina* by 0.4–6.7%, and from *C. notatus* × *C. amethystina* by 0.5–24%. Measurements of the hybrid are closer to the parental midpoint of *C. aureoventris* × *C. amethystina* for 5 of the 7 characters.

In summary, both plumage and external morphology are consistent with the hypothesis that *Calliphlox iridescens* represents a hybrid between *Chlorostilbon aureoventris* and *Calliphlox amethystina*. For taxonomic purposes, *Calliphlox iridescens* Gould is available only for the purpose of homonymy.

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Appendix 1

Species of trochiline hummingbirds that occur in the state of Rio de Janeiro, Brazil (fide J. F. Pacheco, pers. comm.). Vagrant species (less than three records in Rio de Janeiro) are marked by an asterisk. Parentheses enclose a representative list of characters or traits that would probably be expressed in hybrid progeny of these species, but that do not occur in *Calliphlox iridescens* Gould, 1860 (BMNH 1888.7.25.102). Taxonomy follows Sibley & Monroe (1990): *Eupetomena macroura* (violet-blue head and breast, thickened primary rachises); *Melanotrochilus fuscus* (black body plumage, white outer rectrices); *Colibri serrirostris* (purple auricular tufts, subterminal band on rectrices); *Anthracothorax nigricollis* (black ventral plumage, rufous pigmentation on rectrices); **Chrysolampis mosquitus* (brilliant coronal patch, rufous pigmentation on rectrices); *Stephanoxis lalandi* (brilliant coronal patch, elongated crest plumes, blue ventral plumage); *Lophornis magnificus* (rufous crest, contrasting rump band); *Lophornis chalybeus* (white-tipped gorget feathers, contrasting rump band); *Popelairia langsdorffi* (contrasting rump band, attenuated rectrices); **Discosura longicauda* (contrasting rump band, racket-tipped rectrices), *Chlorestes notatus*, *Chlorostilbon* *aureoventris*, **Thalurania furcata* (violet breast and belly); *Thalurania glaucopis* (brilliant coronal patch), *Hylocharis sapphirina* (rufous chin and rectrices, violet head and breast); *Hylocharis cyanus* (white chin, violet head and upper breast); **Hylocharis chrysura* (cinnamomeus chin, golden-bronze tail); *Leucochloris albicollis* (white throat, white-tipped rectrices); *Polytmus guainumbi* (white-tipped rectrices); *Amazilia versicolor* (white throat, dark subterminal band on outer rectrices); *Amazilia fimbriata* (white-margined throat feathers); *Amazilia lactea* (violet-blue throat and upper breast); *Aphantochroa cirrochloris* (dull plumage, large size); *Clytolaema rubricauda* (rufous rectrices); *Heliothryx aurita* (brilliant coronal patch, white outer rectrices); *Heliomaster squamosus* (brilliant coronal patch, white malar mark, white medial stripe from upper breast to vent); *Calliphlox amethystina*.

Appendix 2

General comparative description of definitive plumages of male *Chlorostilbon aureoventris*, *Calliphlox amethystina*, and the hybrid, *C. aureoventris* × *C. amethystina* (=*Calliphlox iridescens* Gould, 1860; BMNH 1888.7.25.102). Descriptions of structural colors are unusually subjective, as color seen by the observer varies according to the angle of inspection and direction of light. For this reason I use general color descriptions.

The dorsal plumage in *amethystina*, from crown to uppertail coverts, is weakly iridescent and dull green to pale bronzy-green in coloration; the iridescence is brighter from a "tail-on" view, as opposed to a "head-on" view. The crown is dull dark green viewed head-on. The dorsum of *aureoventris* is significantly more iridescent than that of *amethystina*, appearing golden-green to bluish-green, depending on the angle of observation. The crown is brilliant golden-green, viewed head-on, with coppery reflections on the periphery.

The quality and brightness of dorsal iridescence in *iridescens* is intermediate to those of the parental species, but closer in overall appearance to *amethystina*. The crown reflects a pale, but variable, bluish-green iridescence when viewed head-on.

The brilliant rosy-red to purplish-red gorget of *amethystina*, which extends from the chin laterally to the eye and posterior to the upper throat, is bordered posteriorly by a white or grayish-white pectoral band that blends posteriorly into dull green on the sides. Gorget feathers are of moderate length (6.1–7.0 mm), medium gray basally bordered distally by a narrow transitional band of gray glossed with green and tipped with a rosy-red terminal disk (from posterior margin of gorget: 2.1–2.4 mm deep, 1.7–2.9 mm wide). Feathers of the lower breast, sides, and flanks are dark gray basally, tipped subterminally with a weakly-iridescent green disk, and fringed (heavily along the midline) with grayish-buff or buff. Vent feathers are white. Tibial plumes, which extend past the base of the hallux, are dark gray, broadly tipped with buffy-white. Undertail coverts are grayish-buff fading to white or pale buffy-white at the margins (subterminally glossed with green in some individuals).

With the exception of white vent plumes, the ventral plumage of *aureoventris* exhibits brilliant iridescence when viewed head-on. Although there is considerable color variation among individuals, iridescence is predominately bluish-green on the throat, upper breast, and undertail coverts, tending toward golden-green on the lower breast, sides and belly. Throat feathers are medium gray basally, becoming dark gray distally, and abruptly tipped with a bluish-green disk (from lower throat, 1.6–2.0 mm deep, 3.0–3.3 mm wide). Gorget feathers (5.1–5.8 mm) are relatively shorter than in *amethystina*. Tibial feathers are dark gray and reach but do not exceed the base of the hallux.

The gorget of *iridescens*, similar in shape to that of *amethystina*, exhibits a peculiar pattern of iridescence, predominately pale silvery-green viewed head-on, but irregularly marked with a coppery hue, especially on the sides of the throat. Closer inspection reveals this is due to coppery or bronze iridescence emanating from barb tips of otherwise silvery-green disks (or silvery-blue in certain lights). Lateral gorget feathers (5.9–6.0 mm long) are dark gray basally, broadly tipped with a silvery-green disk (2.1–2.2 mm deep, 2.7–2.8 mm wide). The depth (usually <1.0 mm) and intensity of coppery disk margins increase laterally, a few gorget feathers lacking coppery iridescence are juxtaposed among margined feathers in the center of the throat. The breast and sides of *iridescens* are dark green (dark gray with only a hint of green iridescence viewed head-on); feather bases are dark gray and grayish feather margins are largely restricted to the lower midline above the vent. Evidence of the white pectoral band of *amethystina* is limited in *iridescens* to a scattering of white and pale gray basal feather barbs. Tibial plumes, which are dark brownish-gray lightly tipped pale buffy-gray, are intermediate in length between those of *amethystina* and *aureoventris*, narrowly passing the base of the hallux. Undertail coverts are buffy gray with a weakly-defined subterminal green spot of variable size and extensively margined with pale buffy-gray.

The tail of *amethystina* is moderately forked. The outer rectrices (R2–R5) are narrow (3.3–3.6 mm wide) and dull purplish-black in coloration. The outer vane is faintly (R3) or moderately (R2) glossed with green. R3–R5 are faintly tipped with green in some individuals (unstriated ramphotheca). Both vanes of R1 are extensively glossed with dark green. Rachises are dark brown on both surfaces. The shallowly forked tail of *aureoventris*, which is shining steel-blue on both surfaces, contrasts highly with the brilliant bluish-green tail coverts. Outer rectrices are 5.4–6.8 mm wide.

The color and shape of the hybrid's tail are intermediate between those of *amethystina* and *aureoventris*. The right outer rectrix (R5) is 4.0 mm wide. The outer vane of R2 and both vanes of R1 are glossed with green.

Remiges of *amethystina* are dark purplish-brown, whereas those of *aureoventris* are bluish-black and significantly glossier. Neither species shows unusual notching or emargination of the primaries and secondaries. The remiges of the hybrid are intermediate in color between those of the hypothesized parental species.

The maxillary ramphotheca in *amethystina* is black, the mandibular ramphotheca is brownish-black distally, medium brown at the base of the bill. Feathering on the maxillary ramphotheca extends to the anterior edge of the nasal operculum but does not obscure it. The mandibular ramphotheca and the proximal ⅔ of the maxillary ramphotheca of *aureoventris* is light yellowish-brown (red in life). Feathering does not reach the anterior edge of the nasal operculum, which is fully exposed. The bill of the hybrid is almost perfectly intermediate in color. The maxillary ramphotheca is dark brown proximally becoming black distally. The mandibular ramphotheca is pale yellowish-brown, gradually darkening to brownish-black on the distal fifth. Feathering extends to the anterior edge of the nasal operculum, which is slightly inflated.

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INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Applications published in the *Bulletin of Zoological Nomenclature*

The following Applications were published on 31 March 1999 in Vol. 56, Part 1 of the *Bulletin of Zoological Nomenclature.* Comment or advice on any of these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary (I.C.Z.N.), c/o The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Case No.

3074 *Eudendrium arbuscula* Wright, 1859 (Cnidaria, Hydrozoa): proposed conservation of the specific name.

3048 NYMPHULINAE Duponchel, [1845] (Insecta, Lepidoptera): proposed precedence over ACENTROPINAE Stephens, 1835.

3054 AUGOCHLORINI Moure, 1943 (Insecta, Hymenoptera): proposed precedence over OXYSTOGLOSSINI Schrottky, 1909.

3069 *Solenopsis invicta* Buren, 1972 (Insecta, Hymenoptera): proposed conservation of the specific name.

3064 *Strongylogaster* Dahlbom, 1835 (Insecta, Hymenoptera): proposed conservation by the designation of *Tenthredo multifasciata* Geoffroy in Fourcroy, 1785 as the type species.

3061 *Hemibagrus* Bleeker, 1862 (Osteichthyes, Siluriformes): proposed stability of nomenclature by the designation of a single neotype for both *Bagrus nemurus* Valenciennes, 1840 and *B. sieboldii* Bleeker, 1846, and the designation of the lectotype of *B. planiceps* Valenciennes, 1840 as the neotype of *B. flavus* Bleeker, 1846.

3020 *Megalotragus* Van Hoepen, 1932 (Mammalia, Artiodactyla): proposed conservation, and *Alcelaphus kattwinkeli* Schwarz, 1932 (currently *Megalotragus kattwinkeli*): proposed conservation of the specific name.

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 31 March 1999 in Vol. 56, Part 1 of the *Bulletin of Zoological Nomenclature.* Copies of these Opinions can be obtained free of charge from the Executive Secretary, I.C.Z.N., c/o The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Opinion No.

1913 *Pila* Röding, 1798 and *Pomacea* Perry, 1810 (Mollusca, Gastropoda): placed on the Official List, and AMPULLARIIDAE Gray, 1824: confirmed as the nomenclaturally valid synonym of PILIDAE Preston, 1915.

1914 *Belemnotheutis* Pearce, 1842, *Geopeltis* Regteren Altena, 1949, *Geoteuthis* Münster, 1843, *Jeletzkyteuthis* Doyle, 1990, *Loligosepia* Quenstedt, 1839, *Parabelopeltis* Naef, 1921, *Paraplesioteuthis* Naef, 1921 (Mollusca, Coleoidea): conserved, and the specific name of *Belemnoteuthis* (sic) *montefiorei* Buckman, 1880: conserved.

1915 *Suchonella* Spizharsky, 1937 (Crustacea, Ostracoda): *Suchonella typica* Spizharsky, 1939 designated as the type species.

1916 BRACHYPTERINAE Zwick, 1973 (Insecta, Plecoptera): spelling emended to BRACHYPTERAINAE, so removing the homonymy with BRACHYPTERINAE Erichson, [1845] (Insecta, Coleoptera); KATERETIDAE Erichson in Agassiz, [1846]: given precedence over BRACHYPTERINAE Erichson.

1917 *Papilio camillus* Fabricius, 1781 (currently *Cyrestis camillus*) and *Limenitis reducta* Staudinger, 1901 (Insecta, Lepidoptera): specific names conserved.

1918 MELOIDAE Gyllenhal, 1810 and NEMOGNATHINAE Castelnau, 1840 (Insecta, Coleoptera): given precedence over HORIDAE Latreille, 1802.

1919 *Polyrhachis* Smith, 1857 (Insecta, Hymenoptera): given precedence over *Myrma* Billberg, 1820.

1920 *Strongylopus* Tschudi, 1838 (Amphibia, Anura): *Rana fasciata* Smith, 1849 designated as the type species.

1921 PETROPEDETINAE Noble, 1931, CACOSTERNINAE Noble, 1931 and PHRYNOBATRACHINAE Laurent, 1941 (Amphibia, Anura): given precedence over HEMIMANTIDAE Hoffman, 1878, and PHRYNOBATRACHINAE: not given precedence over PETROPEDETINAE.

1922 *Loris* E. Geoffroy Saint-Hilaire, 1796 (Mammalia, Primates): conserved, and correction made to the entry for *Choloepus* Illiger, 1811 (Xenarthra) on the Official List.

INFORMATION FOR CONTRIBUTORS

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Cytogeography of Philippine bats (Mammalia: Chiroptera)

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Abstract.—Standard karyotypes of 17 species of Philippine bats representing 12 genera and 5 families are described. Karyotypes of five pteropodid species (*Alionycteris paucidentata, Otopteropus cartilagonodus, Pteropus pumilus, P. leucopterus,* and *Eonycteris robusta*), four rhinolophids (*Rhinolophus arcuatus, R. inops, R. rufus,* and *Hipposideros obscurus*), and two vespertilionids (*Myotis macrotarsus* and *Murina cyclotis*) are reported for the first time. Available data reveal a pattern of distinctive karyotypes among many Philippine bats. In several independent groups, karyotypes are unique at different taxonomic levels. Pteropodid and rhinolophid species endemic to the Philippines have karyotypes that represent major new arrangements for their families or genera. Some species widespread in Asia are chromosomally polymorphic, with major differences between populations from within and outside of the Philippines. The large proportion of unique karyotypes seen among bats from the oceanic Philippines reflects the isolation of the archipelago from mainland southeast Asia.

The bat fauna of the Philippine Islands is large and diverse, consisting of 73 species belonging to 36 genera and 6 families. It also is relatively rich in endemic species, with 25 (Heaney et al. 1998). High levels of species richness and endemism are characteristic of the Philippine terrestrial mammal fauna as a whole, reflecting a history of relative isolation in an ancient tropical island archipelago (Heaney 1986, Heaney & Rickart 1990). Studies of non-volant mammals have revealed a pattern of colonization followed by repeated speciation (Heaney 1986, Musser & Heaney 1992, Rickart & Musser 1993, Heaney & Ruedi 1994). These processes have shaped patterns of distribution and species richness among Philippine fruit bats (Heaney 1991), and similar patterns are likely to exist among other groups of bats, although underlying rates of colonization and speciation are expected to vary among them as a function of dispersal ability (Heaney 1986, 1991).

Cytogenetic studies of mammals can provide insight into phylogenetic and biogeographic relationships. However, previous information on cytogenetics of Philippine bats is limited to a single study on members of one family (Rickart et al. 1989). In many other respects bats constitute one of the most poorly known groups of Philippine mammals (Ingle & Heaney 1992). In this paper, we describe the standard karyotypes (non-differentially stained chromosome complements) of 17 species of Philippine bats representing 12 genera and 5 families, and discuss the significance of chromosomal data with respect to systematics and biogeography.

Methods

Specimens were obtained during field studies conducted from 1987 to 1993. All specimens were collected directly from natural populations and euthanized with sodium pentobarbital or chloroform within 24 h of capture. Karyotypes were prepared from bone marrow and/or spleen cells following standard in vivo methodology (Patton 1967, as modified by Rickart et al. 1989). Fixed cell suspensions were frozen in liquid nitrogen in the field, and standard karyotypes prepared in the laboratory after storage at 0°C to −70°C for several years. Determinations of diploid number were based on chromosome counts from a minimum of 10 mitotic spreads per individual. As used herein, fundamental number (FN) refers to the total number of arms in the autosomal complement. Due to the presence of minute chromosomes, small chromosome arms, or inability to distinguish sex chromosomes, FN values are provisional for some species, as indicated by question marks. Species nomenclature follows Heaney et al. (1998).

Voucher specimens were prepared as skins with partial skeletons, complete skeletons, or preserved in fluid and are deposited in the Field Museum of Natural History, Chicago (FMNH), the National Museum of Natural History, Smithsonian Institution, Washington (USNM), the Philippine National Museum, Manila (PNM), and the Utah Museum of Natural History, University of Utah, Salt Lake City (UMNH). Microscope slides and photomicrograph negatives derived from all specimens examined are housed at UMNH.

Specimens Examined

Alionycteris paucidentata Kock, 1969a.—Mindanao Island, Bukidnon Province, Mt. Kitanglad Range, 16.5 km S, 4 km E Camp Phillips, elev. 1900 m, 8°10′30″N, 124°51′E, 2 females (FMNH 147821, FMNH 147822).

Otopteropus cartilagonodus Kock, 1969b.—Luzon Island, Camarines Sur Province, Mt. Isarog, 5 km N, 20 km E Naga, elev. 900 m, 13°40′N, 123°21′E, 2 females (USNM 573692, USNM 573695).

Pteropus leucopterus Temminck, 1853.—Catanduanes Island, 1 km N, 8.5 km W Gigmoto, elev. 200 m, 13°48′N, 124°19′E, 1 male (USNM 573263).

Pteropus pumilus Miller, 1910.—Negros Island, Negros Oriental Province, 3 km N, 14 km W Dumaguete, elev. 950 m, 9°22′N, 123°11′E, 1 female (USNM 573466), 9 km N, 14 km W Dumaguete, elev. 600 m, 9°23′N, 123°11′E, 1 female (USNM 573749).

Eonycteris robusta Miller, 1913.—Catanduanes Island, 1 km N, 8.5 km W Gigmoto, elev. 200 m, 13°48′N, 124°19′E, 2 females (USNM 573210, USNM 573211).

Taphozous melanopogon Temminck, 1841.—Negros Island, Negros Oriental Province, 4 km N Manjuyod, elev. 20 m, 9°43′N, 123°10′E, 1 female (USNM 459344).

Megaderma spasma (Linnaeus, 1758).—Catanduanes Island, 1 km N, 8.5 km W Gigmoto, elev. 200 m, 13°48′N, 124°19′E, 1 male (USNM 573267); Biliran Island, 5 km N, 10 km E Naval, elev. 850 m, 11°36′N, 124°29′E, 1 female (PNM specimen, EAR field number 1445); Leyte Island, Leyte Province, 10.2 km N, 2.2 km E Baybay, elev. 320 m, 10°46′N, 124°49′E, 1 male (USNM 459392), 10.5 km N, 4 km E Baybay, elev. 700 m, 10°47′N, 124°50′E, 1 female (USNM 459393).

Rhinolophus arcuatus Peters, 1871.—Biliran Island, 5 km N, 10 km E Naval, elev. 850 m, 11°36′N, 124°29′E, 2 males, small morph (USNM 459445, USNM 459446); Luzon Island, Camarines Sur Province, Mt. Isarog, 4 km N, 18 km E Naga, elev. 475 m, 13°40′N, 123°20′E, 1 female, large morph (USNM 573757), 5 km N, 20 km E Naga, elev. 900 m, 13°40′N, 123°21′E, 1 male, large morph (USNM 573758).

Rhinolophus inops K. Andersen, 1905.—Leyte Island, Leyte Province, 8.5 km N, 2.5 km E Baybay, elev. 500 m, 10°46′N, 124°49′E, 1 male (USNM 458606).

Rhinolophus rufus Eydoux & Gervais, 1839.—Catanduanes Island, 1 km N, 8.5 km W Gigmoto, elev. 250 m, 13°47′N, 124°19′E, 1 male (USNM 573588).

Hipposideros ater Templeton, 1848.—Catanduanes Island, 4 km W Virac, elev. 50

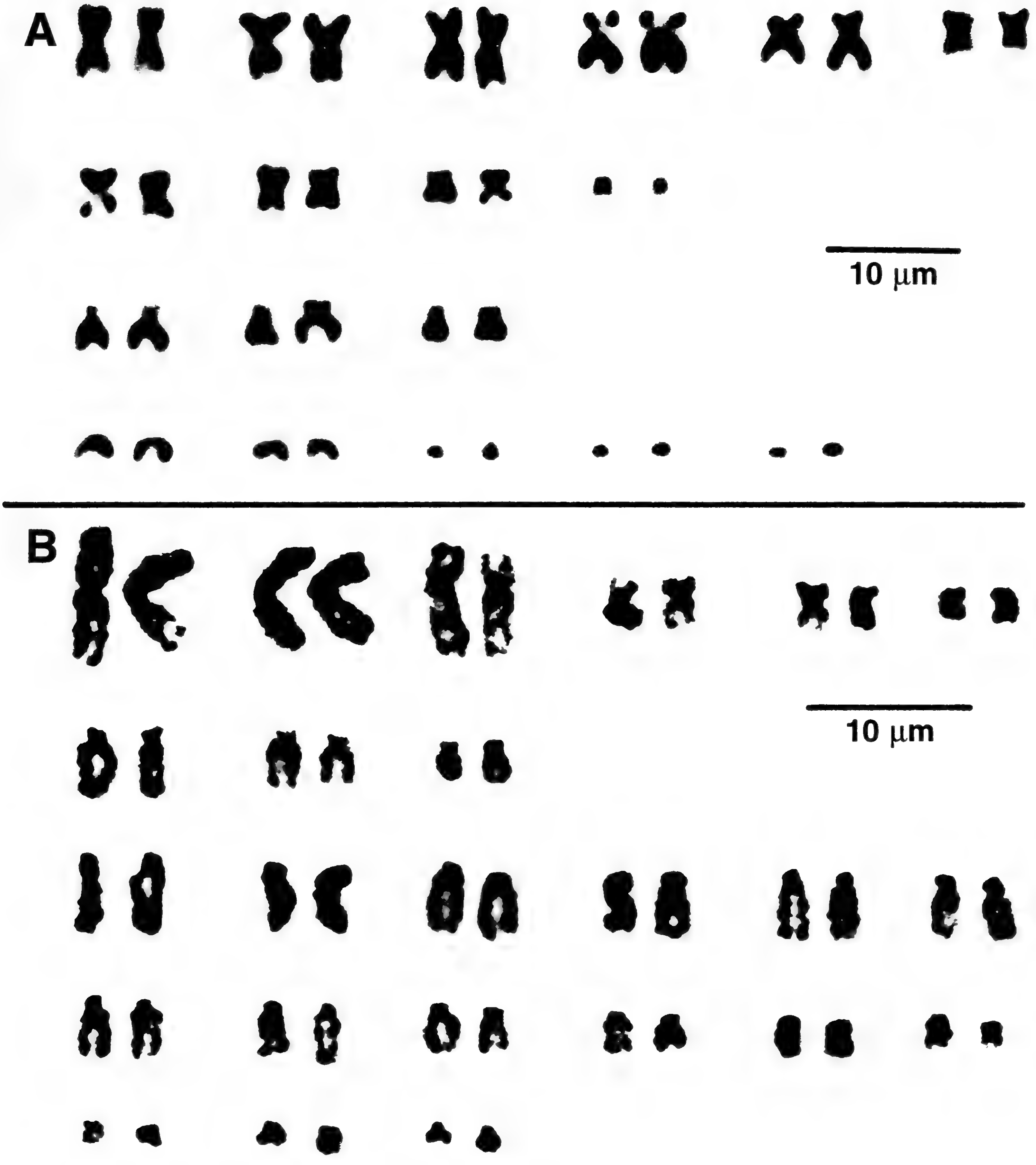

Fig. 1. Karyotypes of: A, *Alionycteris paucidentata* ♀ (FMNH 147821), 2N = 36, FN = 58(?); B, *Otopteropus cartilagonodus* ♀ (USNM 573695), 2N = 48, FN = 62(?).

m, 13°35′N, 124°11′E, 1 female (USNM 573274).

Hipposideros diadema (E. Geoffroy, 1813).—Leyte Island, Leyte Province, 7 km N, 1.5 km E Baybay, elev. 50 m, 10°45′N, 124°48′E, 2 males (USNM 458637, 459418).

Hipposideros obscurus (Peters, 1861).—Catanduanes Island, 1 km N, 8.5 km W Gigmoto, elev. 250 m, 13°47′N, 124°19′E, 1 female (USNM 573280), 1 km S, 4 km W Gigmoto, elev. 600 m, 13°46′N, 124°21′E, 1 male (UMNH 29005); Negros Island, Negros Oriental Province, 3 km N, 14 km W Dumaguete, elev. 950 m, 9°22′N, 123°11′E, 1 female (USNM 459435).

Myotis macrotarsus (Waterhouse, 1845).—Negros Island, Negros Oriental Province, 4 km N Manjuyod, elev. 20 m, 9°43′N, 123°10′E, 2 males (USNM 459739, USNM 459740).

Pipistrellus javanicus (Gray, 1838).—Luzon Island, Camarines Sur Province, Mt. Isarog, 4 km N, 21.5 km E Naga, elev. 1,550 m, 13°40′N, 123°22′E, 2 males (USNM 573822, USNM 573829).

Scotophilus kuhlii Leach, 1821.—Leyte Island, Leyte Province, 7 km N Baybay, elev. 10 m, 10°45′N, 124°47′E, 1 male, 1 female (USNM 458697, USNM 458699); Negros Island, Negros Oriental Province, 2 km E Siaton, elev. 5 m, 9°3′N, 123°3′E, 1 male (USNM 458719).

Murina cyclotis Dobson, 1872.—Luzon Island, Camarines Sur Province, Mt. Isarog, 4 km N, 18 km E Naga, elev. 475 m, 13°40′N, 123°20′E, 1 female (USNM 573776), 4.5 km N, 20.5 km E Naga, elev. 1,125 m, 13°40′N, 123°21′E, 1 female (USNM 573777).

Results

Standard karyotypes for specimens of 14 species are presented in Figs. 1–7 and briefly described below. Karyotypes of 3 additional species are described but not illustrated.

Family Pteropodidae
Subfamily Pteropodinae

Alionycteris paucidentata. 2N = 36, FN = 58(?), Fig. 1A.—This is the first report on the chromosomes of this species, belonging to a monotypic genus endemic to Mindanao Island. The karyotype consists of 13 pairs of metacentric or submetacentric, and 5 pairs of acrocentric chromosomes. The sex chromosomes cannot be determined because females only were examined, but the X chromosomes presumably are metacentric or submetacentric as in other Philippine cynopterines (Rickart et al. 1989).

Otopteropus cartilagonodus. 2N = 48, FN = 62(?), Fig. 1B.—The karyotype of this species, belonging to a monotypic genus endemic to Luzon Island, is reported for the first time. It includes 6 pairs of metacentric or submetacentric chromosomes, 3 pairs of subtelocentric chromosomes, and 15 pairs which appear to be acrocentric. Male specimens were not examined, so the sex chromosomes cannot be determined. However, the X chromosomes presumably are metacentric or submetacentric as in other cynopterines (Rickart et al. 1989).

Pteropus pumilus. 2N = 38, FN = 72, Fig. 2A.—The karyotype of this Philippine endemic is reported for the first time. It is composed entirely of biarmed elements, including 10 metacentric or submetacentric, and 9 subtelocentric pairs. Only females were examined, so the sex chromosomes cannot be determined. However, the X chromosomes presumably are subtelocentric as in congeners sharing this same basic karyotype (Hood et al. 1988, Rickart et al. 1989).

Pteropus leucopterus. 2N = 38, FN = ?, Fig. 2B.—A single male specimen yielded the first available karyotype for this species endemic to the Philippines. Although the preparation quality is poor, basic features of the karyotype are clear: it includes 1 chromosome pair that is submetacentric, and 18 pairs that are either acrocentric or subtelocentric. The sex chromosomes cannot be differentiated and the FN value cannot be determined.

Subfamily Macroglossinae

Eonycteris robusta. 2N = 36, FN = 66(?), Fig. 3A.—The standard karyotype of the endemic Philippine nectar bat is reported for the first time. It includes 17 pairs of small to large-sized biarmed chromosomes, and one pair of small acrocentric elements. The sex chromosomes cannot be distinguished since females only were examined, but the X chromosomes presumably are submetacentric as in *E. spelaea* (Rickart et al. 1989).

Fig. 2. Karyotypes of: A, *Pteropus pumilus* ♀ (USNM 573749), 2N = 38, FN = 72; B, *Pteropus leucopterus* ♂ (USNM 573263), 2N = 38.

Family Emballonuridae

Taphozous melanopogon. 2N = 42, FN = 64(?), not figured.—The karyotype of a single female specimen of this widespread species is consistent with those reported for specimens from India (Ray-Chaudhuri et al. 1971) and Thailand (Hood & Baker 1986). It includes 13 pairs of metacentric or submetacentric, and eight pairs of acrocentric chromosomes. The X chromosomes are presumably submetacentric as reported previously for this species.

Family Megadermatidae

Megaderma spasma. 2N = 46, FN = 64, Fig. 3B.—Philippine specimens of this widespread species have a karyotype that includes 10 pairs of biarmed autosomes and 12 pairs of acrocentric autosomes. The subtelocentric X chromosome is the largest element in the karyotype, and the Y is a small acrocentric chromosome.

Family Rhinolophidae
Subfamily Rhinolophinae

Rhinolophus arcuatus. 2N = 58, FN = 60, Fig. 4A.—Horseshoe bats included under this name are widely distributed among the islands of Southeast Asia (Koopman 1993), and have not been karyotyped previously. Philippine specimens from Biliran and Luzon islands have a uniform standard karyotype consisting of 2 pairs of large metacentric and 26 pairs of small to large acrocentric autosomes, a medium-sized subtelocentric X and an acrocentric Y chromosome. One pair of medium-sized acrocentric autosomes have a secondary constriction.

Rhinolophus inops. 2N = 58, FN = 60, Fig. 4B.—Bats included under this name are endemic to the Philippines and have not been karyotyped previously. A single male specimen from Leyte Island has a standard karyotype that is identical to those seen for specimens of *R. arcuatus* (Fig. 4A).

Rhinolophus rufus. 2N = 40, FN = 60, Fig. 5A.—The karyotype of a single male specimen is the first reported for this endemic Philippine horseshoe bat. It includes 11 pairs of biarmed autosomes, 8 pairs of acrocentric autosomes, a subtelocentric X, and a acrocentric Y chromosome.

Subfamily Hipposiderinae

Hipposideros ater. 2N = 32, FN = 60, Fig. 5B.—The karyotype of a single female specimen of this widespread species closely resembles those reported previously for specimens from India (Ray-Chaudhuri et al. 1971, Sreepada et al. 1993). It consists of 14 pairs of metacentric or submetacentric, and 3 pairs of subtelocentric elements. The X chromosomes cannot be distinguished from the autosomes, but presumably are medium-sized and metacentric as reported previously for this species.

Hipposideros diadema. 2N = 32, FN = 60, not figured.—Standard karyotypes from Philippine specimens of this widespread Asian species consist entirely of biarmed chromosomes, and closely resemble the karyotype reported for a specimen from Borneo (Harada & Kobayashi 1980).

Hipposideros obscurus. 2N = 24, FN = 44, Fig. 5C.—The karyotype of this endemic Philippine roundleaf bat is reported for the first time. It includes 10 pairs of metacentric or submetacentric, and 2 pairs of subtelocentric chromosomes. The sex chromosomes cannot be distinguished with certainty, but the X is presumably medium-sized and either metacentric or submetacentric, as in congeners.

Family Vespertilionidae
Subfamily Vespertilioninae

Myotis macrotarsus. 2N = 44, FN = 50, Fig. 6A.—The karyotype of this species is reported for the first time. It has the arrangement typical for members of the genus *Myotis* (Bickham 1979a, Volleth & Heller 1994), consisting of 3 large metacentric, 1 small submetacentric, and 17 acrocentric autosomal pairs, a submetacentric X and an acrocentric Y chromosome.

Pipistrellus javanicus. 2N = 38, FN = 48, Fig. 6B.—Philippine specimens of this widespread east Asian species have a karyotype consisting of 6 pairs of large biarmed autosomes, 12 pairs of acrocentric autosomes, and acrocentric X and Y chromosomes.

Scotophilus kuhlii. 2N = 36, FN = 48, not figured.—Philippine specimens of the widespread Asian house bat have a standard karyotype that includes seven pairs of biarmed and ten pairs of acrocentric autosomes, a submetacentric X chromosome, and an acrocentric Y chromosome.

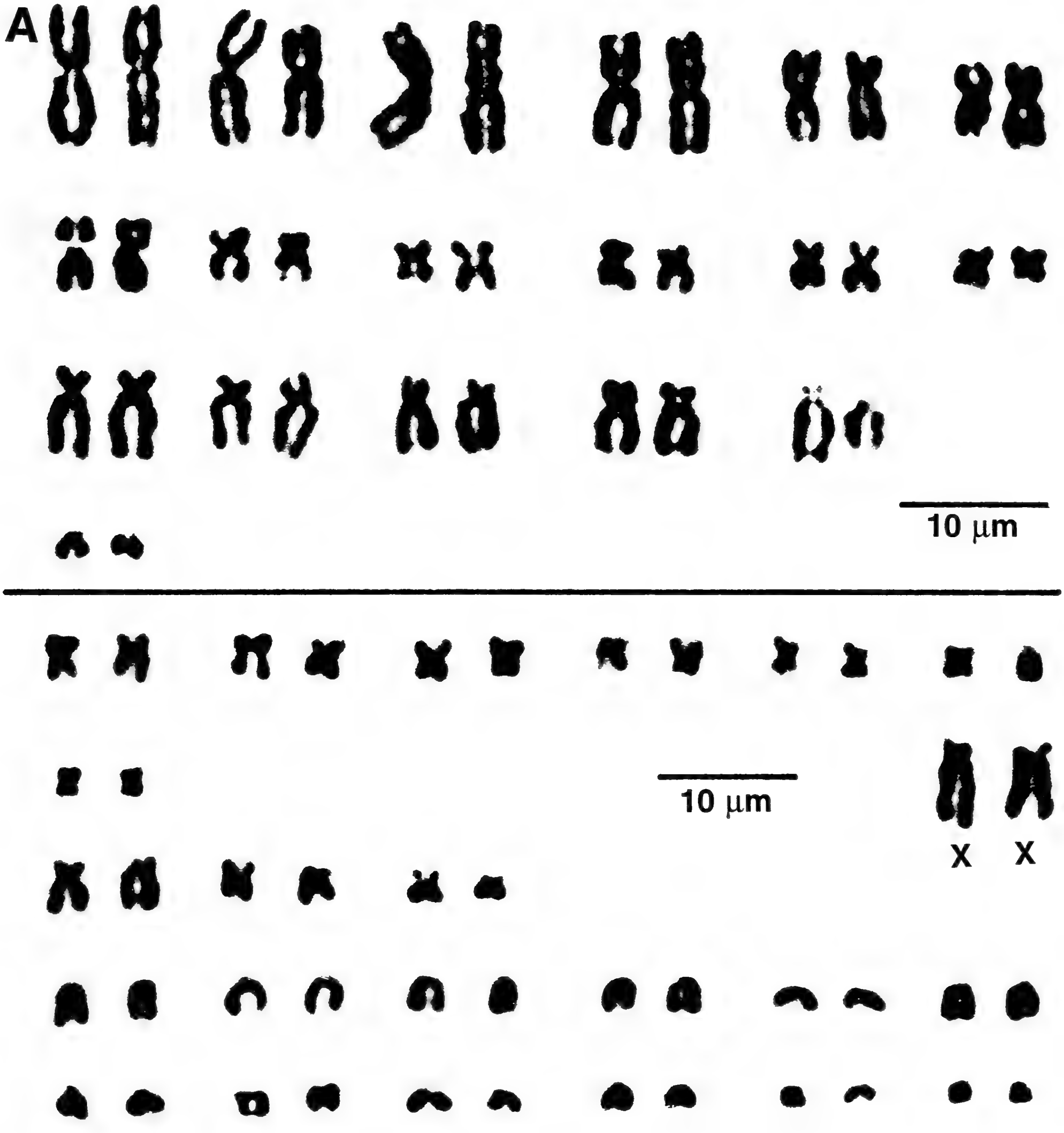

Fig. 3. Karyotypes of: A, *Eonycteris robusta* ♀ (USNM 573210), 2N = 36, FN = 66; B, *Megaderma spasma* ♀ (EAR 1445), 2N = 46, FN = 64.

Subfamily Murininae

Murina cyclotis. 2N = 44, FN = 50(?), Fig. 7.—The karyotype of this widespread Asian species is reported for the first time. The autosomes include three pairs of large metacentric and one pair of small submetacentric elements, and seventeen pairs of small to medium-sized elements that appear to be acrocentric. Females only were examined, so the sex chromosomes cannot be determined with certainty. Based on comparisons with karyotypes of congeners (McBee et al. 1986, Harada et al. 1987), two medium-sized submetacentric elements are tentatively identified as the X chromosomes.

Discussion

Several studies have demonstrated that non-differentially stained chromosomes

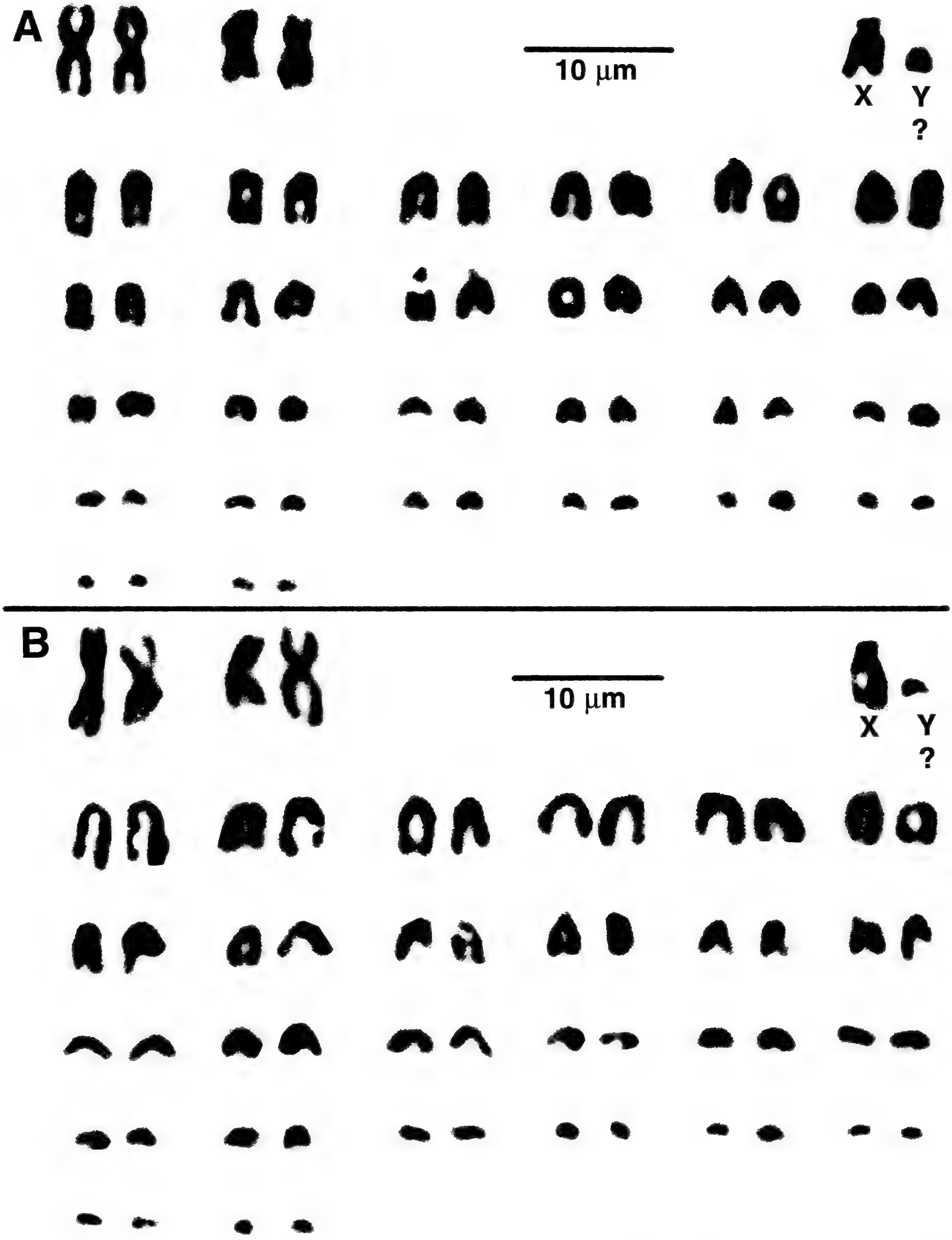

Fig. 4. Karyotypes of: A, *Rhinolophus arcuatus* (small morph) ♂ (USNM 459445), 2N = 58, FN = 60; B, *Rhinolophus inops* ♂ (USNM 458606), 2N = 58, FN = 60.

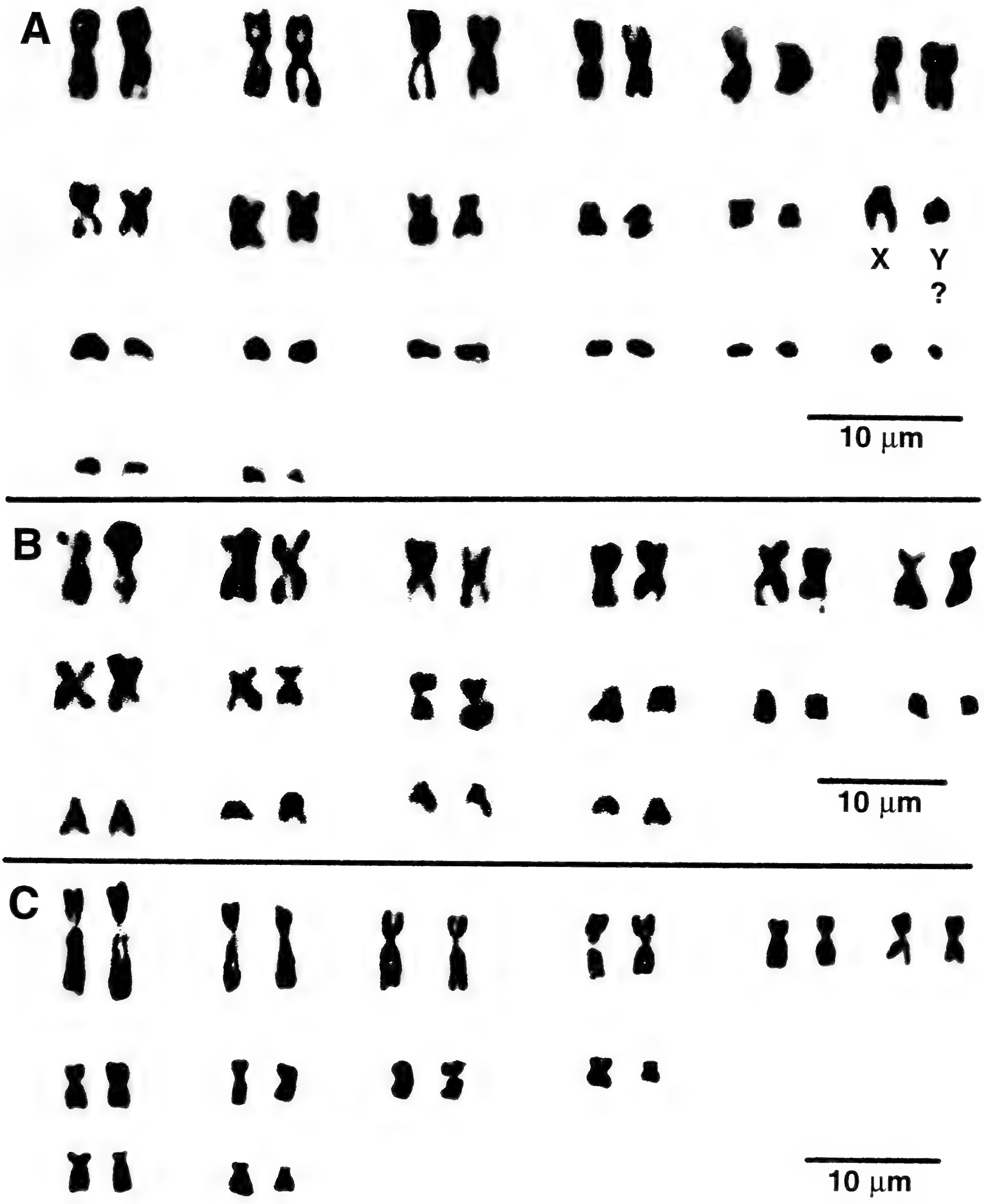

Fig. 5. Karyotypes of: A, *Rhinolophus rufus* ♂ (USNM 573588), 2N = 40, FN = 60; B, *Hipposideros ater* ♀ (USNM 573274), 2N = 32, FN = 60; C, *Hipposideros obscurus* ♀ (USNM 459435), 2N = 24, FN = 44.

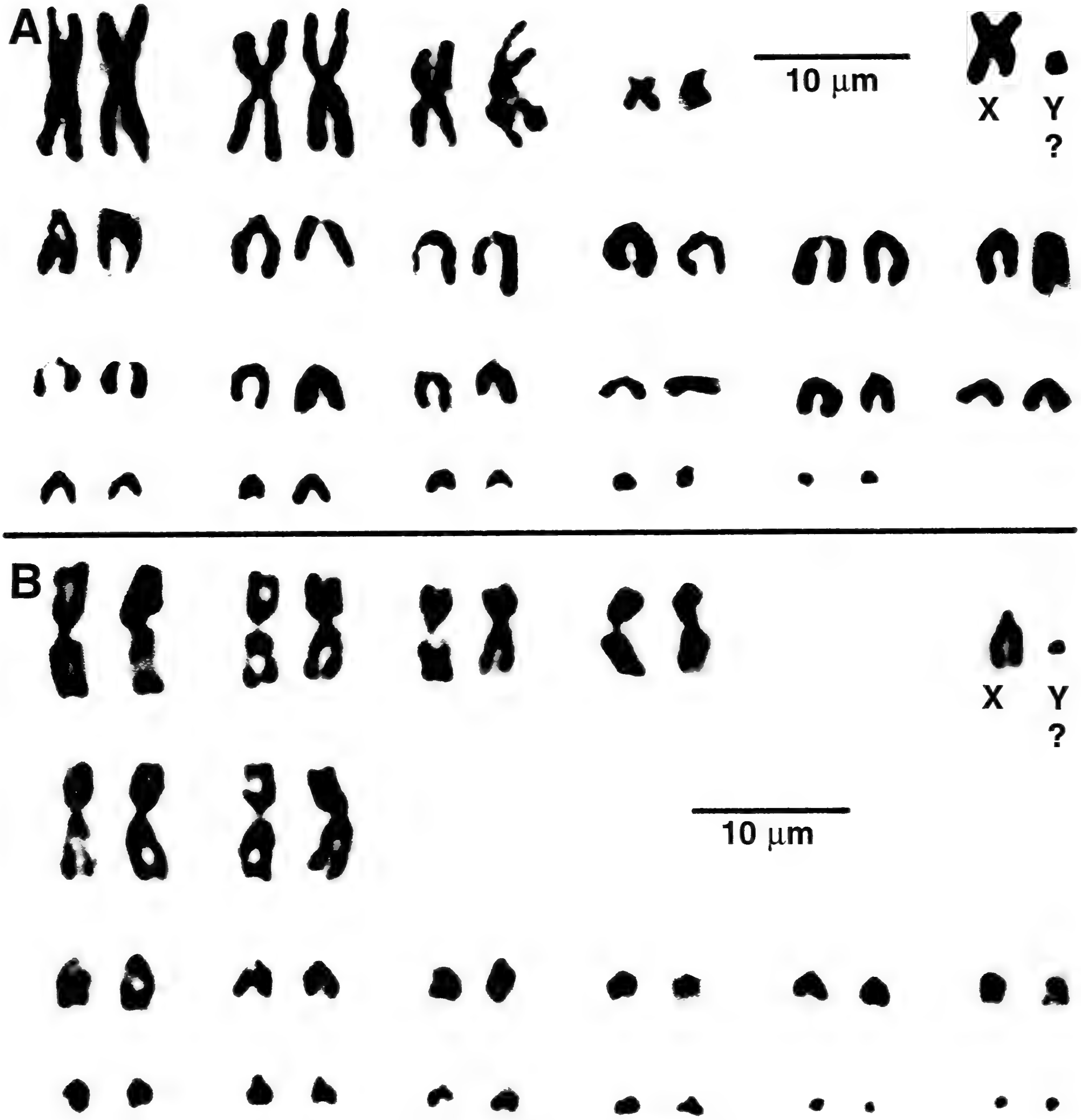

Fig. 6. Karyotypes of: A, *Myotis macrotarsus* ♂ (USNM 459740), 2N = 44, FN = 52; B, *Pipistrellus javanicus* ♂ (USNM 573822), 2N = 38, FN = 48.

may greatly underestimate the magnitude of karyotypic evolution (Haiduk et al. 1981, and references therein). In our analysis of results we therefore consider any observable differences between standard karyotypes to be minimal reflections of actual differences. More importantly, we avoid drawing conclusions based solely on apparent similarities.

With 25 species, the Pteropodidae is one the most diverse mammalian families in the Philippines. It also displays a high level of endemism; 15 species and 4 genera are restricted to the archipelago (Heaney et al. 1998). All five species of pteropodids examined in this study are Philippine endemics, and two belong to monotypic genera.

Alionycteris and *Otopteropus* are part of the diverse cynopterine clade that has undergone substantial radiation in southeast Asia (Rickart et al. 1989:528, fig. 5). Karyotypes of the two genera differ substan-

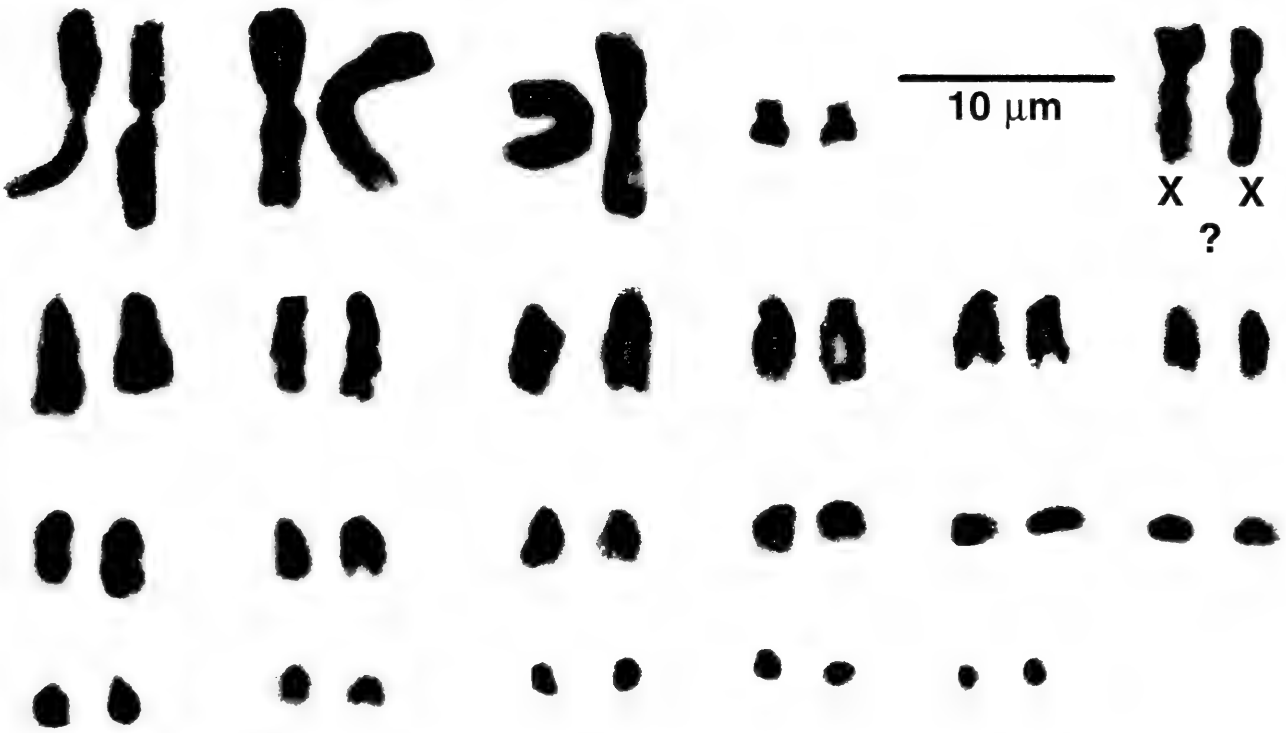

Fig. 7. Karyotypes of *Murina cyclotis* ♀ (USNM 573777), 2N = 44, FN = 50(?).

tially, providing no support for a previously hypothesized sister-group relationship (Rickart et al. 1989, Heaney 1991). The standard karyotype of *Alionycteris* (2N = 36; Fig. 1A) differs from those of other pteropodid genera that have been examined thus far. It most closely resembles karyotypes of *Cynopterus* that have 2N = 34 and FN = 58 (Ando et al. 1980a, Harada & Kobayashi 1980, Rickart et al. 1989), the only apparent difference involving a single Robertsonian translocation. The karyotype of *Otopteropus* (2N = 48; Fig. 1B) also may represent a novel arrangement for the family. It resembles those of *Ptenochirus* (2N = 44–46), another cynopterine genus endemic to the Philippines, and thought to be closely related (Rickart et al. 1989); both genera possess three pairs of large-sized biarmed chromosomes and several smaller subtelocentric and acrocentric elements. The east Asian cynopterine *Penthetor,* considered a more distant relative of *Otopteropus* (Rickart et al. 1989), also reportedly has 2N = 48 (Yong & Dhaliwal 1976), but the karyotype has not been published so comparisons are not possible.

Previous studies on the genus *Pteropus* have characterized it as chromosomally conservative: most species, including *P. pumilus* (Fig. 2A), have karyotypes of 2N = 38 and FN = 72 (Hood et al. 1988, Rickart et al. 1989). The karyotype of the one specimen of *Pteropus leucopterus* (Fig. 2B) represents a major departure from the predominant arrangement for the genus. The absence of large biarmed autosomes and the predominance of acrocentric or subtelocentric elements distinguish this Philippine endemic from all other species of *Pteropus* that have been examined thus far.

The standard karyotype of the Philippine nectar bat, *Eonycteris robusta* (2N = 36; Fig. 3A), is indistinguishable from that of the widespread *E. spelaea* (Harada et al. 1982, Rickart et al. 1989). From the limited perspective of standard karyotypes, there appears to be little chromosomal variation among the few members of the subfamily Macroglossinae that have been examined to date (Haiduk et al. 1980, Rickart et al. 1989).

Our results demonstrate that the widespread Asian ghost bat, *Megaderma spasma,* is chromosomally polytypic. Hood et al. (1988) reported a karyotype of 2N = 38 for specimens from Thailand. Philippine specimens from three islands representing two distinct faunal regions (Heaney 1986) all have 2N = 46 (Fig. 3B). Philippine and Thai specimens have similar sex chromosomes and share FN = 64, indicating that Robertsonian translocations among the autosomes may account for all or most of the observed differences between the karyotypes. *Megaderma lyra,* the only other megadermatid that has been karyotyped, has a very different arrangement: specimens from both India and Thailand have 2N = 54, FN = 104 (Ray-Chaudhuri et al. 1971, Naidu & Gururaj 1985, Hood et al. 1988). The two species also differ substantially in amount and distribution of C-positive heterochromatin and in patterns of G-banding (Hood et al. 1988).

Karyotype differences of the magnitude seen in *Megaderma spasma* suggest that more than one species may be included under this name at present. Although chromosomal polymorphism alone does not preclude possible gene flow between cytotypes (e.g., as occurs in *Uroderma bilobatum*; Baker 1981, Greenbaum 1981), in *M. spasma* it is correlated with geographic isolation by extensive water barriers. Additional data from both mainland and island populations are needed, and a systematic review of the group is warranted.

The genus *Rhinolophus* is one of the most diverse yet poorly known mammalian groups in the Philippines (Heaney et al. 1998). The status of two of the taxa examined herein, *R. arcuatus* and *R. inops,* is uncertain. Both of these taxa have been considered members of the same species group (Andersen 1905, Tate & Archbold 1939). Philippine specimens currently included within *R. arcuatus* probably represent more than one species. Two body size classes are present on most islands, and additional geographic variation is apparent between different islands. Specimens referred to *R. inops* also exhibit geographic variation, and may represent more than one species (Heaney et al. 1991, Ingle & Heaney 1992, Heaney et al. 1998). Data presented here do not help resolve either of these issues. Specimens of both size morphs of *R. arcuatus* and a single example of *R. inops* have the same standard karyotype of 2N = 58, FN = 60 (Fig. 4), which is a common arrangement in the genus (Qumsiyeh et al. 1988, Zima et al. 1992b).

Among the more than 30 species of *Rhinolophus* that have been karyotyped, the limited range in FN values (60 to 64) indicates that Robertsonian rearrangements, that do not alter FN, may account for much of the karyotypic variation (Qumsiyeh et al. 1988, Zima et al. 1992b). A 2N = 62, FN = 60 karyotype has been hypothesized as primitive for the genus. That arrangement predominates among east Asian taxa, whereas karyotypes of 2N = 58, FN = 60–62 predominate in Africa, Europe, and northern Asia (Bogdanowicz 1992, Zima et al. 1992b). With this geographic perspective, the 2N = 58 karyotypes of *R. arcuatus* and *R. inops* are unusual among southeast Asian members of the genus, and may represent novel developments within the oceanic Philippines. Support for this is seen in the phenetic analysis of Bogdanowicz (1992) which places *R. arcuatus* within a group of southeast Asian species that includes several taxa with 2N = 62 karyotypes (Zima et al. 1992b).

The endemic Philippine species *Rhinolophus rufus* (2N = 40, FN = 60; Fig. 5A) has one of the lowest diploid numbers known for the genus, surpassed only by *R. luctus* (2N = 32) and *R. rouxi* (2N = 36) from mainland Asia (Zima et al. 1992b). In a recent phenetic analysis (Bogdanowicz 1982:221, fig. 3), *R. rufus* tentatively clustered with *R. pearsonii* (2N = 42) and *R. yunanensis* (2N = 60), two widespread species from mainland Asia that also have unique karyotypes (Zima et al. 1992b). If reduction in diploid number through centric fusion has been the primary direction of karyotypic evolution in *Rhinolophus,* as hypothesized by Zima et al. (1992b), then the unique arrangement of *R. rufus* may represent a novel derivation within the oceanic Philippines.

Previous work has characterized the genus *Hipposideros* as chromosomally conservative: 14 species, including both *H. diadema* and *H. ater* (Fig. 5B) have standard karyotypes of 2N = 32, FN = 60 with only very minor interspecific variation in arm length ratios (Ray-Chaudhuri et al. 1971, Peterson & Nagorsen 1975, Ando et al. 1980b, Handa & Kaur 1980, Harada & Kobayashi 1980, Harada et al. 1982, Hood et al. 1988, Sreepada et al. 1993). The karyotype of the Philippine endemic *H. obscurus* (2N = 24, FN = 44; Fig. 5C) represents a radical departure from this common arrangement. The low diploid and fundamental numbers of this species distinguish it not only from congeners, but apparently from all other rhinolophids karyotyped thus far which have 2N = 30–62 and FN = 58–64 (Baker et al. 1974, Ando et al. 1980b, Handa & Kaur 1980, Zima et al. 1992b). Given the extent of this FN pattern and the prevailing view on the primary mode and direction of karyotypic evolution in the family (Zima et al. 1992b, Sreepada et al. 1993), the chromosome arrangement of *H. obscurus* may be viewed as another unique derivation within the oceanic Philippines.

All members of the genus *Myotis* karyotyped thus far, including *M. macrotarsus* (Fig. 6A), exhibit the same basic karyotype of 2N = 44, FN = 50–52 that is widely regarded as the primitive arrangement for the family Vespertilionidae (Bickham 1979b, Volleth & Heller 1994). Members of the genus *Murina* that have been examined have karyotypes similar to *Myotis* with 2N = 44 and FN = 50–58 (McBee et al. 1986, Harada et al. 1987, Volleth and Heller 1994, this study, Fig. 7). Very small secondary arms present in some species of *Murina* cannot be discerned in the material available for *M. cyclotis*.

Species of *Scotophilus* examined to date have 2N = 36, and FN = 48–54, with interspecific differences in the size and number of arms on some autosomes (Schlitter et al. 1980, McBee et al. 1986, Ruedas et al. 1990). *Scotophilus kuhlii* (= *S. temmincki* of some authors) is chromosomally polytypic. Specimens from the Philippines examined here have the same standard karyotype of 2N = 36, FN = 48 seen in specimens from Borneo and Thailand (Harada & Kobayashi 1980:91, fig. 5, Harada et al. 1982:274, fig. 2), whereas specimens from India have 2N = 36, FN = 52 (Pathak & Sharma 1969:43, fig. 10). At a minimum, these karyotypes differ by two non-Robertsonian events involving additional arms on the two smallest autosomal pairs. These differences suggest that more than one species may be included under this name at present. Multiple cytotypes are seen elsewhere in *Scotophilus*: the widespread African species, *S. dinganii* and *S. viridis,* show variation comparable to that of *S. kuhlii* (Schlitter et al. 1980, Ruedas et al. 1990).

Our results indicate chromosomal polymorphism within another widespread east Asian vespertilionid, *Pipistrellus javanicus.* Specimens from the Philippines have 2N = 38, FN = 48 (Fig. 6B), whereas those from Malaysia have 2N = 34, FN = 46 (Zima et al. 1992a). These differences suggest the involvement of both Robertsonian and non-Robertsonian events. The autosomal arrangement of Philippine specimens of *P. javanicus* is similar to that reported for Indian *P. mimus* (2N = 38, FN = 48) by Pathak & Sharma (1969:37, fig. 2). However, the acrocentric X chromosome seen in both Philippine and Malaysian *P. javanicus* is distinctive and apparently derived (Volleth & Heller 1994). Acrocentric X chromosomes occur also in *P. abramus* (2N = 26, FN = 44; McBee et al. 1986) and *P. endoi* (2N = 36, FN = 60; Ando et al. 1977). These taxa are considered close relatives of *P. javanicus* (Hill & Harrison 1987), and *P. abramus* has been arranged as a synonym by Koopman (1993). The substantial karyotypic variation seen among these species, and within *P. javanicus,* indicates the need for further study of this group.

Of the 73 species of bats known to occur in the Philippines (Heaney et al. 1998), basic information on standard karyology is now available for 27 (Rickart et al. 1989, this study). These data reveal a geographic pattern of variation at different taxonomic levels within several independent groups. It involves endemic genera with unique karyotypes within the family Pteropodidae (*Alionycteris, Haplonycteris, Otopteropus, Ptenochirus*), endemic species with unique karyotypes within widespread genera that are otherwise chromosomally conservative (*Pteropus leucopterus, Rhinolophus rufus, Hipposideros obscurus*), and widespread species that are chromosomally polytypic, with unique karyotypes observed for Philippine populations (*Megaderma spasma, Pipistrellus javanicus*).

The historical development of the Philippine Islands and their mammal fauna provides the context for understanding these patterns. One part of the Philippines (as a political entity) is the Palawan island group that lies immediately to the north of Borneo. This is the only portion of the Philippines that had dry land connections to the Asian continent during Pleistocene periods of low sea level, and on biogeographic grounds it is considered part of the Sunda Shelf faunal region rather than part of the main body of the Philippines (Heaney 1985, 1986). The remaining Philippine islands are oceanic in origin. Most originated as parts of island arcs far to the southeast of their current position, although a few represent fragments of continental material that dipped below the ocean surface and re-emerged subsequently as effective oceanic islands (Hall 1996, Hamilton 1979, Heaney 1986). The available geological evidence therefore suggests that the fauna of the main portion of the Philippines originated through over-water colonization, and patterns of distribution of the fruit bats and murid rodents are consistent with this (Heaney 1986, 1991; Heaney & Rickart 1991, Musser & Heaney 1992).

Notably, all of the species (or current subspecies) of bats that show distinctive and/or unusual karyotypes occur in oceanic portions of the Philippines. In contrast, species in groups exhibiting little or no karyotypic variation occur mainly in continental Asia (including islands of the continental shelf), although some chromosomally conservative taxa also occur in oceanic areas. Our documentation of unique chromosomal arrangements in 10 of the 27 Philippine bat species that have been karyotyped (37%) implies that the exceptionally high level of endemism among Philippine mammals (34% of the bat species, and about 97% of the rodents; Heaney et al. 1998) resulted from speciation events that included major chromosomal rearrangements as a common feature. Chromosomal rearrangements are thought to arise most often in small, isolated populations (Patton & Sherwood 1983); precisely the conditions that would occur with the rare colonization of oceanic islands.

The presence and consistency of this pattern can be tested readily. We predict that a significant portion of the remaining 46 species of Philippine bats will exhibit standard karyotypes as distinctive as those documented thus far. Banded karyotypes should exhibit additional distinctive arrangements, even among groups showing little or no variation in standard karyotypes. Finally, we predict that studies on population genetics of species with unusual karyotypes will provide evidence of population bottlenecks that are associated with rapid and substantial genetic change.

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On the valid name of the lesser New Zealand short-tailed bat (Mammalia: Chiroptera)

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Abstract.—The lesser New Zealand short-tailed bat, sometimes known as *Mystacina tuberculata* Gray, 1843 was, for 14 years after its description, confounded with the New Zealand long-tailed bat, *Vespertilio* (now *Chalinolobus*) *tuberculatus.* This confusion can be traced to Gray's account, in which he used the name *Vespertilio tuberculatus,* attributing it to G. Forster, but also proposed the new genus *Mystacina* to receive the species. Although Gray did not make available two species-group names, two interpretations of his actions are possible, depending on who is considered to be the author of the name *tuberculatus.* If the author is Gray, *Mystacina tuberculata* Gray is composite, in which case the name must be settled on a part of that composite. If the author is G. Forster, Gray's generic name *Mystacina* is based on a misidentified type species, and there *is* no "*Mystacina tuberculata* Gray". In that case, the specific name must be replaced by the first available name, which is *velutina* Hutton, 1872, and the current usage of *Mystacina* may be preserved by choosing the zoological species before Gray as its type species. We recommend this course of action because G. Forster is properly the author of *Vespertilio tuberculatus,* and because thereby familiar usage of *Mystacina* and Mystacinidae, and current subspecific classification of *Mystacina,* are preserved. The valid name of the lesser New Zealand short-tailed bat is therefore *Mystacina velutina* Hutton, 1872, and we select Hutton's specimen from the Hutt Valley (near Wellington, North Island, New Zealand) as its lectotype.

Résumé.—Durant les 14 années qui ont suivi sa description en 1843, la petite chauve-souris à queue courte de Nouvelle-Zélande, *Mystacina tuberculata* Gray, a été confondue avec la chauve-souris à queue longue de Nouvelle-Zélande *Vespertilio* (maintenant *Chalinolobus*) *tuberculatus,* ce dernier nom lui ayant été attribué soit par Gray, G. Forster ou J. R. Forster. La confusion remonte au compte-rendu initial de Gray dans lequel il utilise le nom *Vespertilio tuberculatus* qu'il attribue à G. Forster. Dans ce même compte-rendu, Gray propose le nouveau genre *Mystacina* pour y classer l'espèce *V. tuberculatus.* Si les travaux de Gray ne rendent pas deux noms de groupes-espèces disponibles, deux autres interprétations sont possibles selon l'identité de l'auteur du nom *tuberculatus.* Si l'auteur est Gray, *Mystacina tuberculata* Gray représente un mélange d'espèces (englobant *Chalinolobus tuberculatus* et *Mystacina tuberculata*). Par contre, si l'auteur est plutôt G. Forster, le genre *Mystacina* créé par Gray est basé sur une espèce-type mal identifiée et "*Mystacina tuberculata* Gray" n'existe pas. Dans ce cas, l'épithète spécifique doit être remplacée par le prochain nom disponible, soit *velutina* Hutton, 1872 (dans le cas présent, il s'agit du premier nom disponible). Cette option permet de préserver l'usage courant du genre *Mystacina* en établissant que l'espèce-zoologique examiné par Gray représente l'espèce-type. Nous recommandons de choisir cette option pour que G. Forster soit à juste titre considéré comme l'auteur de *Vespertilio tuberculatus,* tel que stipulé dans l'article 50 du Code International de Nomenclature Zoologique. Par ailleurs, cette option permet de sélectionner un spécimen type d'un lieu connu pour *Mystacina velutina* et de préserver la classification infraspécifique actuelle de *Mystacina* ainsi que l'utilisation habituelle du genre *Mystacina* et de la famille Mystacinidae. Le seul nom valide de la petite chauve-souris à queue courte de Nouvelle-Zélande est alors *Mystacina velutina* Hutton, 1872, et nous désignons comme lectotype le spécimen de Hutton, récolté à Hutt Valley (près de Wellington, Île du Nord, en Nouvelle-Zélande).

New Zealand is home to but two endemic land mammals, both of which are bats. According to current taxonomy (e.g., Koopman 1993) they are the vespertilionid *Chalinolobus tuberculatus* (Forster, 1844) and mystacinid *Mystacina tuberculata* Gray, 1843. (A second *Mystacina* species, *M. robusta* Dwyer, 1962, first described as a subspecies of *M. tuberculata,* is thought to be extinct—Daniel 1990.) *Mystacina* is of especial interest because of its broad ecological niche, probable nearest relationship with the American noctilionoids, and long history of residence, if not also origin, in New Zealand (Pierson et al. 1986, Hand et al. 1998, Kirsch et al. 1998). In contrast, *Chalinolobus tuberculatus* is clearly a close relative of Australasian species belonging to the same genus and subgenus (Daniel 1979, 1990; Koopman 1993, 1994).

The respective families of the two New Zealand bats are widely separated in current chiropteran classifications (Koopman 1994, Kirsch et al. 1998, Simmons & Geisler 1998), yet for many years the two species were confounded (Tomes 1857). While the history of the specific classification of *Mystacina tuberculata* has several times been recounted, most recently by Hill & Daniel (1985), we believe that the nomenclatural conclusions drawn by most previous authors are incomplete, if not in error. In fact, the correct application of the name *Mystacina tuberculata* is unclear, and it is thus also unclear what the valid name is for the lesser New Zealand short-tailed bat (hereinafter, "the mystacine"). Here we attempt to clarify the history of the species' nomenclature, and to arrive at a resolution of the difficulties encountered that will best promote the stability and universality of nomenclature. We will conclude that the specific name *velutina* Hutton, 1872 must be adopted for the mystacine, and select the zoological species before Gray as the type species of *Mystacina,* so as to preserve the genus and family names in their current and, historically, sole applications.

An Historical Sketch

The first descriptions of the chalinolobe.—In May of 1773, at Queen Charlotte's Sound, South Island, New Zealand, Johann Reinhold Forster, naturalist on Cook's second voyage, shot and subsequently described, and his accompanying son George drew ("a me descriptus et a filio delineatus"—Forster 1844:63), an exemplar of the bat now called *Chalinolobus tuberculatus* (hereinafter, "the chalinolobe"). In his journal, under the date of 21 May, Forster writes, "I shot a a new Shag, never before described", and that, "[i]n the morning I described the new Shag. . . & George drew the Shag & a new Bat, which we had got" (Hoare 1982:283); as Forster used ship's time (i.e., noon of the previous day to noon of the date of entry) in dating his entries, the drawings were made on the morning of 21 May. There appears to be some discrepancy concerning the dates of collection and description of the shag: Hoare (1982) identifies it as *Pelecanus* (= *Phalacrocorax*) *carunculatus,* but Forster (1844) proposed that name under the date of 20 May, the apparent date of the shag's collection; neither Lysaght (1959) nor Hoare (1982) question the date in Forster (1844). However, the dating of events relating to the bat is consistent among Forster's writings.

Despite an Admiralty ban on publication urged by Cook (Quammen 1996), both Forsters published early accounts of their travels, in which allusions to the bat are presented; neither Forster, however, mentions the bat by scientific name in their general accounts of the 1772–1775 voyage. J. R. Forster notes the resemblance of the New Zealand bat to Pennant's "New-York bat" (Forster 1778:130 in the 1996 reprint), while George Forster (1777) is even more casual in his Voyage, stating only that the bat is one of five mammals found in New Zealand.

It was not until nearly 50 years after his death that J. R. Forster's account of the zoology of Cook's second voyage, edited by Lichtenstein, was published (Forster 1844). In it the bat is described as *Vespertilio tuberculatus* under the entry for 22 May. As we know from this description that the bat lived two days after being shot in the wing, 20 May seems probable as the date of its collection. Forster again refers to Pennant, comparing the new species to "*V. noveboracensi* [*s*]", a synonym of *Lasiurus borealis.* That the creature was regarded as a new species of *Vespertilio* is unsurprising: at the time of collection only two genera of bats were recognized—*Noctilio* Linnaeus, 1766 (placed by Linnaeus among Glires) and the vastly heterogeneous *Vespertilio* Linnaeus, 1758 (then and until Erxleben [1777] including even pteropodids, and placed within Primates by Linnaeus). In a footnote on page 62 of Forster (1844), added by the editor, comparison of *Vespertilio tuberculatus* is made to species of *Scotophilos* [sic] and *Miniopterus.* According to Whitehead (1969), no surviving mammal specimens can be traced from any of Cook's voyages, and so George's drawing, now in the British Museum (see below), is the only extant non-written evidence concerning the first bat collected in New Zealand.

While J. R. Forster's description of the bat was not published until 1844, George's illustration, with the name *Vespertilio tuberculatus* written on it, was known to British zoologists prior to posthumous publication of his father's work, as, probably, were some of both of the Forsters' manuscripts (Whitehead 1978). On the basis of this knowledge, a brief description of the chalinolobe appeared in 1843 in an appendix prepared by John Edward Gray for Dieffenbach's Travels in New Zealand. On page 181 of volume two of Dieffenbach (1843), the Forsters' bat is characterized thus:

> Fam. VESPERTILIONIDÆ.
>
> 1. *Vespertilio tuberculatus. G. Forster.* Icon. ined., n. 1.
>
> Yellowish brown; ears small, rounded.
> Inhab. Dusky Bay, New Zealand. *G. Forster.*

Hill & Daniel (1985), like Thomas (1905) before them, were of the opinion that this short characterization is sufficient to make the name available, and we agree (International Commission on Zoological Nomenclature [ICZN] 1985:Art. 12a). As will be seen, parts of this description are inaccurate; however, a description need not be accurate in order to make a name available. Taken on its face, this passage seems to indicate that G. Forster is the author; this impression is reinforced when note is taken of further passages in Dieffenbach in which Gray clearly attributes to himself names he (Gray) therein proposes. Hill & Daniel (1985), however, attribute authorship to Gray (*in* Dieffenbach 1843:181). Thomas

(1905:423) was a bit more equivocal in his attribution, giving the full citation as "Gray (ex Forst.)". Gray incontestably attributes responsibility for the name and locality (which, as we know from J. R. Forster [1844], is incorrect) to George Forster. As will become evident, the critical nomenclatural question is whether the whole of the description is attributable to George, thus establishing him as the one responsible both for the name and for satisfying the criteria that make it available (ICZN 1985:Art. 50a), or whether some part is attributable to Gray.

George Forster's drawing of the New Zealand bat.—No illustrations, by George or otherwise, appear in Forster (1844), so that Hill & Daniel's (1985) statements that George Forster's drawing was published in 1844, if intended to refer to the Lichtenstein edition, are apparently in error. George's drawing of the bat has, to our knowledge, been published only once, and then incompletely, including just one of the two figures on the drawing (Andrews 1986:28). Through the courtesy of the authorities of the British Museum (Natural History), we have been able to examine the original in London, and here publish it fully for, we believe, the first time, as Fig. 1.

The drawing of the bat is number 1 of a series of 271 zoological drawings from Cook's second voyage bound in two volumes (Whitehead 1978). Although a few of these drawings are by other artists, it is well attested that the drawing of the bat is by George (Forster 1844, Whitehead 1978, Hoare 1982). In a catalogue of these drawings ("Catalogue B" of Whitehead 1978) by one of Joseph Bank's associates, probably Dryander (A. Wheeler, pers. comm.; Whitehead [1969] agreed, but later [1978] thought Solander was its author, although this seems unlikely given Diment & Wheeler's [1984] failure to discuss this catalogue), the notation "Vespertilio tuberculatus, N. Zel. Charlotte Sound" is made in reference to the drawing. The recto of the drawing has two views of the bat, one ventral, the other lateral with wings folded. The drawing is in pencil, and the bats have been colored. The body of the upper bat is colored dark brown and a lighter shade of brown. The wings are gray. The lower bat is a more uniform dark brown, and appears to be lit from behind, with a shadow falling towards the viewer. Figure 2 is a reproduction of a sketch made from Forster's drawing which includes details not obvious in the reproduction in Fig. 1.

Below the bats, also in pencil, is written "Vespertilio tuberculatus"; in the upper right is the number "1.", and in the lower left "Geo Forster", both of the latter in ink. According to Whitehead (1978; see also Lysaght 1959), scientific names were written on the drawings by George or J. R. Forster, while George Forster's name was added later by Dryander, it being uncertain by whom and when the drawings were numbered (although certainly prior to 1843). On the verso, "New Zealand Charlotte's Sound" is written in pencil. Apparently different hands are responsible for the scientific name, artist's name, and locality. Whitehead (1978) failed to record any writing on the verso of the bat drawing, but also did not note that two figures are present, nor the notation of locality in "Catalogue B". It is possible that the verso locality was added later, perhaps even after the first publication of the correct locality by J. R. Forster in 1844; Whitehead (1978) notes that a number of later annotations were made to various of the drawings, but we consider it more likely that Whitehead inadvertently omitted this information than that the verso locality was added after 1978. Wheeler (pers. comm.) believes that the verso locality may be in the hand of J. R. Forster; if Whitehead's (1978; see also Lysaght 1959) attribution of the scientific names is to be credited, then the binominal is in the hand of George Forster.

The first description of the mystacine.—The account of *Vespertilio tuberculatus* on page 181 is not the only passage in Dieffenbach (1843) concerned with bats. In an

Fig. 1. George Forster's colored drawing of the bat obtained at Queen Charlotte's Sound, South Island, New Zealand, on or about 20 May 1773. Reproduced from a transparency, by permission of the authorities of the British Museum (Natural History), a.k.a. The Natural History Museum, London. The insets are enlarged and computer-enhanced to show more clearly some of the writing on the drawing.

Fig. 2. Pencil sketch of Forster's drawing by JG showing details not evident in the reproduction in Fig. 1. The shadowing in the lateral view of the bat has been omitted, and the distance between the two views reduced. Scale line is 2 cm.

appended note on page 296, prepared after earlier pages were already printed, Gray returns to a consideration of the Chiroptera of New Zealand, where he provides the first description of a mystacine:

> *Vespertilio tuberculatus,* p. 181.—I have just received two specimens of this bat: it is a new genus, differing from *Embalonura* [sic], Kuhl, and *Urocryptus,* Temm., in having only two large cutting teeth in the middle of the upper jaw; the fur is close, erect, dark brown, with minute white tips to the hair; the under surface is paler; the face has a series of short, rigid, black bristles round the base of the muzzle, the wings near the body and bones of the limbs are thickened and tranversely grooved; the tragus is elongate, subulate. It may be called *Mystacina tuberculata.*—J. E. GRAY.

While this account makes it clear that the two specimens before Gray were mystacines (although, significantly, it does not distinguish between the living species and the then-extant *M. robusta*), it also demonstrates that Gray believed he was describing further specimens of a bat already known: the one described for the first time on page 181. His intent on page 296 was not to name a second species, but to point out this previously known species' generic distinctness from *Vespertilio,* proposing for it the new genus *Mystacina.* (Such a separation from *Vespertilio* here is not audacious: by 1843 over 40 genera of bats had been described, many simply representing subdivisions of the once-comprehensive *Vespertilio.*)

There is only the slightest hint that Gray in 1843 might have thought there to be more than a single species of bat in New Zealand. On page 182 of Dieffenbach, following the account of *Vespertilio tuberculatus,* Gray presents two quotations with parenthetical and interpolated comments:

> "The *Pekápeká,* or Bats, and various small batlets, are very common in the Island, but none of the Vampire species. (Pteropus? or Glossophaga?) They

> are among the smallest of the Australian species."—*Polack,* i. 304. I am not aware that any of these animals have reached Europe; they would be interesting, and doubtless new. "There is, apparently, only one species; probably the one figured by Forster."—*Dieffenbach.*

Hill & Daniel (1985) reproduce only the second of the remarks quoted by Gray, as evidence that he did not (then) believe in the existence of additional New Zealand species, yet Gray's inclusion of the quotation from J. S. Polack (1838:304; imprecisely and incompletely transcribed by Gray) might suggest otherwise. But in any case, we reiterate there can be no doubt that Gray considered his two new specimens to be exemplars of the Forsters' bat. Thus Gray confounded two very different species, with consequences to be explored below.

Dieffenbach's work, with the zoological appendix entitled "Fauna of New Zealand", was published in January 1843 (Sherborn 1932); later in 1843, Gray published a List of the Specimens of Mammalia in the Collection of the British Museum, wherein he reiterated his belief in the identity of *Mystacina tuberculata* and *Vespertilio tuberculatus* (Gray 1843a; the introduction is dated "May-Day, 1843", and a copy in the library of the Field Museum of Natural History bears the manuscript annotation "May 13", without a year).

Once more in 1843, Gray returned to consider, at least briefly, the mystacine, in his contribution to The Zoology of the Voyage of H.M.S. Sulphur (Gray 1843b). While sometimes cited as the first description of *Mystacina* (e.g., Dobson 1878, Miller 1907), this work undoubtedly appeared after Dieffenbach (1843) and Gray (1843a), although, contrary to Hill & Daniel (1985), apparently not as late as 1844. The Zoology of the Sulphur was issued in parts from 1843 to 1845 (Zimmer 1926). A copy of the third part (on birds) in original wrappers in the library of the Field Museum bears the date October 1843, while the fourth part (also on birds), dated January 1844, has on the wrappers an advertisement stating that parts 1 and 2 on mammals and part 3 on birds have already been published. A bound copy of the first two parts (including the "Summary of the Voyage" in part 1, as well as the complete mammals) in the same library has a "Temporary Title" page with the date 1843. The section on mammals is also cited as 1843 by earlier authors (e.g., Tomes 1857, Dobson 1878, Miller 1907). The British Museum Catalogue's (1903–1915) date of 1844, cited by Hill & Daniel (1985), is simply in error; and there seems to be no confusion of the Zoology of the Sulphur and Captain Belcher's general account, as suggested by Hill & Daniel (1985). While thus appearing before 1844, parts 1 and 2 of the Sulphur nonetheless seem to have appeared after Gray's List (1843a; and thus also after Dieffenbach 1843), as in the main text of the List Gray cites the Sulphur by unnumbered plates, rather than by precise page and plate numbers as he does for his other works, and states (page vii) that the Zoology of the Sulphur is "now in the course of publication." He does give precise plate references to the Sulphur in a page (196) of "Corrections" likely added to the List shortly before it was published; in the Sulphur, by contrast, he gives precise page references to his List throughout. These facts indicate that the Sulphur was in preparation but not yet complete or published at the time of the writing of Gray's List (1843a).

Gray's remarks in the Sulphur also give no indication that they are intended to name a taxon. In his account (page 22), Gray explicitly states that he is only mentioning *Mystacina* and related genera "[f]or the purpose of showing the natural relations, and the distinctive characters of the two new genera [*Mosia* and *Centurio*] figured". The entire account of *Mystacina* is but three lines long, and read in context is clearly synoptic rather than descriptive: "MYSTACINA, Gray.—Nose rather produced, surrounded at the base with a series of short rigid bristles. Interfemoral membrane truncated. Cutting teeth $2/6$, upper large. *M. tuberculata,* New Zealand." Further, as Hill & Daniel (1985) remark, the *Sulphur* did not visit New Zealand, and no specimens of *Mystacina* were described in the Zoology.

Subsequent recognition of two species.—Gray (1843a), in his List, had restated his belief in the identity of *Mystacina tuberculata* and *Vespertilio tuberculatus.* The confounding of these two very different species was not recognized until Tomes' (1857) treatment of New Zealand bats, which was based on specimens in the College of Surgeons, British Museum, and Leiden collections. Therein, Tomes also reassigned *Vespertilio tuberculatus* to *Scotophilus.* Both New Zealand bat species were figured by G. H. Ford for Tomes. In coloring, Ford's plate of *Vespertilio tuberculatus* corresponds more closely to George's 1773 drawing and the characterization in Forster (1844), which Tomes accepts as the first published description of the chalinolobe, than to the description given in Dieffenbach (1843:181). Ford's lithograph is clearly not a copy of Forster's drawing, and, contrary to Andrews (1986:64), there is no indication that it is of the Forsters' specimen: as noted earlier, all of the mammal specimens from Cook's voyages appear to have been lost (Whitehead 1969).

While lamenting that the specific names of *Scotophilus tuberculatus* and *Mystacina tuberculata* were so similar, Tomes (1857: 135) realized that this was an irrelevant consideration, as the bats were undoubtedly different:

> As the above-mentioned zoologists have certainly been the first describers of two distinct animals, the names imposed by them will of course be retained; but it is much to be regretted that their specific names are similar; and the more so, as the one most recently given was clearly intended as a reference to the earlier known species.

Thus Tomes accepted Gray's description and naming of the mystacine in Dieffenbach (1843) as valid, but either discounted or (less probably) was unaware of the characterization of the chalinolobe on page 181 of the same work, while also recognizing that knowledge of the chalinolobe dates from much earlier.

Hill & Daniel (1985) note the presence of both species, properly labeled as such, among material registered by Gray in 1844 (and sent in 1843 by Dr. F. Knox from Port Nicholson [= Wellington]), which suggests that Gray had come to recognize their distinctness on the basis of his own comparisons. Nonetheless, much later Gray (1875: 12b), in the Zoology of the Voyage of the H.M.S. Erebus & Terror, acknowledged Tomes' analysis, and gave no indication that he, Gray, had distinguished the bats by himself:

> I at first thought this was the little Bat named and figured as *Vespertilio tuberculata* [sic] by Forster, collected during Cook's voyages, the drawings of which are in the Banksian Library, British Museum, and of which Lichtenstein published Forster's MS. descriptions and notes in 1844, but Mr. Tomes, who has found in the British Museum two kinds of Bats from New Zealand, believes that the one which is a *Scotophilus* is the one which Forster described, on account of the number of incisors he indicates, and describes it as *Scotophilus tuberculatus,* P.Z.S., 1857, 154 [sic: 135], *pl.* 43 [sic: 53], and he also describes and figures the one that I have described as *Mystacina tuberculata,* P.Z.S., 1857, 138, pl. 44 [sic: 54].

Gray's comments here are accompanied by a plate in which the mystacine is figured (Gray 1875:plate 22, fig. 1; probably by Waterhouse Hawkins, who did others in the series). Although not published till 1875, this plate was prepared much earlier (probably in 1844—see Günther [1875] and Hill & Daniel [1985] on the publication history of the Erebus & Terror), and had been seen by Tomes (1857), but is unlikely to be of the specimen figured in Ford's drawing in Tomes. The Erebus & Terror mystacine is shown apparently in flight, and from the dorsal aspect (presumably to show the emballonurid-like penetration of the uropatagium by the tail), "flying" from the upper left toward the lower right of the page, and with its head thrown backwards—either because that was the case in the specimen or in order better to display the face. However, details of the patagia (as well as the position of the head) are different from those in the more hieratic dorsal view in Ford's figure.

Later considerations of the chalinolobe.—Although the later nomenclatural history of the chalinolobe is not entirely without incident (Dobson [1878] confounding it with the Australian species *morio* Gray [Thomas 1889, 1905]), the details of this history need not detain us. From the point of view of our inquiries, the important action is Peters' (1867; as noted by a reviewer, though often cited as 1866, pages 657 ff. of this volume were published in 1867) proposal of the genus *Chalinolobus,* type by monotypy *Vespertilio tuberculatus.* Peters credits Forster with this binominal, but neither specifies which Forster nor gives any bibliographic citation. Fifteen species are currently included in *Chalinolobus,* six in the nominate subgenus (Koopman 1993), and the stability of their names is potentially affected by resolution of the proper application of the species-group name *tuberculatus.*

Later considerations of the mystacine.–Subsequent authors have accepted the existence of two New Zealand bat species, and have been more concerned with the peculiar ecology and broader phylogenetic affinities of the mystacine (reviewed by Daniel 1979, 1990; Kirsch et al. 1998) than with nomenclature. Important exceptions, however, are Hutton (1872), Thomas (1905), and Hill & Daniel (1985).

Hutton (1872) briefly reviewed New Zealand's bats, and, like Tomes, regretting the similarity of the specific names of the chalinolobe and mystacine, proposed the species-group name *velutina* for the mystacine; his comments were based on two specimens of the mystacine then in the Colonial Museum. Thomas (1905), having had his attention called to the two passages on bats in Dieffenbach (1843), which he had previously overlooked, concluded that the brief description of the chalinolobe under the name *V. tuberculatus* on page 181 preempted Gray's page 296 usage of the specific name for the mystacine, and therefore Thomas adopted Hutton's name *velutina* for the mystacine. Thomas was likely influenced by the fact that, although published in the same work, and thus simultaneously, the account on page 181 was clearly written before that on page 296, and so held a sort of temporal, as well as page, priority. (Oddly, while Thomas credits Miller and Palmer with alterting him to Dieffenbach, Miller [1907] does not himself cite that publication in his account of the mystacine, and uses the specific name *tuberculatus* for it.)

Both Thomas and Miller used the generic name *Mystacops* Lydekker for the mystacine. *Mystacops* had been proposed as a replacement name by Lydekker (*in* Flower & Lydekker, 1891) in the belief that *Mystacina* was preoccupied by *Mystacina* Boie, 1822 (a genus of birds). However, as pointed out by Simpson (1945) and Dwyer (1962), Boie's (1822) name was *Mystacinus,* and the difference in ending is sufficient to prevent homonymy (ICZN 1985: Art. 56b).

Hill & Daniel (1985), in a study of geographic variation in the mystacine which included a careful study of extant specimens at the British Museum and a review of the species' nomenclature, differed with Thomas (1905). While accepting his conclusion that the chalinolobe had been properly named in Dieffenbach, they rejected his conclusion that this necessitated the adoption of *velutina* for the mystacine. They rejected this on two grounds: first, on the irrelevant basis that Thomas' proposal had not been generally adopted; and, second, on the ground that no provisions of the Code required such a change. As we shall see, this latter point is problematic. The essence of their analysis is that, in Dieffenbach, Gray proposed two different species-group names for two different zoological species. But, as we have already seen in this historical review, and will explore further below, such was certainly not the case.

Analysis

Two species-group names or one?—The two bat descriptions in Dieffenbach—that on page 181 relating to George Forster's drawing, and the one on page 296 referring to the two mystacine specimens—create a nomenclatural problem, as was first appreciated by Thomas (1905). Are two species-group names proposed in Dieffenbach or only one? The preceding historical sketch makes it certain that Gray regarded both the bat illustrated by George Forster and the two specimens Gray later received as members of the same species. Thomas (1905: 423) also saw this clearly, noting that when Gray discussed the mystacine on page 296 he did so "distinctly stating his opinion that it was the same bat" as was mentioned on page 181. On page 296, Gray had no intention of naming a second species, and in fact did not do so. We can thus state categorically that only one specific name was proposed in Dieffenbach (1843).

Given that but one name is proposed, much depends on who we suppose the author of that name to be. If it be Gray, as Hill & Daniel (1985), and, somewhat less emphatically, Thomas (1905) concluded, then *Mystacina tuberculata* is composite (the syntypical series including a chalinolobe and two mystacines), and the name must be fixed on one part or the other. If, on the other hand, the author is George Forster, as Sherborn (1931), definitely, and Dwyer (1962), apparently, concluded, then the name refers unequivocally to the chalinolobe, and the mystacine requires a name. A further consequence of G. Forster's authorship would be that the genus *Mystacina* would then be based on a misidentified type species (ICZN 1985:Art. 70b), as Gray mistakenly believed his two mystacines to be conspecific with the chalinolobe in George's drawing.

The question of authorship hinges upon who provided the name and the conditions that make it available (ICZN 1985:Art. 50a), and this in turn depends on the interpretation of the passage on page 181 of Dieffenbach. In order for authorship of a name to be attributed to someone other than the author of the work in which it appears, the Code requires that the evidence for this attribution be "clear from the contents of the publication" (ICZN 1985:Art. 50a). A straightforward reading of page 181 seems to indicate that this requirement is met: Gray is attributing the name and the conditions that make it available to G. Forster. It is undeniable that Gray attributes both the name and the locality to George, and the name appears on George's drawing, likely in his own hand, and thus George surely has provided at least one of the two elements that the Code requires; but, it might be contended that Gray has provided the description that makes the name available. The question is, in short, who wrote the five words of description on page 181?

Whose words are they?—That Gray cites G. Forster on two of the lines on page 181 could mean that the intervening line containing the five words was his (i.e., Gray's); but it could equally plausibly mean that Gray merely wanted to make clear the source of the name, as distinct from the other information, which he also attributed to George. Gray need not have put Forster's name at the end of every line in order to make an attribution to George. Indeed, in his account in Dieffenbach (1843) of the "Sea Bear" (*Arctocephalus ursinus* [Linnaeus, 1758], now *Arctocephalus forsteri*), Gray gives information which comes directly from the Forsters (which we know because the Forsters' notes survive on George's drawing or in "Catalogue B"—Whitehead 1978) without immediate attribution, showing that he did not always put Forster's name after every line derived from him. In the account of the bat, Gray was, if anything, more careful and explicit in citing George twice, perhaps because a newly proposed name was involved, whereas the "Sea Bear" had been named previously.

Gray does himself name and describe several new species in Dieffenbach, but when doing so follows the new species' name with "Gray, n.s.", then the locality, and finally the description; this is not the format he follows on page 181, in which the words of description are enclosed within attributions to G. Forster. Since the only plausible interpretation of Gray as the author would have him describing George's drawing, it is significant that one of the new species names proposed by Gray (*Balaena antipod*[*ar*]*um,* now *Eubalaena australis*) is based on the description of a drawing, and that Gray is quite explicit about that basis (page 184): "The above short description of this species is taken from a very good drawing . . .". No such statement of derivation accompanies the account of the bat.

The description might credibly be attributed to Gray if it consisted of a characterization of George's drawing. The fact that the locality given on George's drawing does not match that cited as from G. Forster on page 181 suggests that Gray was working from some written notes by George, and not just the drawing. Perhaps even more persuasive evidence that Gray was not working from the drawing alone is that its color does not correspond to that given in Dieffenbach ("Yellowish brown"; cf. Fig. 1). These notes could not have been J. R. Forster's manuscript descriptions (eventually published in 1844), because the latter give a locality ("in estuario reginae Charlottae" [Queen Charlotte's Sound]—Forster 1844: 63) and color description ("Alae . . . fuscae, ... Vellus ubique . . . fusco-ferrugineum" [Wings . . . dusky, ... Fur dark-rusty brown all over]—Forster 1844:64) different from those on page 181 of Dieffenbach, and, in any event, Forster's manuscript had long been in Berlin by the time Gray was writing. Unless he was simply making things up, Gray must have been working from written material by George, because the source is clearly neither the drawing nor J. R.'s manuscript. That some of the Forsters' manuscripts have been lost is undeniable: Whitehead (1978) records that the Forsters furnished information to Joseph Banks, the documents of which no longer survive, and George's extant journal ends at 11 May, eight days before the Resolution reached Queen Charlotte's Sound (Hoare 1982).

How might George have been the source of erroneous locality and color information? Dusky Bay was visited by the Resolution, and it figures prominently in George's extant journal (Whitehead 1978); it is also, as H. Spencer (in litt.) has pointed out to us, the locality of the "Sea Bear", the subject of the second of George Forster's drawings, on the verso of which the locality is written, and Gray (*in* Dieffenbach 1843:182) did cite this drawing in his account. Gray may just have made a hasty inference or transcription error. As regards the color, notes from the Forsters in "Catalogue B", reproduced in Whitehead (1978), make it clear that their remarks on coloring often consisted of critiques of the drawings; thus "Yellowish brown" could be an admonition for modulation of the applied color, rather than a description. Gray, never having seen the bat, could not have known the import of such a note.

Absent written evidence, we cannot now know for sure whether the five words of description are Gray's or George's but given the citation of G. Forster, both following the name and at the account's conclusion, it was clearly Gray's intent to attribute the name and description, and thus authorship of *Vespertilio tuberculatus,* to the younger Forster. This conclusion is strengthened by looking at Gray's List published a few months later (1843a:34), which reads "The Mystacine. Mystacina tuberculata, Gray, Dieffenb. Jour. App. 296. Vespertilio tuberculatus, G. Forster, Icon. ined. in Brit. Mus. t. 1." As is clear from the form of citation Gray uses in his List, this passage indicates that Gray attributes to himself the combination *Mystacina tuberculata,* while he attributes the specific name *tuberculatus* to G. Forster (which also demonstrates, as we believe is patent from Gray in Dieffenbach as well, and as Sherborn [1931] also indicated, that Gray did not consider himself to have proposed a new species *tuberculata* in the genus *Mystacina,* but rather to have placed Forster's species *V. tuberculatus* in the new genus *Mystacina*). It is clear that the name came from G. Forster, that all knowledge Gray had of the species came from Forster's work (the drawing and perhaps manuscripts), and that Gray attributed the name and the description to Forster. We should not cast aside these certainties as to the source of the name, knowledge of the species, and Gray's own attribution.

Thus, it is our judgment that the description is more likely to be George's than Gray's—and therefore that George not only named the bat, but also satisfied the conditions that make that name available. All the internal evidence of the contents of the publication—of Gray's attributions, citations, and format—indicates that, under Article 50a, authorship should be attributed to George Forster. The external evidence—the lack of correspondence between the drawing and the published account, Gray's later publications—even if it were admissible under Article 50a (which it is not), also fails to support the contention that Gray is the author. The name is thus properly cited as *Vespertilio tuberculatus* G. Forster *in* Dieffenbach, 1843:181.

The consequences of G. Forster as author.—On the interpretation that the description as well as the name on page 181 are George Forster's, and therefore that he and not Gray made that name available, an inescapable conclusion is that there is no such name as "*Mystacina tuberculata* Gray *in* Dieffenbach, 1843"; there is only *Mystacina tuberculata* (G. Forster *in* Dieffenbach, 1843) sensu Gray, 1843 (ICZN 1985: Art. 51b(i)). Gray confused the two specimens before him, and thus also the type species of *Mystacina,* with Forster's *Vespertilio tuberculatus.* This leaves the bats before Gray without a species-group name, and the genus *Mystacina* with a misidentified type species. We consider these two issues in turn.

The species-group name of the mystacine.—"*Mystacina tuberculata* Gray *in* Dieffenbach, 1843:296", being a misidentified type species, rather than the proposal of a new species, cannot possibly be the name for this bat. Gray did use this combination in several other publications (e.g., 1843a, 1843b), and it might be argued that these accounts make the name *tuberculata* available in *Mystacina* as of these publications. The Code, however, explicitly prohibits this: Article 49 states that "[a] previously established species-group name wrongly used to denote a species-group taxon because of misidentification cannot be used for that taxon even if it and the taxon to which the name correctly applies are in, or are later assigned to, different genera . . .".

The valid species-group name of the mystacine must thus be the next available name, which, in this case, is actually the first available name (ICZN 1985:Art. 23e): *velutina* Hutton, 1872. This name was introduced by Hutton to replace "*tuberculata* Gray". It is not, however, strictly speaking, a replacement name in the sense of the Code. A replacement name is proposed to replace an available name, but "*tuberculata* Gray" is not an available name, and was not intended to be one by Gray. Thus Article 72e, on the typification of replacement names, does not apply. Article 72b(ii) and (iv), on the type series of names based in whole or part on previously published misidentifications or unavailable names, does apply, and thus the type series of *Mystacina velutina* consists of all specimens before Hutton, plus Gray's two specimens.

Gray's specimens cannot now be traced (see below), and, given the recognized geographic variation in the lesser mystacine, and the existence in the 1840s of a second species of mystacine (*M. robusta*) in the environs of the South Island, their lack of specific locality data makes them a poor choice to be name bearers. The current whereabouts of the two specimens examined by Hutton in 1871 are also not known. They are not in the National Museum in Wellington; the earliest extant bats currently in that collection were presented in 1877, virtually all the earlier collection having been destroyed by damp and mold in the 1880s–1890s (C. Paulin, in litt.). It was the practice of the Colonial Museum to send type specimens from New Zealand to the British Museum, but such specimens were often not clearly labeled as such, and may have been accessioned into the British Museum collection under some other name, and without their nomenclatural importance being noted (C. Paulin, in litt.). Dobson (1878) records two specimens in the British Museum, "e" and "f" of his list, from "Wellington, New Zealand" received from the Colonial Museum. Hill & Daniel (1985) note that only one of these two was registered, in 1876: BM(NH) 76.4.8.1. It seems quite possible that Dobson's "e" and "f" (including BM(NH) 76.4.8.1) were those before Hutton from the Colonial Museum ("Wellington" recording from where they were sent, rather than the exact locality), but we cannot now be certain of this.

Although they cannot be traced with certainty, Hutton's specimens do have exact localities: "the Hutt Valley, near Wellington" and "Milford Sound, on the southwest coast of the South Island." This is fortunate, as Hill & Daniel (1985:290) have based their subspecific arrangement on a conception of the nominate form as occurring near Wellington. We thus ratify and preserve the nomenclatural stability of their arrangement by selecting as lectotype of *M. velutina* Hutton, 1872 the specimen from the Hutt Valley, near Wellington (ICZN 1985:Art. 74c). Being on the North Island, this locality also excludes the possibility of confusion with the extinct *M. robusta,* as Wellington is outside its historic range (Daniel 1990).

It is worthwhile noting here that the use of *velutina* is in no way in violation of the presumptive statute of limitation which gives the benefit of the doubt to stability when it conflicts with priority (ICZN 1985: Art. 79c). This provision applies to the proposed substitution of an unused senior synonym for a junior synonym, not the substitution of an available name for an unavailable name. Nor does it violate the stronger injunction against the displacement of names in the fourth edition of the Code (ICZN 1999), which again does not apply to unavailable names; and in any event, *velutina* has been used as a valid specific name after 1899 (Minelli & Ride 1997).

The generic name of the mystacines.—In the following, we apply the provisions of the fourth edition of the Code (ICZN 1999), on the recommendation of Dr. P. Tubbs, Executive Secretary of the ICZN, to use these provisions during the interregnum between publication of the new edition and its effectuation, as during this time action by the Commission under Article 70 of the third edition of the Code is no longer possible or, indeed, necessary under the new edition. Explicit provision is made for cases where an author erects a new genus on the basis of specimens to which he has applied the wrong specific name, the applicable section in the fourth edition being that on misidentified type species in Article 70. The article lays out two courses of action which an author discovering such a case may take: either to let the species mentioned by the author of the genus, regardless of misidentification, remain as type species of the genus (i.e., *Vespertilio tuberculatus* G. Forster would be the type species of *Mystacina*); or, to designate the species actually before the author of the new genus as the type species. The principle that we believe should guide action in this case is that types of taxa are zoological objects, not names (Mayr 1969). Thus we believe that the species actually before Gray should be the type of *Mystacina.* We have already noted that Gray's description, while diagnostic to genus, does not exclude the possibility that he may have had a specimen of *M. robusta,* and the locality, "New Zealand", ascribed to Gray's specimens in his List does not allow us to exclude *M. robusta* on geographic grounds, either. However, in historic times the lesser mystacine (*M. tuberculata* auctorum) has been more widespread and abundant than *M. robusta,* and no specimens of the latter are certainly known to have been collected in the 19th century. In addition, the specimens provided by Sir George Grey, which we believe may have been Gray's specimens (see below), are of the lesser mystacine. We are thus confident that at least one of the two specimens before Gray was of the lesser mystacine, and this species, of which we have shown *velutina* Hutton, 1872 to be the valid species-group name, should be the type species of *Mystacina.*

This action would also promote the stability and universality of nomenclature. Were the misidentified species to remain the type species of the genus, it would disassociate *Mystacina* Gray, 1843 from all zoological species with which it has ever been associated; make *Mystacina* Gray, 1843, by virtue of its becoming a senior objective synonym of *Chalinolobus* Peters, 1867, the valid generic name for the chalinolobe and its fourteen congeners, forcing a change in the names of these species; make Mystacinidae a family name in a section of the Microchiroptera distant from its usual application in or near the Noctilionoidea; and leave the mystacines without a generic or family name, leading to further nomenclatural changes. (*Mystacops* Lydekker, 1891, and the family name based on it, Mystacopidae Miller, 1907, do not help here, inasmuch as *Mystacops,* being a replacement name sensu stricto, takes the same type species as *Mystacina,* and would thus also apply to the chalinolobe—ICZN 1985:Art. 67h.)

In contrast, having the species actually before Gray as type species of the genus would allow the name *Mystacina* to continue to be the valid generic name for the endemic noctilionoid bats of New Zealand, as it has been assumed to be since 1843; allow Mystacinidae to continue in its familiar application; and lead to no changes in the nomenclature of the chalinolobe and its congeners. We thus hereby designate the zoological species we believe to have been before Gray, the valid specific name of which is *velutina* Hutton, 1872, as the type species of *Mystacina* Gray, 1843. Should it later be shown that both of Gray's specimens were *M. robusta*—an eventuality we consider highly improbable—then *M. robusta* Dwyer, 1962, as the only zoological species before Gray, would be the type species of *Mystacina,* and familiar usages of the generic and familial names would again be preserved.

What if Gray were the author?—Though we believe that a preponderance of the evidence, including, most trenchantly, the contents of Dieffenbach (1843), leads to the conclusion that George Forster is the author of the description of the chalinolobe, we acknowledge the possibility that it might be Gray. It is therefore useful to explore the implications of this assignment of authorship. We believe that these implications, though not admissible in deciding authorship, offer additional justification for our choice in favor of George.

On the interpretation that Gray is the author, *Mystacina tuberculata* is a composite species because Gray considered the Forsters' bat and the two later-received specimens to be conspecific, thus forming a compound syntypical series (ICZN 1985: Art. 72b); although the two mystacines were seen later by Gray, publication on the three specimens (i.e., the mystacines and the Forsters' bat), because in the same work, was simultaneous. In this case, *Mystacina tuberculata* must be settled on one or the other part of Gray's composite series.

We imagine that most zoologists would agree that the (or a) mystacine would be the logical choice to bear the name, as this was the zoological species before Gray. But before we can decide this issue, we should consider the implications of the two alternatives, and whether a previous author may have already settled the issue. There are two candidates: Dobson (1878), who, apparently inadvertently, attempted to fix the name *tuberculata* on the mystacine; and Thomas (1905), who deliberately chose the chalinolobe.

Dobson's view.—Dobson (1878:445), although not at all appreciating the nomenclatural conundrum (he in fact seems to have been unaware of Dieffenbach [1843]), comes near to settling the issue by referring to specimen "a" in his list of specimens of *Mystacina tuberculata* as the "type". Were this one of the two specimens which Gray had mentioned in Dieffenbach (presumably "a" and "b" in Gray's 1843 List), this would be a valid designation of a lectotype (ICZN 1985:Art. 74a), and the name would be fixed on the mystacine. It is unlikely, however, that Dobson's "a" was one of Gray's specimens. Dobson further states that "a" is the specimen figured in The Zoology of the Erebus & Terror. In the text accompanying this figure, Gray (1875:12b; see quotation above) does not identify the specimen figured, and certainly does not indicate that it is part of his original series. Because much, if not all, of Gray's mystacine material had been turned over to Tomes for the latter's use in writing his 1857 paper, and was seemingly not returned to the British Museum until 1905 (Hill & Daniel 1985), it may be that Dobson never viewed all of the British Museum specimens; and Gray was dead by the time Dobson's catalogue appeared. Thus it is distinctly possible that Dobson's statements are merely conjectural.

Hill & Daniel (1985) have looked carefully into the question of the identity and location of Gray's specimens, examining the accession registers and specimen labels, but unfortunately they have not been able to ascertain with certainty which, if any, of the specimens currently present in the British Museum are Gray's two bats, nor the identity of Dobson's specimen "a". They did, however, uncover evidence which appears to rule out Dobson's specimen "a" from being one of Gray's specimens, thus invalidating it as a lectotype. Thomas annotated specimen "a" in a copy of Dobson's Catalogue at the British Museum with the following note: "Dr. F. J. Knox(P).—see Trans. N.Z. Inst. IV, p. 186, 1871" (Hill & Daniel 1985:286). If Thomas's annotation is correct, then specimen "a" cannot be the type, as Knox (1872) states that he sent his shipment to the British Museum in or following July 1843, after Gray had already published in Dieffenbach. Perhaps Knox, writing in 1871, misrecalled what he had done almost 30 years earlier, in which case his specimen could have been before Gray in 1842, but there is no independent evidence of this, and Knox in his 1872 article refers to notes he had written in 1843 or earlier. Hill & Daniel (1985) have suggested that BM(NH) 44.10.29.7, sent by Knox, may be Dobson's specimen "a", but the date of accession (29 October 1844) lends no support to the notion that it might have been before Gray in 1842. The only thing about which we can be certain is that for Dobson's "a" to be the type, one or more authorities must be mistaken about the identity of the specimen and/or the circumstances surrounding it.

Given that a number of errors in specimen identification and labeling have been discovered in Dobson's Catalogue (Thomas 1905), we are reluctant to assume that Dobson was correct in this case, as no supporting evidence in Gray's publications, the accession registers, specimen labels, or Thomas's subsequent inquiries, is forthcoming; and, if Thomas's annotation is correct, specimen "a" cannot be the type. Hill & Daniel (1985) consider other possibilities for the types, but do not seriously entertain that a specimen ("c" of Dobson's Catalogue) from 1842 provided by Sir George Grey might be one of the type series (even though Gray [1843a] specifically mentions Grey's collection), perhaps because it is not an adult and Hill & Daniel's subspecies-level taxonomy depends heavily on size differences. The accession number of Grey's specimen indicates that it had been at the Museum since at least February, although

Gray was unaware of it when writing the main body of his contribution to Dieffenbach (1843), which is dated "15th August, 1842" on page 181. We do not now know if Gray became aware of the specimen between this date and the publication of Dieffenbach, so that Grey's specimen could have been one of the two specimens referred to on page 296. Sir George Grey also provided a second still-extant specimen (labeled "c*"—Hill & Daniel 1985), catalogued in 1849; if this specimen was a duplicate from 1842 catalogued later, Grey may well have provided both of Gray's bats.

W. D. L. Ride (in litt.) has suggested that Dobson's (1878) specimen "b", attributed by Dobson to Captain Belcher of the *Sulphur,* may have been one of Gray's specimens. Although the *Sulphur* did not call at New Zealand, and Gray (1843b) does not refer to any mystacine specimens, Ride notes that Belcher was an avid collector, and could have received a specimen from his assistant surgeon Andrew Sinclair. Sinclair left the *Sulphur* voyage early to return to England via New Zealand, and collected at the Bay of Islands in 1841, where he may have obtained mystacine specimens. That Knox, Grey, and Belcher (through Sinclair) can all be argued to have provided Gray's bats shows how difficult it is to identify their source or possible current whereabouts.

Hill & Daniel (1985) ultimately concluded that they could not identify the types, and based their conception of the nominate form on BM(NH) 44.10.29.7, a specimen which, if Knox is to be believed, could not possibly be a type.

A further problem with all of the candidates is that none has exact locality data. This is a serious shortcoming, because Hill & Daniel (1985) base their subspecific taxonomy of *M. tuberculata* on the supposition that the nominate form occurs in the Wellington area. As noted earlier, it is even conceivable that Gray's specimens might have included *M. robusta.* At least some early specimens, including perhaps Gray's, came from the South Island and vicinity, and thus within or near the historic range of the now-extinct *M. robusta*; both Hutton and Knox mention a specimen (probably the same one) from as far south as Milford Sound, bats at least occasionally being caught in the rigging of ships plying the South Island coast. Ascribing authorship to Gray and fixing the name on the mystacine thus results not only in the name having a vague locality, but also injects some uncertainty into its specific identity.

Fixing *tuberculata* on the mystacine would give authorship of *Vespertilio tuberculatus* for the chalinolobe to J. R. Forster (1844), although there is some question as to whether *tuberculatus* might be preoccupied in *Vespertilio* by Gray's usage of it in Dieffenbach (1843). The Code is not explicit on this point, but the implication of Article 51c(ii) seems to be that since the proposal of *Mystacina* was not conditional, then *tuberculatus* is not preoccupied. J. R. Forster is cited as the author ("Forster, 1844") in Koopman's authoritative list of 1993 (but not in Koopman's 1994 monograph, prepared earlier than the 1993 list, where he attributes the names of both New Zealand bats to Gray, 1843, apparently accepting the judgments of Hill & Daniel [1985]).

In short, accepting Gray as the author and settling the name of the resulting composite on the mystacine leaves us without a type specimen or type locality, and thus also even without unequivocal correspondence of the name with the extant mystacine species, though it has a superficial appeal in that it would preserve one version of current usage and attribution for both the mystacine and chalinolobe.

Thomas's view.—Of all authors who have considered the mystacine problem, Thomas (1905) came closest to understanding the situation. He realized that both New Zealand bats had been discussed in Dieffenbach (1843), but that only one species-group name had been proposed, so that the name could apply to only one or the other. He apparently regarded the description of *Vespertilio tuberculatus* on page 181 of Dieffenbach as originating with Gray, and therefore that the same author's later description of *Mystacina tuberculata* on page 296 was invalidated by page priority. He thus settled what he took to be Gray's specific name on the chalinolobe. Thomas's claim to have acted as first reviser and settled the question is strengthened by his having clearly been the first to realize that a choice between two courses of action was necessary, and to have made one; and his mention of Forster's figure, and citation of Gray's name as "ex. Forst.", comes close to (although, because he did not use the word "type", not quite) designating a lectotype. It is clear that he intended to restrict application of *tuberculatus* to the chalinolobe, and may have done so according to the nomenclatural standards then prevailing, even if his actions are not conclusive under today's Code.

While appreciating Thomas's insight, we hasten to add that, unless we are willing to consider that an author (in this case Gray) may have misidentified a type species which he himself has authored in the very same publication (a possibility whose illogic makes us loath to contemplate it), Thomas's restriction leads necessarily to all of the unfortunate consequences enumerated above which flow from having the chalinolobe as the type species of *Mystacina.* Thomas overcame these difficulties, in part, by using *Mystacops* for the mystacine, which may have sufficed under nomenclatural rules as then understood; but, as we have already shown, under the current Code, *Mystacops* must always be an objective synonym of *Mystacina,* and thus the unpleasant consequences still follow.

What is to be done?

We believe the weight of the evidence indicates that the description of the chalinolobe on page 181 of Dieffenbach (1843), and hence authorship of *Vespertilio tuberculatus,* should be attributed to George Forster. It is clear from the contents and format of Dieffenbach (1843) that Gray was attributing the species' name and description to another, and thus that "some other person is alone responsible both for the name and for satisfying the criteria of availability" (ICZN 1985:Art. 50a)—that other person being George Forster. Gray never subsequently explicitly attributed the name to himself. Attempts to attribute the conditions of availability to Gray by appealing to the contention that he was describing George's drawing fail on the ground that the description does not correspond to the drawing, and also run afoul of Article 50a's specific admonition that such questions of authorship are to be determined by the "contents of the publication", and not by reference to external evidence. We are not entirely alone in honoring George Forster: Sherborn (1931:6670) cites the name as "G. Forster in J. E. Gray in Dieffenbach, Trav. N. Z. II. 1843, 181." Dwyer (1962) also appears to accept George as author, for he attributes the name to G. Forster in his first mention of the chalinolobe (and elsewhere just to "Forster"). Having once settled authorship upon George Forster, all else follows unambiguously: all species-group names have a firm basis in either extant types (*robusta, aupourica, rhyacobia*) or well-established type localities (*tuberculatus, velutina*) which are in harmony with the current subspecific and specific arrangement, insuring the nomenclatural stability of these names into the indefinite future; the names *Mystacina* and Mystacinidae continue in their familiar applications; and no changes of name are required in the genus *Chalinolobus.* The only drawback of this decision is that it requires use of the specific name *velutina* Hutton for the lesser mystacine, which has not been used since earlier in this century.

The other route, supposing Gray to be the author, makes us choose between Dobson and Thomas: it leads to a chain of uncertainties and difficulties, concerning the specimens before Gray, and whether any of these are still extant; whether Dobson's supposed type was one of these specimens, and thus if he had fixed the specific name on the mystacine; whether Thomas's annotations to Dobson's catalogue are accurate; whether Knox in 1871 correctly recalled the circumstances of his shipment of specimens to the British Museum almost 30 years earlier; and whether Thomas validly settled *tuberculatus* on the chalinolobe. Although by judicious resolution of these several uncertainties we might retain *tuberculatus*(*a*) as the specific name of both extant New Zealand bats, we might also lose some type localities; upset the subspecific classification of *Mystacina,* even introducing uncertainty into its specific classification; make *Chalinolobus* an objective synonym of *Mystacina*; transfer the latter name to a segment of the Chiroptera phylogenetically distant from that to which the name has long applied; leave the mystacines without generic or family names, thus requiring the proposal of new names; and, unlike our proposed course of action, might well require exercise of the plenary power by the Commission. And, whatever resolution we might come to, it would be based on a series of doubtful inferences: a compounding of uncertainties, a multiplication of improbabilities. We thus prefer to resolve the initial uncertainty in favor of G. Forster, as we believe that this is not only correct and historically true, but will do the most to promote the stability and universality of nomenclature.

Synonymy.—Adopting the course here recommended leads to the following synonymies of the names concerned. For the chalinolobe, only the specific synonymy is given, as the generic synonymy would lead us far astray from New Zealand. For the mystacines, familial, generic, specific, and subspecific synonymies are given. They are complete, we believe, as regards synonyms and combinations, but only a few of the more salient citations to each name or combination are given. Further citations may be found in the references in Hill & Daniel (1985), Daniel (1979, 1990), Hand et al. (1998), and Kirsch et al. (1998).

Chalinolobus tuberculatus (G. Forster)

Vespertilio tuberculatus G. Forster *in* Dieffenbach, 1843:181. "Dusky Bay, New Zealand", in error; correctly given as "in estuario reginae Charlottae" (= Queen Charlotte's Sound, South Island, New Zealand) by J. R. Forster, 1844:63. Type lost (Whitehead 1969); drawing of type by George Forster in British Museum (Natural History).

Mystacina tuberculata.—Gray, 1843a:34 (part).

Scotophilus tuberculatus.—Tomes, 1857: 135; Hutton, 1872.

Chalinolobus tuberculatus.—Peters, 1867: 680; Dobson, 1878 (part); Thomas, 1905; Dwyer, 1962; Hill & Daniel, 1985.

Miniopteris [sic] *morio.*—Gray, 1875:12a (?part). Although Gray states "Inhab. Australia", Hill & Daniel (1985:288), following unpublished notes by Thomas, suggest that the specimen illustrated (as *Scotophilus morio*; see next entry) was from New Zealand.

Scotophilus morio.—Gray, 1875:plate 19, fig. 2 (?part). Placed in the genus *Miniopteris* [sic] in the text; supposed by Hill & Daniel (1985) to be of a specimen from New Zealand (see previous entry). The plate may have been prepared as early as 1844 (Tomes 1857), and thus represents Gray's earlier opinion concerning the species' generic position.

Chalinolobus morio.—Thomas, 1889:462 (part); Flower & Lydekker, 1891 (part).

Chalinolobus tumorio Flower & Lydekker, 1891:671 (part; apparently a lapsus for *Chalinolobus morio,* but perhaps arising from an incomplete striking of "tuberculatus", which was overwritten by "morio"; not an available name).

Mystacinidae Dobson

Mystacinae Dobson, 1875:349. Type *Mystacina* Gray. Proposed as a "Group" (=

tribe, and thus a family-group name [ICZN 1985:Art. 35a]).

Mystacopidae Miller, 1907:239. Type *Mystacops* Lydekker (a replacement name for *Mystacina* Gray).

Mystacinidae.—Simpson, 1945:60. First use with correct suffix (ICZN 1985:Art. 11f).

Mystacina Gray

Mystacina Gray *in* Dieffenbach, 1843:296. Type *Vespertilio tuberculatus* G. Forster *in* Dieffenbach, 1843:181 sensu Gray *in* Dieffenbach, 1843:296 = *Mystacina velutina* Hutton, 1872.

Mystacops Lydekker *in* Flower & Lydekker, 1891:671. Replacement name for *Mystacina* Gray, erroneously thought by Lydekker to be homonymous with *Mystacinus* Boie, 1822. Type *Vespertilio tuberculatus* G. Forster *in* Dieffenbach, 1843:181 sensu Gray *in* Dieffenbach, 1843:296 = *Mystacina velutina* Hutton, 1872.

Mystacina velutina Hutton

Mystacina tuberculata.—Gray *in* Dieffenbach, 1843:296; Gray, 1843a (part), 1843b, 1875; Tomes, 1857; Dobson, 1878; Hill & Daniel, 1985.

Mystacina velutina Hutton, 1872:186. "[T]he Hutt Valley, near Wellington", North Island, and "Milford Sound, on the southwest coast of the South Island", New Zealand. Lectotype herein designated to be the Colonial Museum specimen from the Hutt Valley (see text for the fate of this specimen).

Mystacops velutinus.—Thomas, 1905:423.

Mystacops tuberculatus.—Miller, 1907: 241.

Mystacina tuberculata tuberculata.—Dwyer, 1962:3.

Mystacina velutina velutina Hutton

Mystacina velutina velutina, New combination.

Mystacina velutina aupourica Hill & Daniel

Mystacina tuberculata aupourica Hill & Daniel, 1985:294. "Omahuta Kauri Sanctuary, Northland, North Island, New Zealand". Type Auckland Institute and Museum (AIM) M309.

Mystacina velutina aupourica, New combination.

Mystacina velutina rhyacobia Hill & Daniel

Mystacina tuberculata rhyacobia Hill & Daniel, 1985:295. "Te Rimu area, upper Waimarino River, Kaimanawa Forest Park, SE of Lake Taupo, central North Island, New Zealand". Type AIM M304.

Mystacina velutina rhyacobia, New combination.

Mystacina robusta Dwyer

Mystacina tuberculata robusta Dwyer, 1962:3. "Big South Cape Island", Stewart Island region, New Zealand. Type Dominion Museum 1083. Daniel, 1979.

Mystacina robusta.—Hill & Daniel, 1985: 297; Daniel, 1990.

Acknowledgments

We wish to express our thanks to the authorities of the British Museum (Natural History) for facilitating inspection of George Forster's drawing, granting permission to reproduce it, and discussing Forster's work, especially to A. Datta, V. Skeet, and A. Wheeler; B. Williams (Field Museum of Natural History) for providing access to earlier literature and assistance in dating it; C. Paulin (National Museum, Wellington) for information about specimens in the Colonial Museum; W. D. L Ride and P. Tubbs (ICZN) for advice concerning the fourth edition of the Code; D. Lee and H. Spencer for reminding us of Andrews (1986); T. Griffiths for providing copies of literature; W. Feeny and D. Lintner for reproducing the figures; M. Clayton for nautical advice; T. Griffiths and L. Ruedas for comments on the manuscript; and especially to W. D. L. Ride for extensive discussions.

Late in the preparation of the manuscript we became aware that H. Spencer and D. Lee (Otago) were pursuing a parallel investigation of the nomenclature of New Zealand's bats. We are most grateful to them for sharing their views with us, and for much discussion of the issues involved. We are encouraged that our independent analyses agree on many points, but regret that certain points of difference remain.

Although as yet unpublished, Spencer and Lee are making an application to the International Commission on Zoological Nomenclature (Case No. 3095 "*Mystacina* Gray, 1843, *Chalinolobus* Peters, 1866, *M. tuberculata* Gray, 1843 [currently *C. tuberculatus*] [Mammalia, Chiroptera]: proposed conservation of usage." BZN 55: 205). Note that Case No. 3095 does not support the arguments and resolution here proposed. Also, an application means (under Article 80) that current usage is to be maintained until a ruling is made.

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Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 8. A provisional hypothesis for the hybrid origin of *Zodalia glyceria* (Gould, 1858)

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Abstract.—*Zodalia glyceria* (Gould, 1858), supposedly from the vicinity of Popayán, Colombia, is hypothesized to be a hybrid between *Lesbia victoriae* and *Chalcostigma herrani,* which are sympatric in shrublands and timberline ecotones in the Andes from southern Colombia to northern Peru. Those portions of the capital, spinal, and ventral feather tracts that exhibit green iridescence in the parental species are greenish-blue to purple in the hybrid, depending upon the angle of observation. For example, the dominant wavelength reflected from back plumage is much shorter in the hybrid (505 nm) than in either of the parental species (561–576 nm). This color shift is thought to have been caused by a developmental aberrancy, possibly associated with hybridization, which affected melanin granules that produce iridescence in feather keratins. Rectricial measurements of the hybrid fall between the character means for *L. victoriae* and *C. herrani* whose tails differ markedly in shape.

Among the many puzzling species of hummingbirds described by John Gould, *Cometes glyceria* stands apart in taxonomic obscurity (Gould 1858: opposite plate 176):

> "During the many years that I have given attention to the Trochilidae, I have not met with a bird which has caused me more thought, and I may say perplexity, . . . it is intimately allied to the members of the genera *Lesbia, Cometes* and *Cynanthus,* partaking as it does, either in form or colouring, of characters pertaining to each of those genera. Sometimes it has occurred to me that it might be a hybrid between either two of them, but I am perfectly at a loss to say which two species would be likely to produce such a cross. Such an idea has entered my mind, but when I have again and again reconsidered the matter, it has appeared to me that it is a distinct species, and that it may ultimately prove to be the female or young male of some gorgeous bird with which we are at present unacquainted."

As a consequence of evolving generic definitions, *glyceria* was placed first in *Sparganura* (Cabanis & Heine 1860, Sclater & Salvin 1873) and later transferred to *Zodalia* (Mulsant & Verreaux 1876, Elliot 1878, Salvin 1892, Boucard 1893, Sharpe 1900, Oberholser 1902, Cory 1918). Simon (1921) considered *Zodalia glyceria* to be a senior synonym and immature plumage of *Z. ortoni* (Lawrence 1869), a position embraced by Peters (1945). The taxonomic validity of *Zodalia glyceria* was not formally challenged until Meyer de Schauensee (1947) declared both *Z. glyceria* and *Z. ortoni* to be hybrids of *Lesbia victoriae* and *Ramphomicron microrhynchum.* This conclusion was followed by subsequent authors (e.g., Morony et al. 1975, Greenway 1978, Fjeldså & Krabbe 1990, Sibley & Monroe 1990, Collar et al. 1992). Meyer de Schauensee's (1947) evaluation of *Z. ortoni* appears to be valid (Graves 1997); however, the holotype of *Zodalia glyceria* seems to represent a different, and previously unreported, intergeneric hybrid. Here I provide a detailed hybrid diagnosis employing the methods and assumptions outlined in Graves (1990) and Graves & Zusi (1990). In recognition of its 120-year association with *glyceria,* I use *Zodalia* as a generic identifer instead of *Cometes.*

Materials and Methods

The holotype of *Zodalia glyceria* (The Natural History Museum; formerly British Museum of Natural History, BMNH 1888.7.25.184) was procured by M. Mossa before 1853 in the vicinity of Popayán, Colombia (Gould 1858). Although Salvin (1892) considered *Z. glyceria* a juvenile and Simon (1921) believed it to be an immature of *Z. ortoni,* the holotypes of neither of these species exhibit striations on the maxillary ramphotheca typical of juvenile hummingbirds (see Ortiz-Crespo 1972). Instead, both specimens appear to be males in definitive plumage based on the presence of elongated rectrices and a brilliant, narrow gorget that extends from the chin to the upper breast. The unique appearance of *Z. glyceria* (Figs. 1–3) cannot be attributed to a developmental or geographic variation of any known taxon. Two other possibilities exist—it represents a valid species or a hybrid. Because hybrids lack formal standing in zoological nomenclature, hybridity must be ruled out before species status is granted. As this paper demonstrates, I was unable to reject the plausibility of a hybrid origin for *Z. glyceria.*

Assuming a hybrid origin, the pool of potential parental species (Appendix 1) includes all species of trochiline hummingbirds (subfamily Trochilinae: Zusi & Bentz 1982, Sibley & Monroe 1990, Bleiweiss et al. 1997) that occur in southern Colombia and northern Ecuador (Chapman 1917, Hilty & Brown 1986, Fjeldså & Krabbe 1990, Schuchmann & Heindl 1997, Krabbe et al. 1998). Notes, photographs, and videotape of *Zodalia glyceria* were compared with similar material for the holotypes of *Zodalia ortoni* (=*Lesbia ortoni*; American Museum of Natural History, AMNH 156651; Graves 1997), *Zodalia thaumasta* (National Museum of Natural History, Smithsonian Institution, USNM 173911), *Chalcostigma purpureicauda* (AMNH 483931), *Aeronympha prosantis* (Field Museum of Natural History, FMNH 11852), and *Heliangelus zusii* (Academy of Natural Sciences of Philadelphia, ANSP 159261; Graves 1993). The type of *Z. glyceria* was compared with specimens of all trochiline species deposited in the Natural History Museum.

Measurements of the aforementioned type specimens and of selected species were taken with digital calipers and rounded to the nearest 0.1 mm: wing chord; bill length (from anterior extension of feathers); rectrix length (from point of insertion of the central rectrices to the tip of each rectrix), and rectrix width (at widest point). Pairs of rectrices are numbered from the innermost (R1) to the outermost (R5). Lengths of crown and gorget feathers were measured by sliding a slip of paper to the feather base and then marking the position of the feather tip on the paper (Appendix 2). Data judged to be most relevant to the hybrid diagnosis are presented in Table 1. Untransformed measurements and least squares regression lines were projected on bivariate plots to illustrate size differences (Fig. 4) (Wilkinson 1989).

I evaluated the color of the dorsal plumage (center of back) with a calibrated colorimeter (CR-221 Chroma Meter, Minolta Corporation) equipped with a 3.0 mm aperture. The measuring head of the CR-221 uses 45° circumferential illumination. Light from the pulsed xenon arc lamp (C illuminant, 2° observer) is projected onto the specimen surface by optical fibers arranged in a circle around the measurement axis to provide diffuse, even lighting over the measuring area. Only light reflected perpendicular to the specimen surface is collected for color analysis. Colorimetric data from iridescent feathers are acutely dependent on the angle of measurement, the curvature of plumage surfaces in museum skins, and the degree of pressure applied to the plumage surface by the Chroma Meter aperture. In order to reduce measurement variation, I held the aperture flush with the plumage surface without depressing it. The default

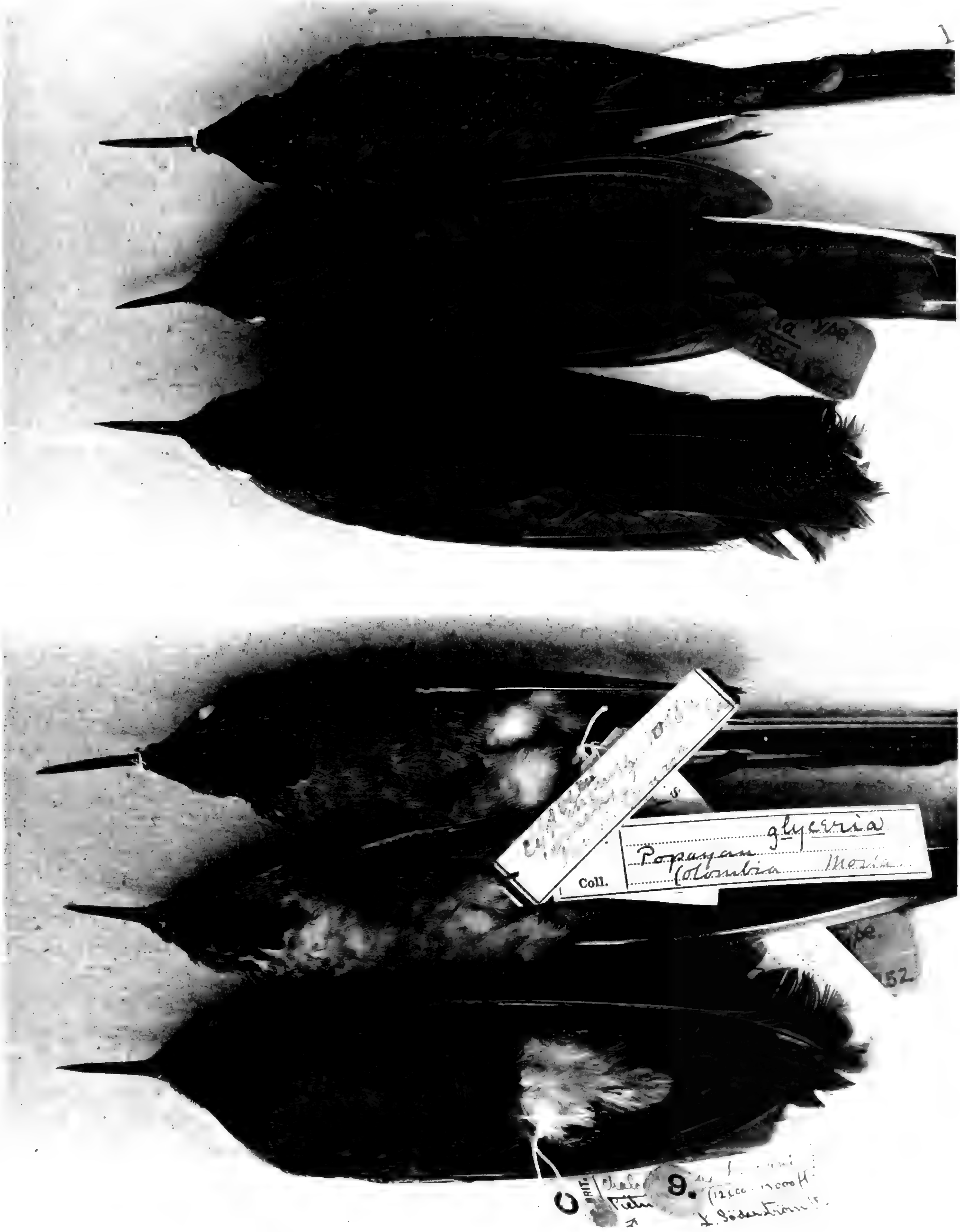

Fig. 1. Dorsal and ventral views of male *Lesbia victoriae* (top), *Chalcostigma herrani* (bottom), and a probable hybrid, *L. victoriae* × *C. herrani* (=*Zodalia glyceria* [Gould, 1858]; BMNH 1888.7.25.184).

setting for the CR-221 Chroma Meter displays mean values derived from three sequential, in situ measurements. I repeated this procedure three times for each area of plumage, removing the aperture between trials. Each datum summarized in Table 2 thus represents the mean of three independent measurements.

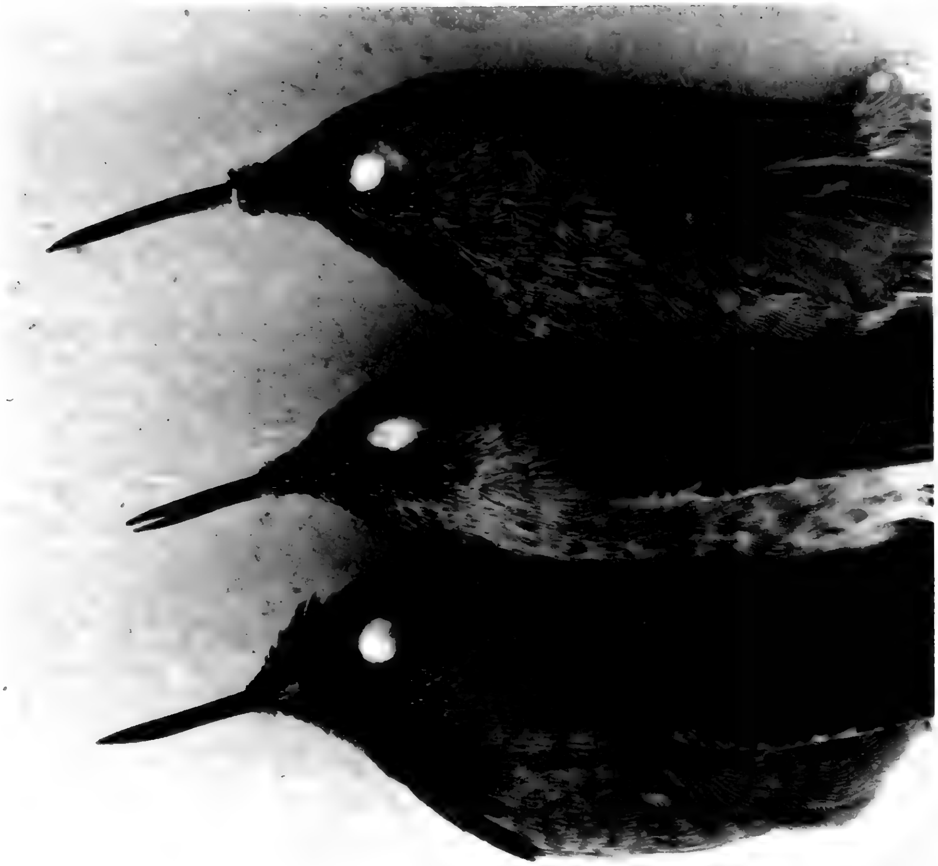

Fig. 2. Lateral view of male *Lesbia victoriae* (top), *Chalcostigma herrani* (bottom), and a probable hybrid, *L. victoriae* × *C. herrani* (=*Zodalia glyceria* [Gould, 1858]; BMNH 1888.7.25.184).

Colorimetric characters were described in terms of opponent-color coordinates (*L, a, b*) (Hunter & Harold 1987). This system is based on the hypothesis that signals from the cone receptors in the human eye are coded by the brain as light-dark (*L*), red-green (*a*), and yellow-blue (*b*). The rationale is that a color cannot be perceived as red and green or yellow and blue at the same time. Therefore "redness" and "greenness" can be expressed as a single value *a,* which is coded as positive if the color is red and negative if the color is green. Likewise, "yellowness" or "blueness" is expressed by *b* for yellows and $-b$ for blues. The third coordinate *L,* ranging from 0 to 100, describes the "lightness" of color; low values are dark, high values are light. The more light reflected from the plumage the higher the *L* value will be. Visual systems in hummingbirds (e.g., Goldsmith & Goldsmith 1979) differ significantly from those of humans. The relevance of opponent color coordinates to colors perceived by hummingbirds is unknown. General color descriptions presented in Appendix 2 were made under natural light.

The hybrid diagnosis was approached in a hierarchical manner. A hypothesis of parentage was first derived from comparison of plumage pattern, color and feather shape. As a second step, the restrictive hypothesis was tested with an analysis of size and external proportions. Concordance of results is regarded as strong support for the hypothesis (Graves 1990, Graves & Zusi 1990).

Results and Discussion

Characters of *Zodalia glyceria* that permit its parental species to be identified include: (a) moderately lengthened crown feathers broadly margined with rufous; (b) partially white outer vane of outermost rectrices (R5); (c) deeply forked tail (fork

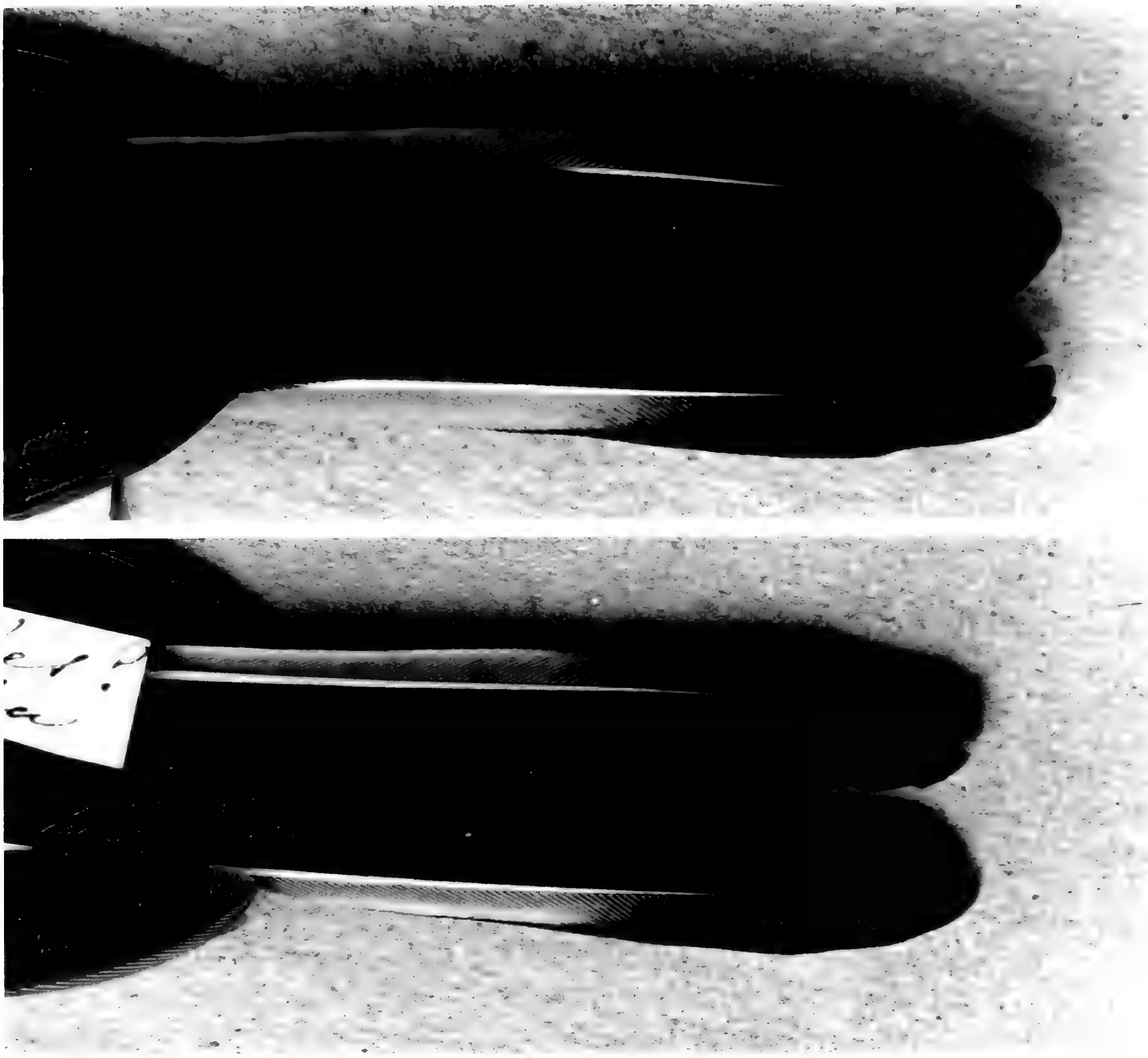

Fig. 3. Dorsal (top) and ventral (bottom) view of rectrices of *Zodalia glyceria* [Gould, 1858]; BMNH 1888.7.25.184.

depth = 51.6 mm); (d) broad rectrices (all >10 mm wide); (e) narrow brilliant gorget; and (f) short tibial plumes. This suite of characters (Figs. 1–3, Appendix 2) can be recovered from a particular pairwise combination of species, but not from any single species.

The pool of potential parental species (a maximum of $\binom{86}{2}$ = 3,655 possible pairwise combinations) may be quickly narrowed by focusing on the elongated rufous-margined crown feathers of *Z. glyceria.* Meyer de Schauensee's (1947) hypothesis, *Lesbia victoriae* × *Ramphomicron microrhynchum,* is unlikely because neither of those species possesses a rufous or chestnut crown patch. Only two species in the geographic source pool (Appendix 1) have rufous or chestnut crowns: *Chalcostigma herrani* and *C. ruficeps.* The latter species can be ruled out as a parent of *Z. glyceria* on the basis of external measurements (see below).

The partially white outer vanes of the outermost rectrices (R5) of *Z. glyceria* were contributed by the other parental species. Five species in the geographic source pool (*Ocreatus underwoodii, Lesbia victoriae, L. nuna, Aglaiocercus kingi, A. coelestis*) have deeply forked tails. *Ocreatus* can be eliminated from consideration because *Z. glyceria* shows no evidence of racket-tipped rectrices or elongated tibial plumes. Neither

Table 1.—Ranges (mean ± standard deviation) of measurements (mm) of adult males of *Lesbia victoriae*, *Chalcostigma herrani*, and a probable hybrid, *L. victoriae* × *C. herrani* (=*Zodalia glyceria* [Gould, 1858]; BMNH 1888.7.25.184). Measurements of adult male *Lesbia nuna* are included for comparison.

	victoriae (*n* = 12)	*nuna* (*n* = 12)	*herrani* (*n* = 15)	Hybrid BMNH 1888.7.25.184
Wing chord	58.7–62.2 (60.3 ± 1.1)	50.3–52.8 (51.8 ± 0.6)	66.7–72.7 (69.8 ± 1.7)	65.9
Bill length	13.5–15.3 (14.5 ± 0.6)	7.5–9.0 (8.2 ± 0.4)	9.8–12.2 (11.3 ± 0.5)	10.7
Rectrix 1	22.1–24.9 (23.5 ± 0.9)	19.8–22.4 (21.0 ± 0.7)	43.8–47.9 (45.8 ± 1.4)	33.8
Rectrix 2	26.2–31.1 (28.8 ± 1.2)	25.9–28.1 (27.0 ± 0.7)	48.5–52.5 (49.9 ± 1.4)	41.9
Rectrix 3	39.2–44.4 (42.1 ± 1.7)	36.0–40.4 (38.0 ± 1.4)	49.9–56.3 (52.7 ± 1.6)	51.0
Rectrix 4	62.1–68.5 (65.2 ± 2.3)	51.3–57.6 (54.3 ± 1.9)	50.3–56.4 (50.4 ± 1.6)	63.3
Rectrix 5	149.0–189.0 (173.7 ± 10.4)	94.1–109.0 (99.9 ± 4.1)	47.1–56.2 (51.8 ± 2.6)	85.4

species of *Aglaiocercus* possesses white outer rectricial vanes in male definitive plumage. A species of *Lesbia* is thus implicated, although I doubt that the specific identity of the "trainbearer" parent can be determined from plumage color or pattern alone. In brief, details of plumage pattern and color are consistent with the hypothesis that *Zodalia glyceria* is a hybrid between a rufous-crowned species of *Chalcostigma* and a species of *Lesbia* (Appendix 2).

Two peculiar aspects of plumage color need to be addressed in greater detail. The greenish-blue iridescence of *Z. glyceria* undoubtedly influenced Meyer de Schauensee (1947) to propose the purple-backed thornbill (*Ramphomicron microrhynchum*) as one of its parental species. However, both *R. microrhynchum* and *Lesbia victoriae*, as well as a robustly documented hybrid, *L. victoriae* × *R. microrhynchum* (AMNH 156651), exhibit green (instead of greenish-blue or purple) iridescence on the breast and sides (Graves 1997). It is usually assumed that hybridization in hummingbirds produces no traits characteristic of genera or species other than those involved in the particular cross (Banks & Johnson 1961). In a recently published exception to this general rule, plumage iridescence of a hybrid specimen, *Aglaiocercus kingi* × *Metallura tyrianthina* (AMNH 146645), was found to be significantly bluer (dominant wavelength, 511 nm) than that exhibited by the parental species (cumulative range, 553–571 nm) (Graves 1998b). The broader implications of this finding are unclear, but the shift in dominant wavelength may result from a developmental aberrancy or mutation, directly related to hybridization, that affects melanin granules that produce iridescence in feather keratins.

The holotype of *Zodalia glyceria* appears to represent another case of the "blueing" phenomenon associated with intergeneric hybridization (Graves 1998b). The dorsal plumage is significantly bluer (dominant wavelength, 505 nm) than that of *Lesbia victoriae* or *Chalcostigma herrani* (cumulative range, 561–576 nm) (Table 2). However, the pattern of greenish-blue iridescence (violet to purple at certain angles) in *Z. glyceria* coincides precisely with the distribution of green iridescence in those species, suggesting a single developmental or mutational event affecting iridescence of the entire plumage (Fig. 5).

A second puzzlement is the absence of terminal white spots on the outermost rectrices (R4–R5) of *Z. glyceria*. Presuming

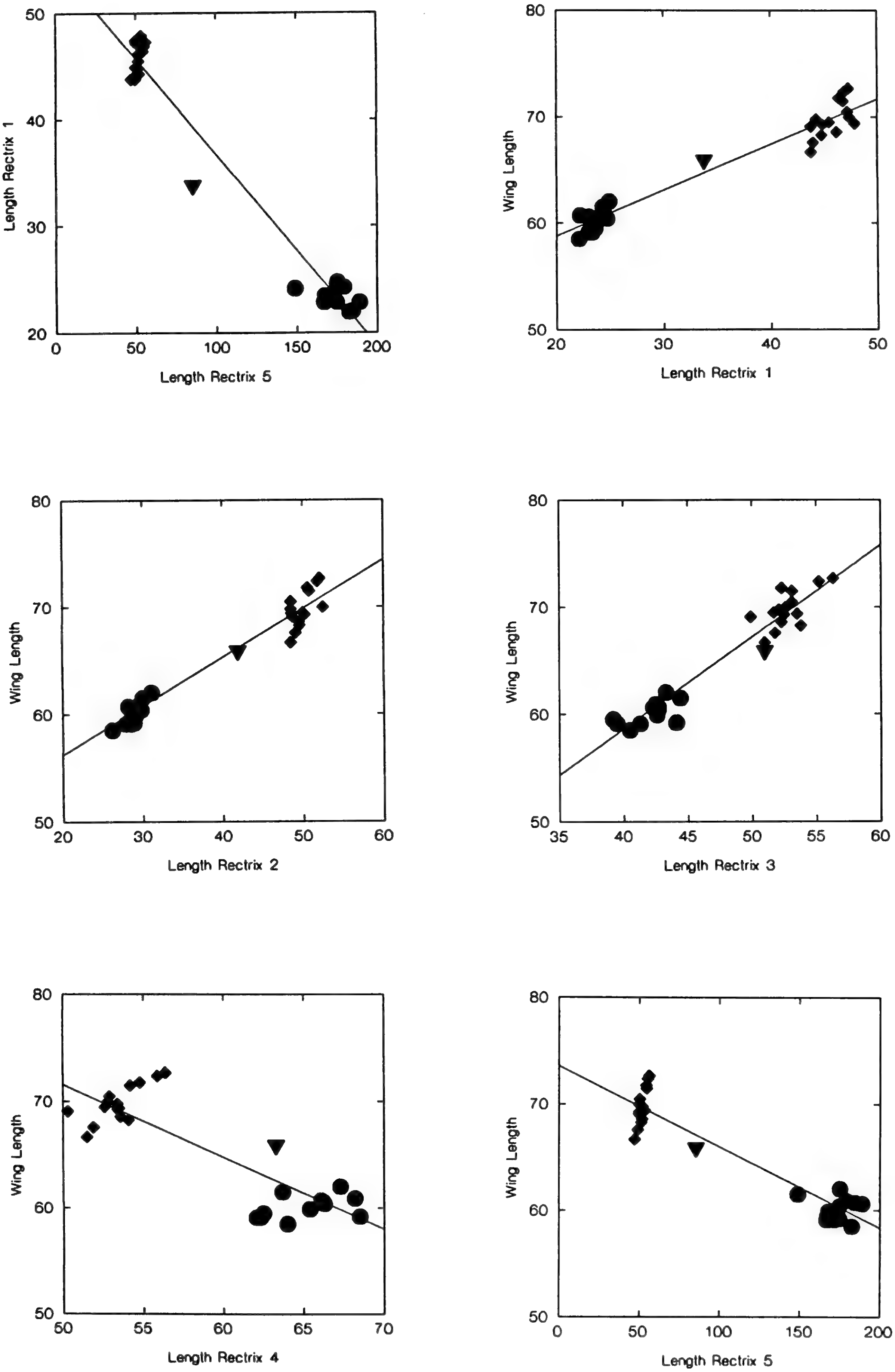

Fig. 4. Bivariate plots of mensural characters of males in definitive plumage: *Lesbia victoriae* (●); *Chalcostigma herrani* (◆); a probable hybrid (▼), *L. victoriae* × *C. herrani* (=*Zodalia glyceria* [Gould, 1858]; BMNH 1888.7.25.184). Least squares regression lines are illustrated for comparison.

Table 2.—Ranges and means (± standard deviation) of opponent color coordinates (*L, a, b*) and dominant wavelength (nm) reflected from dorsal plumage (center of back) in male *Chalcostigma herrani, Lesbia victoriae,* and their probable hybrid, *L. victoriae* × *C. herrani* (=*Zodalia glyceria* [Gould, 1858]; BMNH 1888.7.25.184).

Variables	*C. herrani* *n* = 15	*L. victoriae* *n* = 21	hybrid 1888.7.25.184
Back plumage			
L (Lightness)	20.1–23.3	30.5–36.0	25.3
	21.3 ± 0.9	33.6 ± 1.1	
a (Red [+]/Green [−])	−8.8–(+2.5)	−16.8–(−5.4)	−5.1
	−3.7 ± 3.4	−13.2 ± 2.6	
b (Yellow [+]/Blue [−])	9.6–15.2	19.2 –29.6	1.0
	11.7 ± 1.7	26.4 ± 2.8	
Dominant wavelength (nm)	561–576	563–570	505
	569.0 ± 5.3	564.8 ± 1.7	

Chalcostigma herrani as a parental species, this observation apparently conflicts with assumptions I made in previous papers about the heritability of unpigmented tail spots in trochiline hybrids (Graves 1990, 1998a; Graves & Zusi 1990). This discrepancy seemed to be resolved by a closer examination of *Z. glyceria*'s rectrices, which suggests that the white terminal spots in *C. herrani* were phenotypically expressed as conspicuously white rachises in R4 and R5 (see Appendix 2). Although the basal third of the dorsal rachial surface of R5 is dull white or cream-colored in some female *Lesbia victoriae,* the rachis of R4 is brown in all specimens examined (50+). Consequently the white rachises of R4 and R5 in *Z. glyceria* cannot be attributed to female or immature characters of *Lesbia victoriae.* In summary, details of plumage color and pattern are sufficient to narrow the pool of possible parental combinations: *Lesbia* (*victoriae* or *nuna*) × *Chalcostigma* (*herrani* or *ruficeps*).

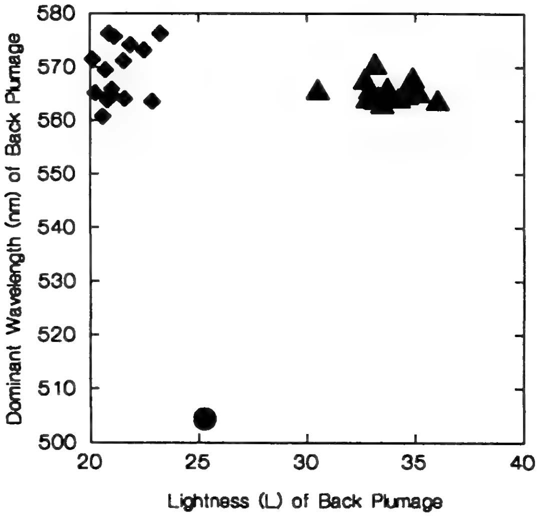

Fig. 5. Bivariate plots of mensural characters of males in definitive plumage: *Lesbia victoriae* (▲); *Chalcostigma herrani* (◆); a probable hybrid, *L. victoriae* × *C. herrani* (●) (=*Zodalia glyceria* [Gould, 1858]; BMNH 1888.7.25.184).

External measurements.—Several straightforward comparisons permit the identification of the parental species of *Zodalia glyceria:* (a) length of R3 (*Chalcostigma herrani* > *Z. glyceria* > *Lesbia victoriae* > *C. ruficeps* > *L. nuna*); (b) length of R4 (*L. victoriae* > *Z. glyceria* > *L. nuna* > *C. herrani* > *C. ruficeps*); (c) width of R5 (*C. herrani* > *Z. glyceria* > *C. ruficeps* > *L. victoriae* > *L. nuna*) (Table 1, unpublished data). Crown and gorget feathers of *C. herrani* and *Z. glyceria* are also significantly longer than those of the other taxa. Because morphological luxuriance (where hybrids are larger than their parental species) has never been observed in trochilines, these data indicate *L. victoriae* and *C. herrani* as the most probable parental species of *Z. glyceria.*

Male *Lesbia victoriae* and *Chalcostigma herrani* in definitive plumage differ markedly in tail shape and rectricial measurements are non-overlapping. The deeply forked tail (fork depth = 83–88% of tail length) of male *L. victoriae* is among the longest in the Trochilidae (319 species according to Sibley and Monroe 1990), with tail/wing ratios ranging from 2.4 to 3.1 in Ecuadorian populations. In contrast, the tail of *C. herrani* is relatively short (tail/wing = 0.7–0.8) and shallowly forked (fork depth = 5–16% of tail length). Bivariate plots of wing length and rectricial measurements of *L. victoriae* and *C. herrani* exhibit both positive (R1, R2, R3) and negative (R4, R5) allometry (Fig. 4). Rectricial measurements of *Z. glyceria* fall between the character means of *L. victoriae* and *C. herrani,* and, in most cases, approximate the values predicted by least squares regression.

In summary, evidence derived from size and shape characters, as well as plumage pattern and color, strongly suggest that *Z. glyceria* represents an intergeneric hybrid between *Lesbia victoriae* and *Chalcostigma herrani.* As such, *Cometes* (=*Zodalia*) *glyceria* Gould is available only for the purposes of homonymy in taxonomy.

Geographic overlap.—The geographic and elevational ranges of the parental species, *Lesbia victoriae* and *Chalcostigma herrani,* overlap broadly in the Andes (Fjeldså & Krabbe 1990). *Lesbia victoriae* inhabits forest edge and brushy slopes at 2600–4000 m elevation, whereas *C. herrani* prefers well-drained rocky slopes, forest edge and *Polylepis* woodland at 2700–3600 m.

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Appendix 1

Species of trochiline hummingbirds that occur in southern Colombia (Cauca, Nariño, Putamayo) and northern Ecuador (Carchi, Esmeraldas, Imbabura): *Androdon aequatorialis, Doryfera johannae, D. ludoviciae, Campylopterus largipennis, C. falcatus, Colibri delphinae, C. thalassinus, C. coruscans, Anthracothorax nigricollis, Klais guimeti, Lophornis chalybeus, Popelairia popelairii, P. conversii, Chlorostilbon mellisugus, Thalurania colombica, T. furcata, Damophila julie, Hylocharis grayi, Chrysuronia oenone, Amazilia fimbriata, A. amabilis, A. rosenbergi, A. franciae, A. cyanifrons, A. saucerrottei, A. tzacatl, Chalybura buffonii, C. urochrysia, Adelomyia melanogenys, Phlogophilus hemileucurus, Heliodoxa imperatrix, H. gularis, H. schreibersii, H. aurescens, H. rubinoides, H. jacula, H. leadbeateri, Topaza pyra, Oreotrochilus chimborazo, Urochroa bougueri, Patagona gigas, Aglaeactis cupripennis, Lafresnaya lafresnayi, Pterophanes cyanopterus, Coeligena coeligena, C. wilsoni, C. torquata, C. lutetiae, Ensifera ensifera, Boissonneaua flavescens, B. matthewsii, B. jardini, Heliangelus strophianus, H. exortis, Eriocnemis vestitus, E. luciani, E. mosquera, E. mirabilis, E. alinae, E. derbyi, Haplophaedia aureliae, H. lugens, Urosticte benjamini, U. ruficrissa, Ocreatus underwoodii, Lesbia victoriae, L. nuna, Ramphomicron microrhynchum, Metallura williami, M. tyrianthina, Chalcostigma ruficeps, C. stanleyi, C. herrani, Opisthoprora euryptera, Aglaiocercus kingi, A. coelestis, Schistes geoffroyi, He-*

liothryx barroti, H. aurita, Heliomaster longirostris, Philodice mitchellii, Myrtis fanny, Acestrura mulsant, A. bombus, A. heliodor, A. berlepschi.

Appendix 2

General comparative description of adult male *Lesbia victoriae, Chalcostigma herrani,* and a probable hybrid, *Lesbia victoriae* × *Chalcostigma herrani* (= *Zodalia glyceria* [Gould, 1858]; BMNH 1888.7.25.184). Descriptions of structural colors are unusually subjective, as color seen by the observer varies according to the angle of inspection and direction of light. For this reason I use general color descriptions.

Dorsal feathering (capital and spinal tracts) of *victoriae* posterior to the upper tail coverts is medium dull green; feather bases are gray and some lateral barbs are narrowly fringed with buff. Crown feathers are unmodified (length, 6.1–7.1 mm, $\bar{X}$ = 6.6 ± 0.3; *n* = 15).

The crown of *herrani* is dark saturated green (matte black when viewed head-on), bisected by a medial stripe of deep lustrous rufous, which begins at the base of the bill, reaches its widest point on the forecrown (where the barbs have a plush-like texture), and narrows (one or two feathers wide) to a thin stripe on the hindcrown. The bases of rufous-tipped crown feathers (length, 8.1–10.6 mm, $\bar{X}$ = 9.6 ± 0.9; *n* = 16) are grayish-black. In males in subdefinitive plumage, the feather barbs are less plush-like, and the rufous crown stripe is considerably wider, often extending laterally to the superciliary region. The back of *herrani* is dark green (sooty green from head-on) becoming dark bronzy-green with reddish (coppery) highlights on the rump and uppertail coverts.

Dorsally, *glyceria* differs considerably in appearance from *victoriae* and *herrani,* or for that matter, all other species of hummingbirds. First, an oval crown patch extends from the base of the bill to the nape. Feathers in this weakly defined patch (~9.2 mm long) are broadly tipped with rufous and possess a shining central spot (imparting a spotted appearance) that, depending upon the angle of inspection, reflects greenish-blue or purple iridescence. The superciliary, nape, back, scapulars, rump, and uppertail coverts are shining greenish-blue to purple; the distal ends of barbs are pale rufous or buff, and not easily seen without magnification.

In *victoriae,* a brilliant, medium-green gorget extends from the chin to the upper breast; the posterior end of the gorget is broadly lanceolate. Feathers at the gorget point are of moderate length (8.4–9.8 mm, $\bar{X}$ = 9.1 ± 0.4; *n* = 15) and width (~2.5–3.2 mm). From base to tip they are grayish-buff proximally, bordered distally by a broad band of pale buff, a narrow transitional band (<0.4 mm) of bronzy green, and broadly tipped with medium green (terminal iridescent tip: length ~2.8–3.0 mm, width ~2.5–3.2). The lores, auriculars, sides of neck, breast, and flanks are green, new feathers are finely margined (10× magnification) with buff. The basal third of feathers on the breast, sides, and belly is dark gray; feathers are narrowly fringed with buff, extensively so along the midline below the gorget and on the abdomen. Vent plumes are white; undertail coverts (13–16 mm long) are buff with a muted and elongated grayish spot along the rachis. Tibial plumes, which extend approximately half way to the toes, are dark grayish-brown, broadly tipped with buff; tibial plumes are buff.

In definitive plumage, *herrani* has a narrow and highly iridescent gorget ("beard"), extending from the chin to the upper breast, that changes color in a stepwise fashion from blue (chin) to red (gorget tail). Although a large fraction of the visible spectrum is reflected in ~20–25 rows of gorget feathers, the exposed portion of individual feathers appears to the eye (viewed head-on) to be rather uniform in color, reflecting a truncated range of wavelengths. The posterior ⅓ of the gorget tail is frequently 1–2 feathers wide. Feathers in gorget tail are relatively long (length, 12.0–15.3 mm, 13.6 ± 0.9; *n* = 16) and narrow (~1.7–2.5 mm), the iridescent red tip is similarly elongated (length ~5.0–6.0 mm, width ~2.0–2.3 mm). These feathers, from base to tip, are sooty gray or black, gradually becoming black glossed with green, and then changing abruptly in an optically smooth gradient (~0.7–1.2 mm) from greenish-gold, to coppery-gold and coppery-orange, and finally to red (depending on the angle of inspection, the terminal portion of the feather can vary from reddish-orange to reddish-magenta when viewed head-on). The auriculars and sides of the throat are dusky green (matte black from head-on), contrasting with the brilliant gorget. The breast, sides, and belly are dusky green becoming buffy toward the midline. In general, ventral feathers are grayish-buff, marked with a diffuse dull green disc, which becomes progressively smaller toward the midline. The vent plumes are white. Undertail coverts are moderately long (20–25 mm), pale buffy-white to buff, marked with grayish smudges, or in some individuals, by an indistinct grayish stripe of variable width. Tibial plumes extend about ⅔ of the way to the toes, and are dark brownish-gray with a scattering of buffy barbs.

The gorget of *glyceria* is uniformly silvery-green (viewed head-on), and is composed of ~20–21 rows of iridescent feathers that extend from the chin to the upper breast. At midpoint, the gorget is about 5 feathers in width. Chin feathers have intermingled buff and greenish barbs. Feathers from the gorget tail most closely resemble those of *victoriae* in color, exhibiting an indistinct lanceolate spot (pale grayish-buff) centered at the rachis near the base of the feather, bordered distally by a broad subterminal band of pale buff, and terminated with a highly iridescent silvery-green tip (length ~3.8 mm, width ~2.0; total feather length

~10.1 mm). Gorget feathers of *glyceria* are intermediate in shape between those of *victoriae* and *herrani.* The color pattern of the ventral plumage of *glyceria* most closely resembles that of *victoriae.* Ventral feathers are dark gray basally, broadly tipped with buff, and marked with an iridescent spot (greenish-blue to violet and purple, depending on the angle of inspection), the size and distinctiveness of which decreases toward the midline. The tibial plumes, which extend approximately half way down the tarsus, are dark grayish-brown, broadly tipped with pale buff and grayish-buff barbs (approximately intermediate in appearance between *victoriae* and *herrani*). The vent feathers are white. Undertail coverts are pale buff, marked with a subterminal lanceolate spot (greenish-purple on largest coverts) whose darkness, color intensity and size increases with covert size.

In *victoriae,* the rectrices (dorsally) are black with brownish-purple reflections in bright light, conspicuously (R1–R4) or inconspicuously (R5) tipped with dark green. The proximal ⅓ of the lateral vane of R5 is gray (dorsally) and grayish-white (ventrally). Rectrices are relatively narrow (R3–R5 < 7.0 mm wide). The dorsal surface of rachises is dark brown (the proximal 10–25 mm of R5 in some specimens is cream-colored). Ventrally, rachises are dark brown, gradually shading to pale brown at the base, except for R5 in which the proximal third of the rachis is grayish-white (the pigmentation of R4 is intermediate). Tips of R5 are slightly subspatulate and "bowed" in cross-section.

The dorsal and ventral surfaces of *herrani* rectrices reflect a metallic iridescence that varies from dark bluish-purple on the outer rectrices (R5) to dark purple on the innermost (R1). The two outer rectrices are tipped with large white spots (length, measured along the rachis), 13.8–16.7 mm (R5) and 10.0–11.7 mm (R4). R3 exhibits a faint white mark near the tip along the rachis. Rachises are dark brownish black, becoming white in the unpigmented spots on both surfaces. Rectrices are relatively wide: (R1) 10.3–13.7 mm; (R2) 11.1–15.8 mm; (R3) 10.9–14.6 mm; (R4) 11.2–13.7 mm; (R5) 10.0–12.8 mm. In cross-section, the rectrices are nearly flat.

The rectrices of *glyceria* are nearly flat and relatively wide: (R1) width = 10.5 mm; (R2) 11.0 mm; (R3) 11.6 mm; (R4) 10.4 mm; (R5) 10.1 mm. Rectrix shape in *glyceria* is approximately intermediate between that of *victoriae* and *herrani.* Dorsally, R1 is dark metallic bronzy-purple gradually shading toward purple about 12 mm from the tip and finally to violet-purple (terminal 3 mm). R2–R4 are similarly colored although the basal bronzy-purple portions are largely obscured in the folded tail. The central part (~24–62 mm from feather tip) of the lateral vane of R5 is dull white on both ventral and dorsal surfaces (dilute pigmentation can be observed at 10× magnification). No traces of white tipping or terminal spotting could be observed on any of the rectrices of *Z. glyceria* under magnification (10×). Dorsally, the rachises of R1–R3 are dark brown becoming light brown proximally. Rachises of R4 and R5 are conspicuously white starting approximately 14 mm and 16 mm, respectively, from the feather tip. All rachises are slighter darker on ventral surfaces.

Remiges are dull dark brown and similar in shape in *victoriae, herrani,* and in *glyceria.* Greater wing coverts and primary coverts are the same color as back plumage in the respective specimens. The bill of *glyceria* is intermediate in shape between that of *victoriae* (slightly decurved in lateral profile, smoothly tapered in dorsal profile) and *herrani* (straight in lateral profile, abruptly tapered in dorsal profile). The ramphothecas and feet of *victoriae, herrani,* and *glyceria* are black.

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A new species of pelican (Aves: Pelecanidae) from the Lower Pliocene of North Carolina and Florida

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Abstract.—A new species of pelican, *Pelecanus schreiberi,* is described from rare fossils from the Lower Pliocene Yorktown Formation of North Carolina. Additional material from the nearly contemporaneous Bone Valley Formation in Central Florida is tentatively referred to the same species, which was much larger than any existing New World pelican and so distinctive in some features that it appears to represent an extinct lineage with no living descendents. The holotype is the distal portion of a femur with dense medullary bone indicating a laying female, so the species presumably bred near the type locality.

Among the tens of thousands of bird fossils recovered from early Pliocene marine deposits excavated in a phosphate mining operation in North Carolina (Olson & Rasmussen 2000), are a few specimens belonging to an extremely large species of pelican (Pelecanidae: Pelecaniformes). These are so distinctive as to leave little doubt that they constitute a previously unrecognized element in the late Tertiary avifauna of North America. With the discovery of additional contemporaneous specimens from Florida that may represent the same species, it was decided that formal description was warranted, despite the paucity of material.

Order Pelecaniformes
Family Pelecanidae

The femora are referable to the Pelecanidae by the combination of the very long, broad anterior surface of the external condyle; the long, squared outline of the fibular condyle in posterior view; the very long, distinct scar for attachment of M. gastrocnemius lateralis; and the distinct, deep depression for the ligamentous loop of M. iliofibularis. The overall aspect of the distal end of the femur in anterior view is somewhat similar in the Cathartidae but the gastrocnemius scar is small and round, the depression for the loop of the iliofibularis is indistinct, and the external condyle is relatively shorter. The Pelagornithidae differ markedly in having the popliteal fossa indistinct (versus very deep), the shaft broader and not constricting above the condyles, and the external condyle much less posteriorly produced. From the illustrations of the femur of *Teratornis merriami* in Miller (1925, plate 4c, d), the Teratornithidae differ in having the popliteal fossa shallower, the fibular condyle much less produced laterally, the gastrocnemius scar smaller, and the intercondylar groove much shallower. Other taxa of large birds in the Lee Creek avifauna such as swans, storks, and cranes (Anatidae, Ciconiidae, and Gruidae) differ even more substantially from the Pelecanidae than the above families.

Pelecanus schreiberi, new species
(Figs. 1–2)

Holotype.—Distal third of right femur of an egg-laying adult female (lumen filled with dense medullary bone), paleontological collections of the National Museum of Natural History, Smithsonian Instution, UNSM 192077; collected about 1972 by

Gerard R. Case; collector's number NC 543.

Type locality.—Texasgulf Inc. Lee Creek Mine, south side of Pamlico River, near Aurora, Beaufort County, North Carolina (35°23′22″ N; 76°47′06″ W).

Horizon.—Basal part of the Yorktown Formation, Lower Pliocene. This determination was made from matrix removed from paratypical femur USNM 263567 and is based on the presence of secondary phosphate, abundant echinoid spines, and the foraminiferan *Nonionella labradorium* (Thomas G. Gibson, USGS, pers. comm., 1999). Most of the avian fossils recovered at Lee Creek are from the basal part of the Yorktown Formation and it is assumed that the other specimens cited here come from that unit as well.

Measurements (mm) of holotype.—Distal width 37.2, depth through external condyle 28.3, depth through internal condyle 22.3, length from proximal edge of scar for M. gastrocnemius lateralis to distal extent of external condyle 34.2, width and depth of shaft at proximal edge of scar of M. gastrocnemius lateralis 23.6 × 15.8.

Paratypes.—The following are topotypical paratypes from the Lee Creek Mine: distal fourth of left femur, USNM 263567; pedal phalanx 1 of digit III, USNM 446506; pedal phalanx 2 of digit III, USNM 421948.

Mainly on the basis of their very large size, the following specimens from the Bone Valley Formation in Polk County, central Florida, are also referred to *P. schreiberi:* right quadrate lacking orbital process, UF 125031 (Seminole phosphate mine); axis vertebra lacking dorsal spine, UF 65677 (Gardinier mine).

Measurements.—See Table 1.

Etymology.—To my late friend and colleague Ralph W. Schreiber (6 July 1942–29 March 1988), former curator of birds at the Natural History Museum of Los Angeles County, authority on and devoted student of pelicans, whose career was ended much too soon (see Woolfenden 1989).

Diagnosis.—Larger than all modern pelicans except the largest individuals of the two largest species (*Pelecanus crispus* Bruch and *P. onocrotalus* Linnaeus). Distal end of femur in distal view with rotular groove narrower and much deeper, anterior crest of external condyle extending anteriorly well beyond the level of that of the internal condyle; in posterior view fibular condyle much more expanded laterally. The pedal phalanges are much more robust than the comparable elements in modern pelicans.

Discussion.—This very large species exceeds in size either of the living North American pelicans (American White Pelican *P. erythrorhynchos* Gmelin and the smaller Brown Pelican *P. occidentalis* Linnaeus). Because medullary bone functions as a calcium reserve, forming 10 to 14 days prior to egg-laying and being quickly resorbed afterwards (see references cited in Ballmann 1979, Mourer-Chauviré et al. 1999), the holotype is certainly from a female. The paratypical femur is essentially the same size as the holotype and thus could be from a non-breeding female. This is turn suggests that males (the larger sex) of the fossil species may have exceeded in size any individuals of modern pelicans.

Pelecanus schreiberi must have been breeding somewhere near the site of fossil deposition in North Carolina, making it a previously unknown member of the resident avifauna of eastern North America, despite its apparent rarity. Size alone precludes its inclusion in any existing species of North American pelican and the qualitative differences in the femur are so great as almost to suggest generic distinction.

Pelican remains are also represented in the nearly contemporaneous Bone Valley Formation of central Florida (Becker 1987), but are likewise very scarce. A single axis vertebra (UF 65677) is too large for *Pelecanus erythrorhynchos* (Table 1) and is here tentatively referred to *P. schreiberi,* although otherwise I could detect no consistent differences from *P. erythrorhynchos* or Old World pelicans. Of three quadrates

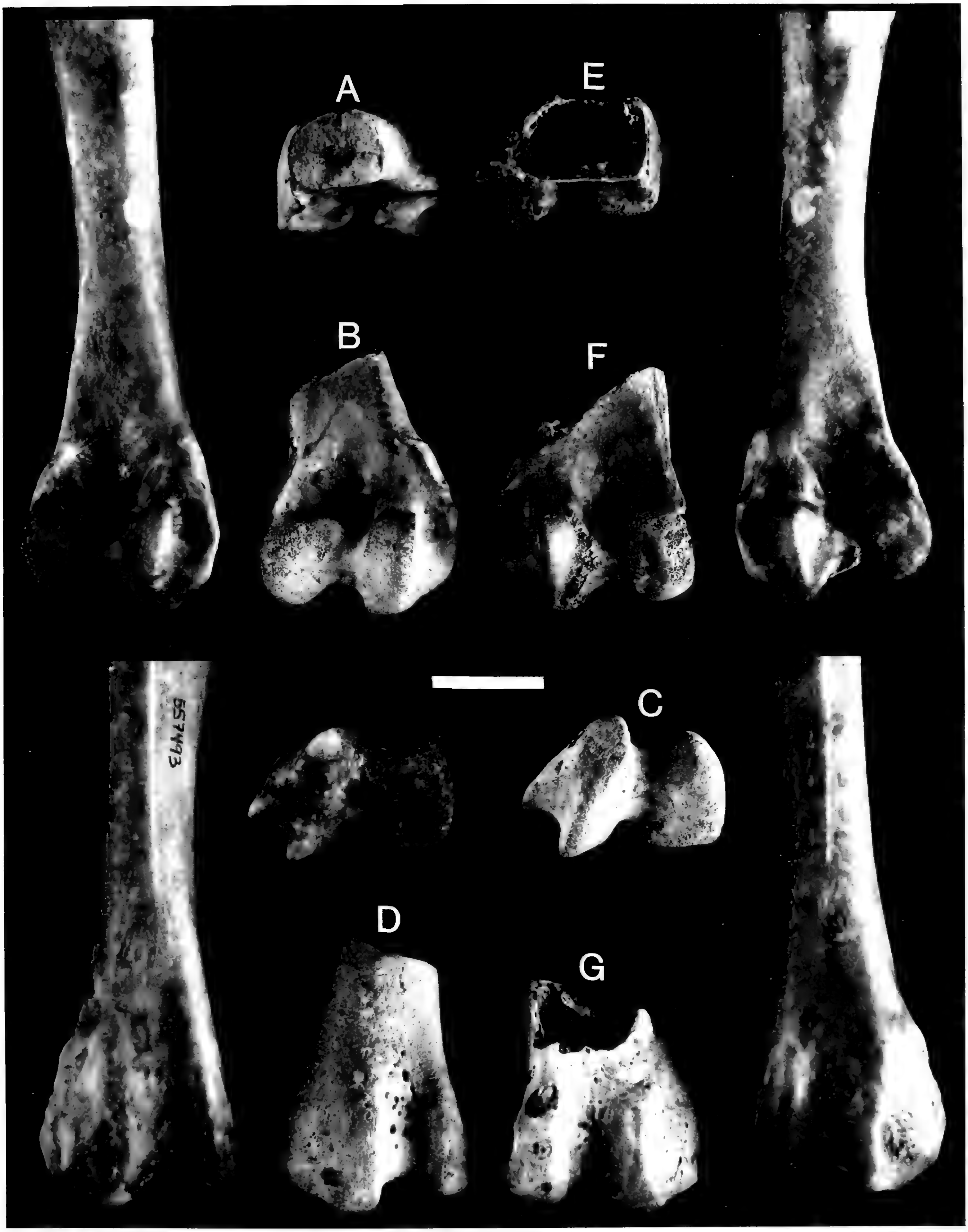

Fig. 1. Femora of *Pelecanus*. A–D, holotype of *Pelecanus schreiberi*, new species (USNM 192007): A, proximal view; B, posterior view; C, distal view; D, anterior view. E–G, paratype of *P. schreiberi*, new species (USNM 263567): E, proximal view; F, posterior view; G, anterior view. Unlettered elements are comparative views of the modern species *P. crispus* (USNM 557493). Note the dense medullary bone in the lumen of the femur of the holotype (A), indicating an egg-laying female, versus the hollow trabeculated lumen of the paratype (E). Scale bar = 2 cm.

Table 1.—Measurements of bones of *Pelecanus*. *P. schreiberi* $n = 1$ or 2; *P. crispus* $n = 2$ (1 unsexed, probably female; 1 male); *P. erythrorhynchos* all are males (the larger sex); $n = 8$ except quadrate and axis $n = 7$.

	P. schreiberi range	*P. crispus* range (mean)	*P. onocrotalus* range (mean)***n***	*P. erythrorhynchos* range (mean)
Quadrate				
Depth	33.0	34.8–37.0 (35.9)	30.4–33.6 (32.0) **2**	28.7–29.8 (29.2)
Length mandibular articulation	25.0	23.9–27.3 (25.6)	25.0–29.4 (27.8) **4**	23.0–23.9 (23.4)
Axis				
Length	38.5	34.5–39.9 (37.2)	35.8–43.7 (39.5) **7**	33.6–35.9 (35.0)
Posterior width	25.1	23.4–25.8 (24.6)	23.5–28.7 (26.2) **7**	21.1–23.3 (22.7)
Femur				
Distal width	37.2–38.2	35.3–37.4 (36.3)	33.5–37.6 (35.9) **7**	30.3–33.2 (31.8)
Depth external condyle	27.3–27.9	25.2–27.9 (26.5)	25.1–27.6 (26.7) **7**	21.5–24.0 (22.5)
Phalanx 1 Digit III				
Length	53.6	48.1–57.3 (52.7)	47.5–57.8 (53.5) **5**	40.7–46.5 (44.5)
Proximal width	13.2	10.5–11.9 (11.2)	10.6–12.6 (11.9) **5**	8.7–11.0 (10.1)
Distal width	8.2	7.1–8.9 (8.0)	7.6–9.5 (8.4) **5**	6.6–7.5 (7.1)
Phalanx 1 digit III				
Length	37.8	37.2–44.5 (40.8)	36.9–45.0 (41.4) **5**	30.1–35.9 (34.1)
Proximal width	9.6		8.4–10.1 (9.0) **5**	7.0–8.5 (7.9)
Distal width	7.3		6.0–8.3 (7.0) **5**	5.0–5.8 (5.6)

from the Bone Valley Formation, one (UF 65699) is smaller than in males of *P. erythrorhynchos* but probably within the range of females of the species, one (UF 125031) is larger than in *P. erythrorhynchos* in one measurement and within the range in another, whereas the third (UF 125030) exceeds that species in both measurements (Table 1) and is therefore referred to *P. schreiberi.* The measurements of three distal ends of tarsometatarsi from Bone Valley (UF 12344, UF 29738, UF 123868) all fall within the range of variation of *P. erythrorhynchos.* The quadrates and axis in the Brown Pelican (*P. occidentalis*) differ markedly in morphology from those of other pelicans, and are unlike those elements found at Bone Valley. If two species of pelican are represented there, one would be referred to *P. schreiberi* and the other would presumably be in the *P. erythrorhynchos* lineage.

The fossil record of Pelecanidae elsewhere in North America is also very meager. Miller (1944) tentatively assigned three poorly preserved fragments of femora from from the Pliocene of Oregon to *P. erythrorhynchos.* A new species, *P. halieus,* was erected by Wetmore (1933) for the proximal portion of a radius from the late Pliocene Hagerman deposits of Idaho said to be similar to *P. erythrorhynchos* but smaller. The radius is usually not considered a very diagnostic element, but when I re-examined the holotype of *P. halieus* (USNM 12233) I could find nothing that it resembled more than a pelican and it is indeed smaller than in *P. erythrorhynchos.* Becker (1986) assigned additional material from Idaho to this species.

Pelicans are much better represented in the fossil record of Europe, where *Pelecanus gracilis* Milne-Edwards is known from fairly abundant remains from the early Miocene of France. Cheneval (1984) made this the type of a new genus, *Miopelecanus,* and also suggested that *Pelecanus intermedius* Fraas, from the Middle Miocene of Germany might be conspecific with *Miopelecanus gracilis,* although he did not use the former in a new combination, contra Mlíkovsky (1992:435). These pelicans were

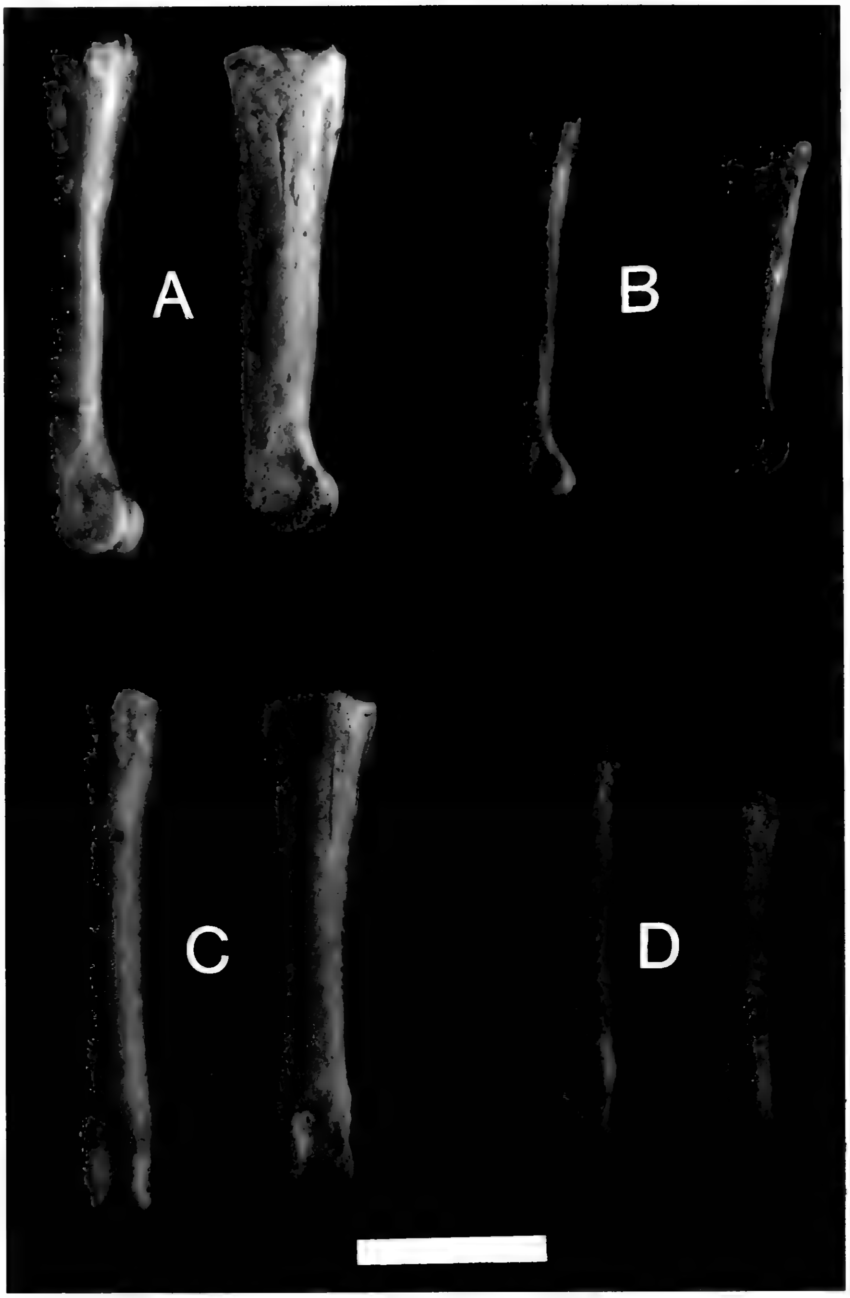

Fig. 2. Pedal phalanges of *Pelecanus crispus* (USNM 557493) on the left in each pair compared with paratypes of *Pelecanus schreiberi,* new species, on the right in each pair. A, pedal phalanx 1, digit III (USNM 446506), lateral view; C, same, dorsal view; B, pedal phalanx 2, digit III (USNM 421948), lateral view; D, same, dorsal view. Scale bar = 2 cm.

much smaller and more gracile than *P. schreiberi,* and the rotular groove of the femur is figured (Cheneval 1984: pl. 5-2) as quite broad, not narrow and deep as in *P. schreiberi.*

With one exception, discussed below, other named pelicans from Europe, Asia, and Africa would all have been smaller than *P. schreiberi* (see Lydekker 1891, Harrison & Walker 1976). The various fossil pelicans from Australasia, reviewed by Rich & van Tets (1981), likewise were smaller than *P. schreiberi,* with the exception of *Pelecanus conspicillatus novaezealandiae* Scarlett, which Rich & van Tets elevated to full species rank. The width of the femur in this species, from the late Holocene of New Zealand, was the size of that of *P. schreiberi,* although on temporal and geographic grounds it would be highly unlikely for the two to be closely related. Furthermore, Scarlett's (1966: fig. 4) illustration shows the rotular groove of the femur of the New Zealand bird to be very wide and shallow, unlike that of *P. schreiberi.*

Perhaps of greater potential relevancy in the present connection is the almost ethereal taxon *Pelecanus odessanus* Widhalm (1886), which was proposed in an obscure publication that seems to have eluded many researchers. Mlíkovsky (1996), for example, was unable to consult it, and one wonders if Brodkorb (1963) may have taken his information about it from Lambrecht (1933). Beginning at least with Lambrecht (1933), the author's name has most often been incorrectly rendered as "Wildhalm," when in fact it was Germanicized as J. Widhalm (from Ighnatii Martuinovich Vidghal'm).

Widhalm's paper treats a few fossils of waterbirds (the pelican, a toe bone of "*Colymbus,*" which at that time probably meant a loon [*Gavia*], and an assortment of bones of cormorants) from Tertiary deposits at Novaja Slobodka, near Odessa, Ukraine, previously assigned to the Lower Pliocene but now to the Upper Miocene (MN 11–13, Mlíkovsky 1996:749). This was for its time (or even now) an exemplary paper. In the case of the pelican, for example, Widhalm took into account recent views on the complexities of nomenclature of modern species, gave measurements of the fossil and the two relevant modern species, along with fairly detailed comparisons, and provided a superb lithographic plate.

The problem arises with what has been interpreted as Widhalm's apparent failure to conform to binomial nomenclature, but in my opinion this is an unfair appraisal probably arising from other authors' lack of access to the original publication. Brodkorb (1963), for example, considered Widhalm to be nonbinomial and therefore attributed the name *Pelecanus odessanus* to Lambrecht (1933). Mlíkovsky (1996) was of the opinion that Widhalm's apparent treatment of cormorants from the site called into question the validity of Widhalm's nomenclature. Widhalm's exact typography where the new pelican was proposed (p. 6) was as follows: "*Pelecanus odessanus.* fossilis *Widhalm.*". It is evident that Widhalm did not intend the term "fossilis" to be part of the scientific name, but merely an indication that his pelican was a fossil, as opposed to a modern taxon. The situation with cormorants is a little more complex but again I believe does not involve anything that can be considered formal nomenclature as on page 8 they are referred to as: "Haliaeus fossilis, var. Odessana major, medius, und minor. *Widhalm.*", which I interpret as simply a provisional way of saying that there were three sizes of fossil cormorants from Odessa (*Halieaus* Illiger, 1811, is a synonym of *Phalacrocorax* Brisson, 1760).

Regardless of its authorship, *Pelecanus odessanus* was a very large pelican, the length of the tarsometatarsus being given as 150 mm (that in the largest specimen of *P. crispus* that I examined was 131 mm, and in the two largest *P. onocrotalus* it was 138 and 145 mm). This species was temporally quite close to *P. schreiberi* and was probably of similar size. Unfortunately it is not known what became of Widhalm's specimens (Lambrecht 1933, Mlíkovsky 1996). Absent comparable elements it would not be possible to determine the distinctness of *P. odessanus* from *P. schreiberi* in any case.

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

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Abstract.—A new species, *Platymantis sierramadrensis,* from the Sierra Madre Mountains in the provinces of Aurora and Isabela, Luzon Island, Philippines, is described. This species is distinguished from other Philippines species of *Platymantis* (*hazelae* group) by its pale color, smooth skin, advertisement call, and other characters given in the diagnosis.

Recent field work in the Sierra Madre Mountains, northeastern Luzon Island, conducted separately by us in 1996 and 1997 resulted in the collection of 22 specimens (16 adults and 6 juveniles) of this distinctive frog. These specimens are platymantine frogs based on structure of the pectoral girdle (Brown 1952) and are referred to the *hazelae* group of *Platymantis* based on digital structures (Brown et al. 1997). This species is an addition to the list of eight other species occurring on Luzon and the Central and Western Visayas and currently assigned to this group. The specimens are deposited in the California Academy of Sciences (CAS) and Philippine National Museum (NMPH).

Materials and Methods

Materials examined included holotypes of all other species of the *hazelae* group of *Platymantis* from the Philippines. These holotypes with the exception of *P. panayensis* are in the CAS collections. The holotype of *P. panayensis* is in the NMPH.

Morphometric characters.—Snout–vent length (SVL), head length (HL), head breadth (HW), snout length (SnL), diameter of eye (ED), diameter of tympanum (TD), tibia length (TiL), third finger length from proximal edge of basal tubercle (3FL), diameter of third finger disk (3FD), and diameter of third toe disk (3ToD).

Advertisement calls (Fig. 1) were recorded and analyzed, using a Kay Electrics SonaGraph (Model #550) and SIGNAL Sound Analysis System software.

Platymantis sierramadrensis, new species
Fig. 2

Holotype.—NMPH 6465, an adult female, collected by Marisol Pedregosa in disturbed lowland forest at Sitio Mapidjas, Barangay Umiray, Municipality of General Nakar, Quezon Province, Luzon Island on 29 May 1996.

Paratypes.—CAS 204738, 204742–45 and NMPH 5980, 6461–63, 6466–67, CMNH 05678–79, collected in disturbed lowland forest in Sitio Mapidjas, Barangay Umiray, Municipality of Dingalan, Aurora Province, Luzon Island at the southern end of the Sierra Madre mountains.

Referred specimens.—CAS 204739–41 and NMPH 6464, 6470–74 from Palanan, northern Sierra Madre Mountains, Isabela Prov., Luzon Island. These specimens are in close agreement morphologically and in

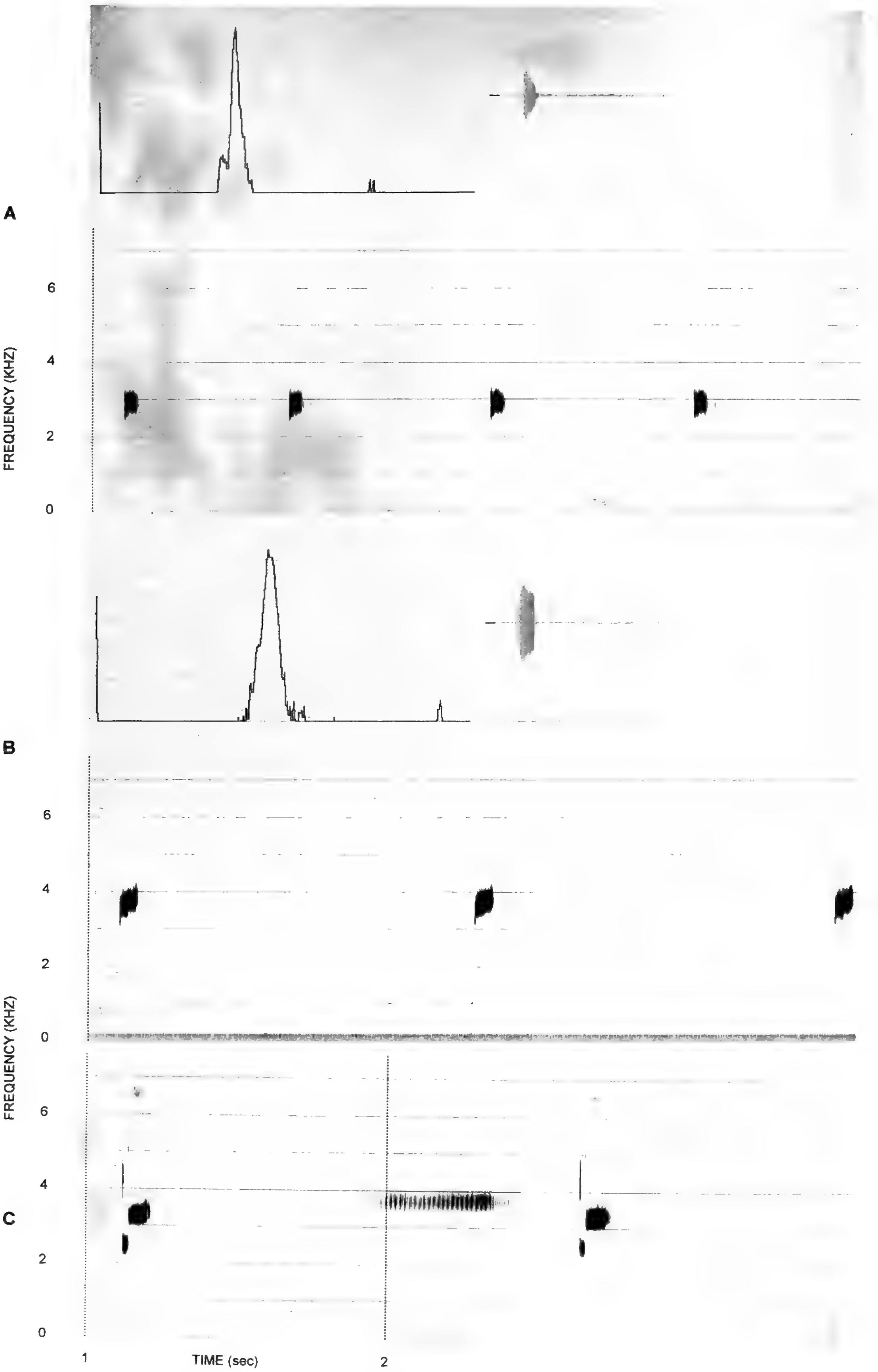

Fig. 1. Audiospectrograms of advertisement calls of (A) *Platymantis sierramadrensis* (NMPH 6472), (B) *P. subterrestris* (CAS 204322), (C) *P. montanus* (CAS 201705).

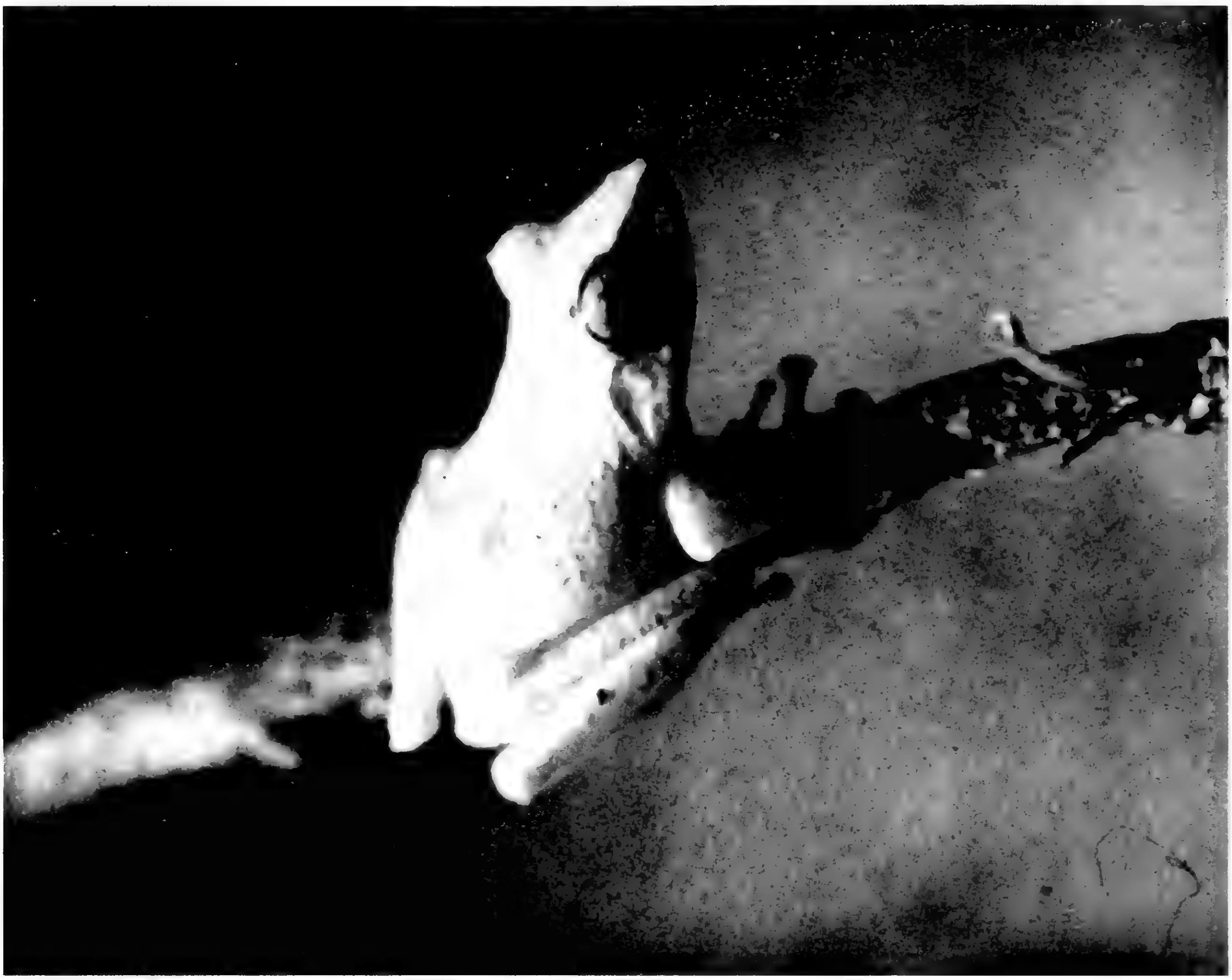

Fig. 2. *Platymantis sierramadrensis* (NMPH 6464) from Sierra Madre National Park, Isabella Province, Luzon Island. Color (in life), pale yellowish without dark markings on either body or limbs, is shown in this photograph of a male clinging to a branch of a forest shrub.

advertisement call with the type and paratypes. This population at the northern end of the Sierra Madre needs further investigation. It may prove to be a valid subspecies.

Diagnosis.—*Platymantis sierramadrensis* differs from other members of the *hazelae* group in having a pale creamy color without dark brown or blackish markings on body or limbs. In preserved specimens, faint, scattered brownish flecks are evident on dorsal and lateral surfaces. Other characters are: smooth skin, terminal phalanges rounded, and finger disks broader than those on toes, SVL 22.7–25.2 for mature males and 25.7 for one mature female; HL (39% of SVL) about equal to HW (40% of SVL) for 10 males and one female.

Description of holotype.—A gravid female; dorsum uniformly off white; dorsum and venter smooth; abdomen translucent, some internal organs visible; a conical tubercle on heel; measurements in mm: SVL 25.7, HL 10.0, HW 9.9, SnL 4.6, ED 3.6, TD 1.5, TiL 13.3, 3FL 3.7, 3FD 1.4, 3ToD 0.9.

Description.—SVL 22.7–25.2 for 10 mature males and 25.7 for one mature female: HL 37–42% (mean 39%) of SVL; HW 37–42% (mean 40%) of SVL; SnL 17–21% (mean 19%) of SVL; ED 12–15% (mean 14%) of SVL; TD 5–8% (mean 6%) of SVL; TiL 49–56% (mean 52%) of SVL; 3FL 14–17% (mean 15%) of SVL; 3FD 5–7% (mean 6%) of SVL; 3ToD 3–5% (mean 4%) of SVL; tympanum exposed; lore moderately oblique, concave; vomerine teeth only slightly protruding, patches widely separated; fingers with minute webs at base; fingers except first with broad disks; fingers with shallow circum-marginal grooves; first finger shortest, third finger longest, and second and fourth about equal in length; subarticular tubercles large, round, low; a row of low, inconspicuous supernumerary tubercles on palm; inner, middle and outer metacarpal tubercles oval, vague, inner and middle about equal in size; larger than outer; hind limb long; toes webbed to distal edge of tubercle on first and second, to distal edge of basal tubercle on third, and to midway between tubercles on fifth; disks of toes narrower than those of fingers, subarticular tubercles rounded, low; plantar area smooth; inner metatarsal tubercle elongated, outer vague; dorsum smooth, without tubercles; venter generally smooth, coarsely granular in some specimens.

Variations.—Based on the limited sample available to us, there are a few small differences in the body proportions between the northern (Isabela Province) and the southern (Aurora Province) populations. However, it is not possible to say whether these differences are significant because of the small samples. The northern population has barely overlapping values for HL/SVL (40–42 versus 37–40%) and TD/SVL (5–6 versus 6–8%) and non-overlapping values for 3FD/SVL (16–17 versus 14–15%). The two general collecting sites are far apart (ca. 200 km) and the forest environment is no longer continuous. These populations may not interact in any way.

Color (in life).—Pale cream without dark bars or other marks on limbs or body and without areolations.

Color (in preservative).—Pale cream without dark bars or other marks. Small brownish pigment flecks are scattered on dorsal and lateral surfaces. The specimens from the northern Sierra Madre (Isabela Province) appear slightly darker.

Reproduction.—The only mature female in the collections has about 10 ovarian eggs of various sizes, the largest being 2.8 mm in diameter. The eggs are yellow in color and are devoid of dark pigments, suggesting that the species undergoes direct development like other members of *Platymantis.* This female was collected in May, 1996 in Aurora Province. However, rainfall occurs throughout the year, and breeding activities may also be non-seasonal.

Advertisement call.—The call of this frog sounds like "pek-pek-pek" produced in a forceful manner. Each note ranges from 2500 to 3250 Hz with a duration of 0.05 to 0.06 of a second. The time interval between notes is about 0.53 to 0.64 seconds (Fig. 1).

Ecological notes.—Specimens of this species were collected in virgin and disturbed lowland forest at altitudes of 55 to 550 m. They were observed on leaves of low shrubby plants and screw pines from 0.5 to 2.5m above the ground. In Palanan, Isabela (northern part of Sierra Madre), adult males were observed and heard calling in March–April, 1997 while sitting on leaves of shrubs.

Etymology.—The species name is derived from Sierra Madre Mountains, the type locality.

Comparisons.—Platymantis sierramadrensis, based on digital characters, belongs in the *hazelae* group. This species differs from the other species of the group primarily in the distinctive color pattern. In life, the color appears cream to creamy yellow (Fig. 1) without the dark markings and/or areolations on the body and limbs that characterize other species of this group (Brown et al. 1997). This species also differs in the appearance of the ventral body wall. It permits a partial view of underlying organs, especially eggs in gravid females.

In terms of size (SVL) at maturity, based on those species with samples of fine or more specimens, this species is among those with ranges from about 20 to 28 mm for males and with ranges widely overlapping when species are compared (Brown et al. 1997).

The species of the *hazelae* group of *Platymantis* are known only from the central and northern islands of the Philippines in contrast to the ranges exhibited by the *guentheri* group (throughout the Philippines), and the *dorsalis* group (Philippines, Palau Islands, Melanesia, and New Guinea). Three of previously recognized species of the *hazelae* group are known from the central islands and five species are known from mountain ranges or isolated mountains on the northern island of Luzon. *Platymantis sierramadrensis* does not change this zoogeographic concept. It simply adds a sixth species of the group for Luzon Island, a species apparently isolated in a previously little known mountain range, the Sierra Madre. *Platymantis sierramadrensis* is not the first new species of this genus to be described from the Sierra Madres. It is preceded by *Platymantis pygmaeus* (*dorsalis* group, Brown et al. 1998).

Advertisement calls have been recorded for three species of the *hazelae* group (*sierramadrensis, montanus,* and *subterrestris*). The note structure is similar for these three species, but the frequencies and intervals between notes differ (Fig. 1).

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Two new species of the *Eleutherodactylus rugulosus* group (Amphibia: Anura: Leptodactylidae) from Honduras

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Abstract.—Two new species of *Eleutherodactylus, E. pechorum* and *E. olanchano,* of the *E. rugulosus* group are described from Honduras. The following combination of characters will distinguish *E. pechorum* from the remaining *E. rugulosus* group members: male vocal slits present; male nuptial thumb pad absent; finger II < I; female loreal length/eye length ratio ≤1.00; keels present on unwebbed portions of toes; toes with basal webbing; canthus rounded; posterior surface of thighs marked with numerous pale spots and blotches; anteroventral and posteroventral surfaces of tibial segments barred; ventral surfaces pale yellow; and size moderate. *Eleutherodactylus olanchano* is distinguished from all other *E. rugulosus* group species by the following combination of characters: male vocal slits and nuptial thumb pads absent; finger II > I or II ≈ I; tympanum length/eye length ratio ≥1.00; and male size very small (females unknown).

Recent fieldwork in Honduras has resulted in the discovery of two new species of the *Eleutherodactylus rugulosus* group. One of these species is a streamside dweller, as are most members of the group. However, the other species occurs on forested hillsides, well above streams that are inhabited by *E. aurilegulus,* another *rugulosus* group member. The forest dwelling species represents only the third known member of the *rugulosus* group occurring in that type of habitat (Campbell et al. 1994, Johnson & Savage 1995).

Materials and Methods

All morphological and color pattern traits discussed herein follow the character states and terminology defined by Savage (1975). Comparative data for *E. azueroensis, E. taurus,* and *E. vocalis* were taken from Savage (1975). Comparative material examined is listed in Appendix I. The name *rugulosus* is in quotes in this appendix because work in progress by J. A. Campbell and J. M. Savage will likely severely restrict the geographic distribution of *E. rugulosus.* Thus, the specific identity of the Honduran and Nicaraguan material of *E. "rugulosus"* examined is unresolved at this time. Abbreviations used in each species description are EL (eye length), E–N (anterior border of eye to posterior edge of nostril; equals loreal length of Savage 1975), HL (head length; tip of snout to angle of jaw), HW (greatest width of head), LL (leg length), SL (snout length; anterior border of eye to tip of snout), SVL (snout–vent length), TL (tibia length), and TM (tympanum length). Measurements were made to the nearest 0.1 millimeter under a dissecting microscope. Museum acronyms follow those of Leviton et al. (1985) and color codes are those of Smithe (1975-1981).

Systematics

Eleutherodactylus pechorum, new species

Fig. 1

Holotype.—National Museum of Natural History (USNM) 530000, an adult male,

Fig. 1. Adult male holotype of *Eleutherodactylus pechorum* (USNM 530000), SVL 33.5 mm.

from near a small dam along a small tributary of the Quebrada de Las Marías (15°17.64′N, 85°21.29′W), about 12 airline km NNE La Colonia, Departamento de Olancho, Honduras, 680 m elev., collected 2 Aug 1998 by J. R. McCranie, K. L. Williams, and L. D. Wilson. Original number LDW 11375.

Paratype.—USNM 529999, and adult female with the same locality data as the holotype, except collected 1 Aug 1998.

Referred specimen.—BMNH 1985.1454, an adult female from along the Río Cuyamel, Departamento de Colón, Honduras.

Diagnosis.—The combination of the presence of vocal slits and the absence of nuptial thumb pads in males will distinguish *E. pechorum* from all other described members of the *E. rugulosus* group, except for *E. anciano, E. azueroensis, E. taurus,* and *E. vocalis. Eleutherodactylus pechorum* is distinguished from *E. anciano* by having finger II shorter than finger I (finger II longer than or equal in length to finger I in *E. anciano*), toe keels on toe IV of females (weakly infolded fringes on at least one side of toe IV in all four females), shorter female snouts (E–N/EL $\leq$ 1.000 versus $\geq$1.000, n = 4), and larger female size (to 59 mm SVL versus to 41 mm, n = 4). In addition, *E. anciano* is known only from remnants of broadleaf cloud forest (Lower Montane Moist Forest formation of Holdridge 1967) at 1770 to 1840 m elevation in southwestern Honduras. The new species differs from *E. azueroensis* of the Peninsulá de Azuero, Panama, in having the posterior surface of the thighs marked with numerous pale spots and blotches (a few small pale spots in *E. azueroensis*), the anteroventral and posteroventral surfaces of the tibial segments barred (uniformly brown), the canthus rounded (moderately sharp), and basal toe webbing (moderately webbed; webbing formula II 2–3 1/2 III 3–4 1/3 IV 4 1/3–3^- V in *E. pechorum* versus II 2^-–3 1/4 III 2 2/3–4 IV 4–2 1/2 V in *E. azueroensis*). *Eleutherodactylus pechorum* differs from *E. taurus* of southwestern Costa Rica and adjacent Panama in having toe keels on unwebbed portions of toes (well developed fleshy toe fringes in *E. taurus*), four and one-third segments on toe IV free of webbing (<4), definite toe discs (barely expanded), and females to 59 mm SVL (females to 80 mm). The new species can be distinguished from *E. vocalis* of western Mexico by having finger II shorter than finger I (finger II longer than or equal in length to finger I in *E. vocalis*), ventral surfaces pale yellow (white), and the anteroventral and posteroventral surfaces of the tibial segments barred (suffused).

Description of holotype (alcohol after formalin).—An adult male with the following measurements (percentages of SVL in parentheses): SVL 33.5 mm; HL 13.1 mm (39.1); HW 12.5 mm (37.3); EL 3.9 mm (11.6); SL 5.6 mm (16.7); E–N 3.4 mm (10.1); TM 3.5 mm (10.4); LL 56.5 mm (168.7); and TL 19.6 mm (58.5). Dorsum smooth with several enlarged tubercles on upper eyelids, short postorbital ridges also present; snout nearly rounded in dorsal aspect, rounded in profile; canthus rostralis rounded; tympanum prominent; first finger longer than second; finger discs definite, a little over twice width of digit just proximal to discs on fingers III–IV; well developed inner tarsal fold; heels rugose; plantar tubercles absent; inner metatarsal tubercle elongated, elevated, visible from above; outer metatarsal tubercle small, round, barely elevated; toe discs definite, that on toe IV about 1.6 times width of digit just proximal to disc; toes with marginal ridge; toes basally webbed, webbing formula I 2–2 1/2 II 2–3 1/2 III 3–4 1/3 IV 4 1/3–3^- V; vomerine tooth patches on elevated, nearly triangular-shaped ridges located posteromedially to ovoid choanae, tooth patches separated by distance less than width of either patch; paired vocal slits present; nuptial pads absent. Belly cream, lightly flecked with dark brown; throat and chest cream, moderately flecked with dark brown; dorsum brown with indistinct dark brown mottling, several white spots scattered on back; postorbital ridges slightly darker brown than adjacent dorsum; dark line absent along canthal ridges; loreal region brown; upper and lower lips with dark brown bars separated by white lines, dark lower lip bars not extending onto chin; top of head brown with slightly paler interorbital bar anterior to median portion of orbit; supratympanic fold slightly darker brown than adjacent area; groin mottled with dark brown and white; posterior surface of thighs dark brown with numerous cream spots and blotches; anterior surface of thighs pale brown with dark brown vertical bars; underside of thighs and tibial segments cream with very sparse dark brown flecks, barred with dark brown along margins.

Color in life (based on a Kodachrome® slide, except for ventral coloration, which was recorded in life): dorsal surfaces of head and body Verona Brown (223B), with slightly darker brown mottling and slightly paler brown, scattered spots; postorbital ridges mottled Verona Brown (223B) and slightly darker brown; dorsal surfaces of limbs Raw Umber (23), with darker brown crossbands; interorbital region mottled pale brown, medium brown, and dark brown, suggestive of pale interorbital bar outlined with darker brown; dark brown upper lip bars separated by pale brown; tympanum intermediate between Verona Brown (223B) and darker brown mottling; iris coppery brown, reticulated with black; belly and ventral surfaces of thighs pale yellow.

Variation in paratype (alcohol after formalin).—Color is described as follows: belly, chest, and throat cream, lightly flecked with grayish-brown; dorsum grayish-brown with distinct dark brown mottling and elongated, narrow spots; several dirty white small spots also present on lower back; postorbital ridges distinctly darker brown than adjacent dorsum; dark line absent along canthal ridges, although several dark flecks present just anterior to eye; loreal region pale brown; upper and lower lips with medium brown bars separated by dirty white lines, dark lower lip bars not extending onto chin; top of head grayish-brown with slightly paler brown interorbital bar, pale bar bordered anteriorly and posteriorly by dark brown; supratympanic fold darker brown than adjacent area; groin mottled with grayish-brown and pale brown, several dark brown spots also present; posterior surface of thighs grayish-brown with numerous cream spots and blotches; anterior surface of thighs pale brown with grayish-brown vertical bars; underside of thighs and tibial segments cream, barred with grayish-brown along margins.

The following measurements (percentages of SVL in parentheses) were recorded: SVL 41.2 mm; HL 17.0 mm (41.3); HW 16.0 mm (38.8); LL 70.7 mm (171.6); and TL 24.8 mm (60.2).

Comments on referred specimen.—A single adult female (BMNH 1985.1454; SVL 59.1 mm) from about 50 airline km NNE of the type locality of *E. pechorum* is referred to this species. This specimen is very similar in color pattern and morphology to the female paratype of *E. pechorum.* Also, although the type locality for *E. pechorum* is in the headwaters of the Río Wampú, the locality is only some 15 km from the headwaters of the Río Paulaya. The locality for the BMNH specimen is along a tributary of the latter river. Additionally, *E. epochthidius,* another streamside *Eleutherodactylus* (*E. milesi* group), is known from both the *E. pechorum* type locality and from a locality very near that for BMNH 1985.1454.

Natural history notes.—Both type specimens were collected at night alongside a small stream flowing through nearly pristine forest at 680 m elevation. However, at 660 m elevation, the former forest around this stream has been cleared, as have most of the hillsides surrounding the forest on both sides of the stream. The forest alongside this portion of the stream remains intact only because water from that portion of the stream is piped to several villages below the stream. This extensive deforestation is taking place even though the region is part of the Río Plátano Biosphere Reserve, established as a World Heritage Site in 1980. The type locality is in the Premontane Wet Forest formation of Holdridge (1967).

Etymology.—The name *pechorum* means "belonging to or pertaining to" the Pech, in reference to this frog inhabiting an area long, but sparsely populated by the indigenous Pech tribe.

Eleutherodactylus olanchano, new species

Fig. 2

Holotype.—National Museum of Natural History (USNM) 529998, an adult male, from a hillside above the Quebrada El Pinol (15°07′N, 86°44′W), Parque Nacional La Muralla, Departamento de Olancho, Honduras, 1200 m elev., collected 14 Aug 1994 by J. R. McCranie and L. D. Wilson. Original number LDW 10319.

Paratypes.—USNM 529991–97, all adult males, all from the type locality, 1180–1200 m elev., collected 21 Jul 1993 (USNM 529996–97) or 12–14 Aug 1994 (the remaining specimens).

Referred specimens.—USNM 529989–90, both adult males, from near Río de Enmedio (14°52′N, 86°48′W), Montaña El Armado, Departamento de Olancho, Honduras, 1350 m elev., collected 13 Jun 1993.

Diagnosis.—The combination of small adult male size (SVL 18.7–29.8, $\bar{X}$ = 24.8; females unknown), large male tympanum (TM/EL 1.00–1.14, $\bar{X}$ = 1.06), finger II longer than or equal in length to finger I, and males lacking vocal slits and nuptial thumb pads will distinguish *E. olanchano* from all other described species of the *E. rugulosus* group. *Eleutherodactylus olanchano* is the smallest known member of the *E. rugulosus* group. Males of all other species reach at least 33 mm SVL (the single known adult males of *E. anciano* and *E. pechorum*), 38 mm SVL (*E. vocalis*), or 40 mm or longer (the remaining *E. rugulosus* group species: Savage 1975, Savage et al. 1988, Campbell et al. 1994, Johnson & Savage 1995).

Description of holotype (alcohol after formalin).—An adult male with the following measurements (percentages of SVL in parentheses): SVL 29.8 mm; HL 13.1 mm (44.0); HW 11.7 mm (39.3); EL 3.5 mm (11.7); SL 4.8 mm (16.1); E–N 3.0 mm (10.1); TM 4.0 mm (13.4); LL 55.6 mm

Fig. 2. Adult male holotype of *Eleutherodactylus olanchano* (USNM 529998), SVL 29.8 mm.

(186.6); and TL 17.6 mm (59.1). Dorsum smooth to weakly granular, with several distinct tubercles on lower back and upper eyelids; postorbital ridges absent; canthus rostralis rounded; tympanum prominent; first finger equal in length to second; finger discs definite, about 1.8 times width of digit just proximal to discs on fingers III–IV; well developed inner tarsal fold; toe discs definite, that on toe IV about 2.0 times width of digit; toes with marginal ridge; toes moderately webbed, webbing formula I 2–2 1/2 II 2–3 1/3 III 3–4 IV 4–2 3/4 V; vocal slits absent; nuptial pads absent. Belly cream, very lightly flecked with dark brown; chest cream, heavily flecked with dark brown; throat heavily flecked with dark brown; dorsum dark brown with several very dark brown markings in postocular region; dark line absent along canthal ridges; loreal region mottled pale and dark brown; upper and lower lips with dark brown bars separated by cream lines, dark lower lip bars not extending onto chin; top of head pale brown with a few dark brown small spots in interocular region near mid level of orbit; supratympanic fold very dark brown; groin cream, heavily flecked with dark brown; posterior surface of thighs dark brown, with indistinct pale brown blotches; anterior surface of thighs pale brown, with slightly darker, incomplete vertical bars; underside of thighs and tibial segments cream, with very sparse dark brown flecks, barred with dark brown along margins.

Color in life (based on a Kodachrome® slide, except for ventral coloration, which was recorded in life): dorsal surfaces of head and body Cinnamon-Rufous (40), with several dark brown spots in postorbital and interorbital regions and slightly darker brown mottling on lower back; dorsal surfaces of limbs Cinnamon-Rufous (40), with darker brown, somewhat indistinct, crossbands; dark brown upper lip bars separated by pale brown; supratympanic folds dark brown; tympanum pale brown; iris reddish-brown, reticulated with dark brown on upper half, grayish-brown, reticulated with dark brown on lower half, both halves not separated by dark band; belly and ventral surfaces of thighs pale yellow.

Variation in type series (alcohol after formalin).—Belly coloration of all paratypes is similar to that of holotype; most specimens have less brown flecking on chest and throat than does holotype; however, one specimen (USNM 529992) has throat and chest more intensely punctated with dark brown; dorsal surfaces of head and body vary from grayish-brown to dark brown, with varying amounts of dark brown spots or lines present in postorbital and interocular regions, these dark marks indistinct in darker specimens; one specimen (USNM 529992) has a rather broad, pale brown middorsal stripe extending from tip of snout to just above vent; most specimens have indistinct pale brown blotches on posterior surface of thighs; however, these blotches can be rather distinct in a few specimens (e.g., USNM 529991–92); underside of thigh and tibial segments similar to that of holotype in all specimens, except that one specimen (USNM 529992) has slightly more flecking medially on thighs near knees than does the holotype.

Morphological measurements of the entire type series include SVL given in millimeters and other measurements as percentages of SVL, range followed by mean in parentheses: SVL 18.7–29.8 (24.8); HL 40.3–44.6 (43.5); HW 37.1–40.1 (38.6); LL 168.8–208.6 (191.0); and TL 56.4–62.9 (59.4). Additionally TM/EL ranges and means are 1.00–1.14 (1.06) in the entire type series, and finger II varies from being longer than finger I to being equal in length to finger I. Examination of the testes of two specimens (USNM 529993–94; 28.1 and 23.1 mm SVL, respectively) confirmed that they are adults.

Comments on referred specimens.—Two adult males (USNM 529989–90; 26.5 and 24.0 mm SVL, respectively) from about 30 airline km SSW of the type locality agree in all diagnostic features with those of the type series. These specimens were collected by M. R. Espinal. His collection from the Río de Enmedio region also contains two adult females of *E. aurilegulus* (USNM 529987–88; 53.5 and 53.6 mm SVL, respectively). Espinal did not record any habitat information for this collection, but it seems likely that the *E. olanchano* were taken from forested hillsides above the streamside locality where *E. aurilegulus* would be expected to occur.

Natural history notes.—The type series was collected both during the day and at night while active among leaves on the forest floor on a single hillside above the Quebrada El Pinol. Specimens were collected in July and August. Two species of streamside *Eleutherodactylus* (*E. aurilegulus* and *E. stadelmani*; *E. rugulosus* and *E. milesi* groups, respectively) were common alongside the Quebrada El Pinol at the base of the hillside, while *E. lauraster* (*E. rhodopis* group) was found in the same habitat as the *E. olanchano*. This locality is in the Premontane Wet Forest formation of Holdridge (1967), as is the locality for the referred specimens. The known elevational range for this species is 1180 to 1350 m.

Etymology.—The name *olanchano* is Spanish, meaning "native of Olancho," and is used in reference to this Honduran department, in which this species is apparently endemic. The name is a noun used in apposition to the generic name.

Discussion

Members of the *Eleutherodactylus rugulosus* group occur from southern San Luis Potosí, Mexico on the Atlantic versant and from northern Sinaloa, Mexico on the Pacific versant southward to central Panama (Savage 1975). The two new species described herein appear to have relatively small geographical distributions as do many other Central American members of this group (Savage, pers. comm.).

Among the described species of the *E. rugulosus* group, *E. pechorum* appears to be most similar morphologically to *E. azueroensis* of low and moderate elevations (60–940 m) of the Peninsulá de Azuero, Panama. However, the intervening lowlands (with the exception of the Golfo Dulce area of the Pacific versant of southern Costa Rica and adjacent Panama where *E. taurus* occurs) are inhabited by one or more moderately webbed species of the *E. rugulosus* group in which the males lack vocal slits and nuptial thumb pads. No specimens from the intervening territory resemble either *E. pechorum* or *E. azueroensis* in the subtle features that distinguish species in this group. The localities for *E. pechorum* lie in excess of 900 km NNW of the nearest known locality for *E. azueroensis.*

The second new species described herein (*E. olanchano*) possesses a combination of male characters (very small size, very large tympanum, finger II longer than or equal in length to finger I, and the absence of vocal slits and nuptial thumb pads) not shared with any other described member of the group.

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Appendix I
Comparative material examined

Eleutherodactylus anciano. Honduras—Ocotepeque: El Chagüitón, KU 208999–9001, ROM 18076–80.

Eleutherodactylus aurilegulus. Honduras—Atlántida: Lancetilla, AMNH 54792–96, MCZ 16184–88, 16280, 16284–85, 17448–50, 21270; 2.0 km SE Lancetilla, TCWC 30129; mountains S of Lancetilla, MCZ 16191; 7 km NW Las Mangas, UF 90216; Quebrada La Muralla, SMF 77636–39; Quebrada de Oro, KU 209002–32, 209033 (3), LACM 137286–97; Tela, UMMZ 70329 (7). Colón: Balfate, AMNH 45696–703, 45718; Trujillo, CM 63920–21. Olancho: Quebrada La Calentura, USNM 343704; Quebrada Las Cantinas, USNM 343710–14; between El Díctamo and

Parque Nacional La Muralla Centro de Visitantes, USNM 343625–36; Río de Enmedio, USNM 529987–88; Quebrada La Habana, USNM 343705–09; Quebrada de Las Mesetas, USNM 343695–702; Quebrada del Monte Escondido, USNM 343703; near Parque Nacional La Muralla Centro de Visitantes, USNM 343622–24; Quebrada El Pinol, USNM 343657–94; confluence of quebradas El Pinol and Las Cantinas, USNM 343638–56; near Los Planes, USNM 343637; Quebrada Salitre Lajas, USNM 343715–16; Sendero El Pizote, USNM 343717–19. Yoro: Monte Mataderos, MCZ 21287; Portillo Grande, FMNH 21859–60, 34696–97, MCZ 21273–75, 21289, UMMZ 77852 (3); Santa Marta, FMNH 21857–58, MCZ 21271–72, 21288, UMMZ 77851 (3); Subirana Valley, FMNH 21782, MCZ 21283–86; 6.6 km S Yoro, MVZ 171375–76, USNM 217582–83; ca. 3 km W Yoro, TCWC 23619; ca. 32 km W Yoro, MVZ 175800, USNM 217584–85.

Eleutherodactylus "*rugulosus.*" Honduras—Comayagua: between La Misión and Trincheras, AMNH 54752; Siguatepeque, MCZ 26421. Cortés: Agua Azul, AMNH 54951; Río Guayabal, AMNH 54751; Hacienda Santa Ana, FMNH 4661 (3), 4663, 4665–69, 4691–93, 4695–97, MCZ 17433–34, 21282, SMF 29865; Cañon Santa Ana, FMNH 4671, 4674–75; Lago de Yojoa, MSUM 4540, 4637. El Paraíso: ca. 6 km E Danlí, TCWC 23811; Danlí, BYU 18209; Monserrat, AMNH 54814; Montaña del Volcán, MCZ 26433–35. Francisco Morazán: Agua Amarilla, AMNH 54883; San Francisco, AMNH 54750; Cerro Uyuca, MCZ 26440; Rio Yeguare Valley, MCZ 25954–56, UMMZ 94055 (6); El Zamorano, MCZ 26376–77, 26469. Intibucá: 5 km NE Jesús de Otoro, TCWC 23810. Santa Bárbara: Montaña de Santa Bárbara, AMNH 55309–12. "HONDURAS," ZMB 13202 (holotype of *Hylodes laevissimus* Werner). Nicaragua—Atlántico Sur: Río Chiquito, SMF 77825. Granada: Volcán Mombacho, SMF 78222–28. Matagalpa: Selva Negra, SMF 78207–21.

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Taxonomic status and geographic distribution of *Bryconamericus eigenmanni* Evermann & Kendall, 1906 (Characiformes: Characidae)

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Abstract.—*Bryconamericus eigenmanni* Evermann & Kendall (1906) is redescribed on the basis of additional material collected at the type locality, Río Primero, Province of Córdoba, central Argentina. Evidence supporting the validity of *B. eigenmanni* based on morphometric, meristic, and osteological characters is discussed. The geographic distribution of *B. eigenmanni* is analyzed and the species is compared with *Bryconamericus iheringi,* which some authors suggested was conspecific. *Bryconamericus eigenmanni* can be distinguished from *B. iheringi* by the number of maxillary teeth, premaxilla shape, body depth, caudal peduncle length, orbital diameter, and the secondary sexual dimorphism of the pelvic fin of males. The known range of *B. eigenmanni* suggests that it is endemic to endorrheic drainage basins of central Argentina.

Resumen.—Se redescribe *Bryconamericus eigenmanni* en base a material adicional colectado en la cuenca de la localidad tipo, Río Primero, Provincia de Córdoba, Argentina central. Se discute evidencia apoyando la validez de *B. eigenmanni* en base a caracteres morfométricos, merísticos y osteológicos. Asimismo, se analiza la distribución geográfica y se compara con *Bryconamericus iheringi,* la cual fue sugerida como coespecífica por algunos autores. *Bryconamericus eigenmanni* puede distinguirse por el número de dientes maxilares, forma del premaxilar, diámetro orbitario, altura del cuerpo, longitud del pedúnculo caudal, y el dimorfismo sexual secundario en la aleta pélvica del macho. El rango de distribución conocido de *B. eigenmanni* sugiere que es endémica de cuencas endorreicas de la región central de Argentina.

The characid *Bryconamericus eigenmanni* (Evermann & Kendall 1906:83) was originally described on the basis of two specimens from the Río Primero, the main tributary of an endorrheic drainage basin of the Province of Córdoba, in central Argentina. The taxonomic status of this species has been regarded as unclear by a number of authors primarily because of its close similarity with *B. iheringi,* a species widespread through the Plata basin. This similarity was noted by Eigenmann (1927:379), although he preferred to recognize the species as distinct, a practice followed by subsequent authors (e.g., Ringuelet et al. 1967: 116, Géry 1977:390). The lack of additional collections of *B. eigenmanni* prevented further analysis of the question. Malabarba & Kindel (1995:684) explicitly noted the need for a statistical comparison of population samples from within the areas of distribution of both nominal species. However, these authors added uncertainty to the identity of *B. eigenmanni* by erroneously citing its type locality as being within the Río Paraná system, when it is actually a separate drainage.

Bryconamericus eigenmanni, first assigned to *Astyanax* by Evermann & Kendall (1906:83), was transferred to *Bryconamericus* by Eigenmann (1910:434), who had previously proposed the genus (in Eigenmann et al. 1907:139). The current definition of the genus follows Eigenmann (1927), and was summarized by Vari & Siebert (1990:516) and Malabarba & Kindel (1995:679). These authors, among others, pointed out the need for a reconsideration of the monophyly of *Bryconamericus,* including an evaluation of the taxonomic status of the nominal species assigned to the genus. Given those questions, we have focused on the taxonomic identity of the species *B. eigenmanni* as part of a comprehensive revision of the species of the genus *Bryconamericus* in Argentina. We present evidence supporting the distinctiveness of *B. eigenmanni,* redescribe the species, compare it with *B. iheringi,* and discuss its geographic distribution.

Material and Methods

Most of the examined material was collected by members of the Laboratory of Ichthyology of the Institute of Limnology "Dr. Raúl A. Ringuelet" (ILPLA) during field trips to the Province of Córdoba, Argentina, using nets and the ichthyocide Pronoxfish. Measurements were taken using calipers to the nearest 0.05 mm. Caudal-peduncle length was measured from the base of the last anal-fin ray to the last perforated scale of the lateral line. Osteological preparations were made following Dingerkus & Uhler (1977). Meristic data are presented as ranges; the mean is indicated between parentheses when necessary. Counts of gillrakers on the lower portion of the arch includes the element at the corner between inferior and superior arches. The anal-fin ray count includes the last ray divided to its base as a single element. The lateral-line count includes the last pored scale. The following abbreviatures are used: C & S, cleared and stained; F, females; HL, head length; M, males; *n,* number of specimens; and SL, standard length. Institutional abbreviations used in the listing of material examined follow Leviton et al. (1985). The drainage basins follow the terminology of Mazza (1962).

Bryconamericus eigenmanni
(Evermann & Kendall, 1906)
Fig. 1a, b

Astyanax eigenmanni Evermann & Kendall, 1906: 83, fig. 1.

Bryconamericus eigenmanni.—Eigenmann, 1910: 434; 1927: 379, pl. 68, fig. 1, pl. 69, fig. 13.—Pozzi, 1945: 255.—Ringuelet & Arámburu, 1962: 29.—Ringuelet et al., 1967: 116.—Ringuelet, 1975: 82.—Géry, 1977: 390.—Malabarba & Kindel, 1995: 684, fig. 3.—Miquelarena & Aquino, 1995: 560.—López et al., 1996: 6.

Material examined (all localities in Argentina unless noted otherwise).—*Bryconamericus eigenmanni:* USNM 55570 (holotype of *Astyanax eigenmanni* Evermann & Kendall, 1906), Río Primero, Córdoba, 1903–1904. J. W. Titcomb. ILPLA 970 (8 ex.), MLP 6-VII-83-22 (8 ex.), second Arroyo Mallín-Tanti, Córdoba. ILPLA 971 (11 ex. + 8 c&s), MLP 6-VII-83-15 (55 ex.), Arroyo Cachimayo, near Taninga, Córdoba. ILPLA 972 (17 ex.), Bialet Massé, Río Cosquín, Córdoba. ILPLA 973 (11 ex. + 4 c&s), MLP 6-VII-83-16 (54 ex.), Arroyo Niñanquil, Córdoba. ILPLA 974 (5 ex.), MLP 6-VII-83-20 (26 ex.), stream at camping ground Villa Giardino, Córdoba.

Bryconamericus iheringi: ILPLA 297 (50 ex.), ILPLA 298 (7 ex.), ILPLA 595 (27 ex.), Laguna Chascomús, Buenos Aires. ILPLA 975 (18 ex.), Laguna Cochicó, Buenos Aires. MCP 11481 (3 ex.), Arroio do Ouro, along road between Feliz and Caxias do Sul (RS 452), almost 100 m above bridge, Jacui drainage, Rio Grande do Sul, Brazil. USNM 310959, Arroyo Pelotas at

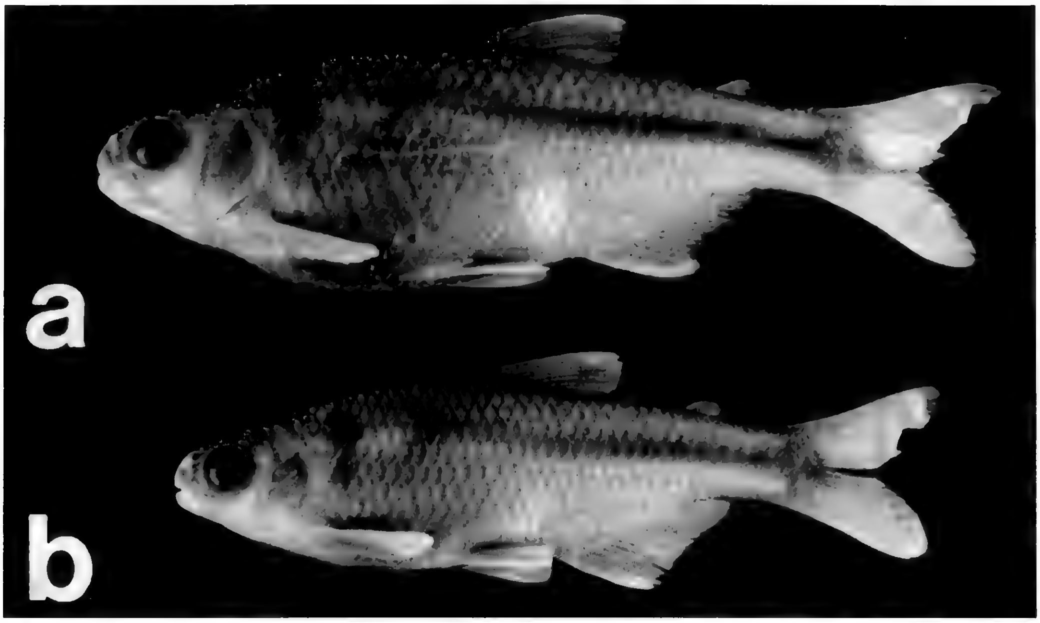

Fig. 1. *Bryconamericus eigenmanni,* ILPLA 970. Left lateral view. a, female, SL = 61.0 mm; b, male, SL = 50.7 mm. Second Arroyo Mallín-Tanti, Córdoba, Argentina.

bridge crossing, along road between Pelotas and Porto Alegre, near Pelotas, Rio Grande do Sul, Brazil. USNM 310947, Rio Grande do Sul, Brazil. USNM 310979, Arroyo Sarandi, Rio Grande do Sul, Brazil.

Description

Body elongate. Dorsal and ventral profiles slightly convex. Head short and robust; snout deep and rounded, blunt. Caudal peduncle deep and moderately long. Anal-fin origin along vertical line through base of last dorsal-fin ray. Mouth slightly inferior. Maxilla approaching or reaching vertical line through anterior border of eye. Infraorbitals well developed, 6, third largest. Ventral and posterior margins of infraorbitals reaching horizontal and vertical limbs of preopercle.

Posterior border of dorsal, pectoral, and caudal fins gently rounded. Pelvic-fin tip rounded in males, pointed in females. Dorsal-fin rays ii, 7–9, typically 8. Second unbranched and first branched dorsal-fin rays almost equal in length. Tip of adpressed dorsal fin not reaching adipose fin. Adipose fin small. Pectoral-fin rays i, 10–12; these occasionally followed by one or two unbranched rays. Ventral-fin rays i–ii, 6–8, typically ii, 7. Principal caudal-fin rays 17+2; dorsal caudal-fin procurrent rays 10–12, and ventral procurrent rays 8–10. Anal-fin rays iv, 15–17.

Cycloid scales regularly distributed on body. Single row of scales on base of 9 to 12 anterior branched anal-fin rays. Scales present on caudal-fin base. Lateral line complete, 38 to 39 perforated scales. Rows of scales from dorsal-fin origin to lateral line 5–6, and 4.5–5.5 from lateral line to anal-fin origin. Vertebrae 36–38, typically 37. Supraneurals 4–6, typically 5. Gill rakers 7–9+10–12. Morphometric characters presented in Table I.

Teeth.—Maxilla elongate, with 3 to 6 teeth along ventral margin (Fig. 2a). Each tooth typically tricuspidate, though teeth with 1 or 4 cusps also occur. Premaxilla ascending process short and slightly curved (Fig. 2b). Premaxilla with an outer row of 4 or 5 tricuspidate teeth, and an inner row of 4 teeth, with 4 or 5 cusps each. Dentary with 8 to 12 teeth: 3 or 4 larger anterior teeth with 4 or 5 cusps, followed by a series of smaller teeth, usually with 1 or 3 cusps (Fig. 2c).

Color in alcohol.—Ground color light tan. Body and head finely dotted, more con-

Table 1.—Morphometric data of *Bryconamericus eigenmanni* presented as percent of standard length (3–11), distance between origins of pectoral and pelvic fin (12), and head length (13–15) (ILPLA 970; ILPLA 971; ILPLA 973; ILPLA 974) (13 M, 7 F).

Character	Range	$\bar{X}$	*SD*	*n*
1 Standard length	46.0–73.0	59.6	5.8	20
2 Total length	58.0–88.0	72.4	6.9	20
3 Body depth	28.7–33.0	31.1	1.1	20
4 Head length	24.1–27.2	25.7	0.8	20
5 Caudal peduncle length	11.4–15.4	13.2	0.8	20
6 Caudal peduncle length	17.9–23.2	20.2	1.1	19
7 Predorsal distance	47.1–53.1	50.3	2.0	20
8 Prepelvic distance	42.5–49.1	46.4	1.8	20
9 Preanal distance	58.8–68.0	63.2	2.1	20
10 Pectoral-pelvic distance	19.5–26.8	23.6	1.6	20
11 Pelvic-anal distance	15.7–25.8	18.9	2.0	20
12 Pectoral length	73.8–125.2	103.9	13.7	17
13 Orbital diameter	21.9–30.7	27.9	1.9	20
14 Interorbital width	30.3–39.6	35.9	2.4	20
15 Snout	16.2–27.4	22.6	2.6	20

centrated along posterior scale margins forming overall reticulated pattern more evident above trunk midlateral line. Dark pigmentation on head, opercle, supraorbitals, maxilla, and along body dorsal of midline relatively more intense. Vertically elongate dark brown humeral mark between second and fourth lateral-line scales. Midlateral band extends from near vertical line through dorsal-fin origin, along second scale row dorsal to lateral line. Band faint anteriorly and becoming darker posteriorly; covering one-third of caudal peduncle depth below adipose fin, and terminating as triangular spot on caudal-fin base. Paired fins light brown. Dorsal and anal fins dark brown, with distal portions of first rays lighter. Middle rays of caudal fin dark.

Sexual dimorphism.—First to fourth or fifth branched pelvic-fin rays of males curved to form a basket-like structure (Fig. 3a). In females ventral fins almost flat (Fig. 3b). Pectoral and pelvic fins larger in males, where tip of pectoral fin reaches or slightly surpasses pelvic-fin origin. Pelvic fin reaches anal-fin origin. In females tip of both pectoral and pelvic fins separated from pelvic- and anal-fin origins, respectively, by two or more scale rows. Margin of anal fin almost straight in males and slightly concave in females, in which first branched rays relatively longer. Males with bony hooks on pelvic and anal fins. Anal-fin hooks short, curved (Fig. 4a), forming smaller angle relative to ray axis than one formed by longer and more pointed pelvic-fin hooks (Fig. 4b).

Distribution.—Known only from the Province of Córdoba in central Argentina (31°00′S; 65°02′W). It was collected in the endorrheic drainage basins of the Río Primero and the Río Pichanas, to the east and west respectively of the Sierras Grandes.

Ecology.—Collected in shallow creeks (ca. 0.5 m deep) over sandy to rocky bottom, and in deeper pools (up to 1.5 m deep) of the same streams. Water in these environments has the anion CO_3H^- and the cations Ca^{++} and Na^+ as the most abundant elements (Menni et al. 1984). Following Cabrera's (1976) phytogeographical scheme, the distribution range of *B. eigenmanni* is the "Chaqueño-serrana" area of the "Chaqueño" dominion.

Discussion and Conclusions

The original description provided by Evermann & Kendall (1906) does not permit an unequivocal discrimination of *B. eigen-*

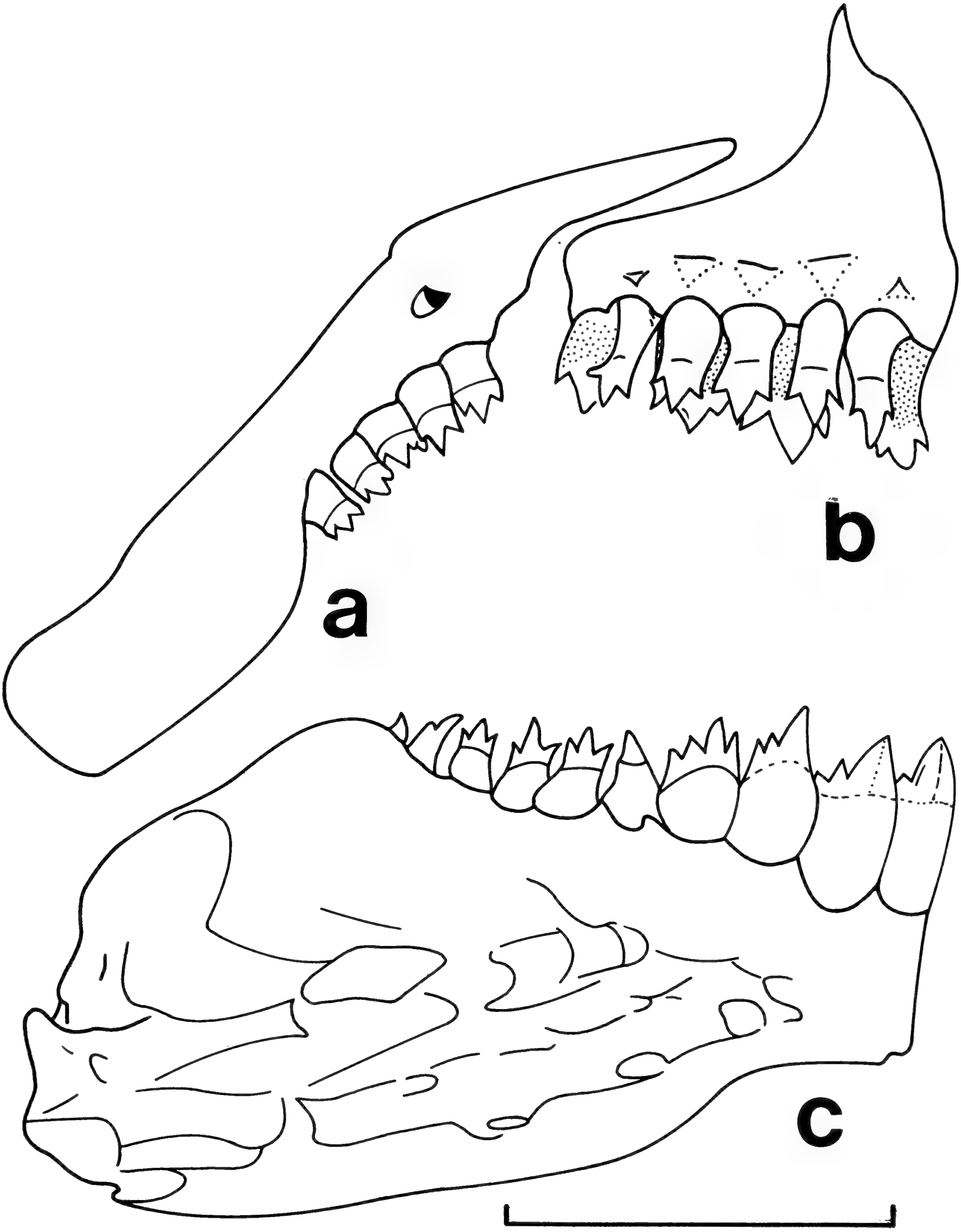

Fig. 2. Jaws of *Bryconamericus eigenmanni*, ILPLA 973. a, maxilla; b, premaxilla; c, dentary. Scale bar: 1 mm.

manni from congenerics. Eigenmann (1927) noted its close similarity to *B. iheringi,* however, indicating that *B. eigenmanni* differed in having less convex dorsal and ventral body profiles, longer pectoral fins, and wider naked area below the infraorbitals. Ringuelet et al. (1967:116) and Malabarba & Kindel (1995:684) pointed out that neither the meristic nor morphometric values of *B. eigenmanni* clearly differed from those of *B. iheringi.* Malabarba & Kindel (1995) erroneously considered the type lo-

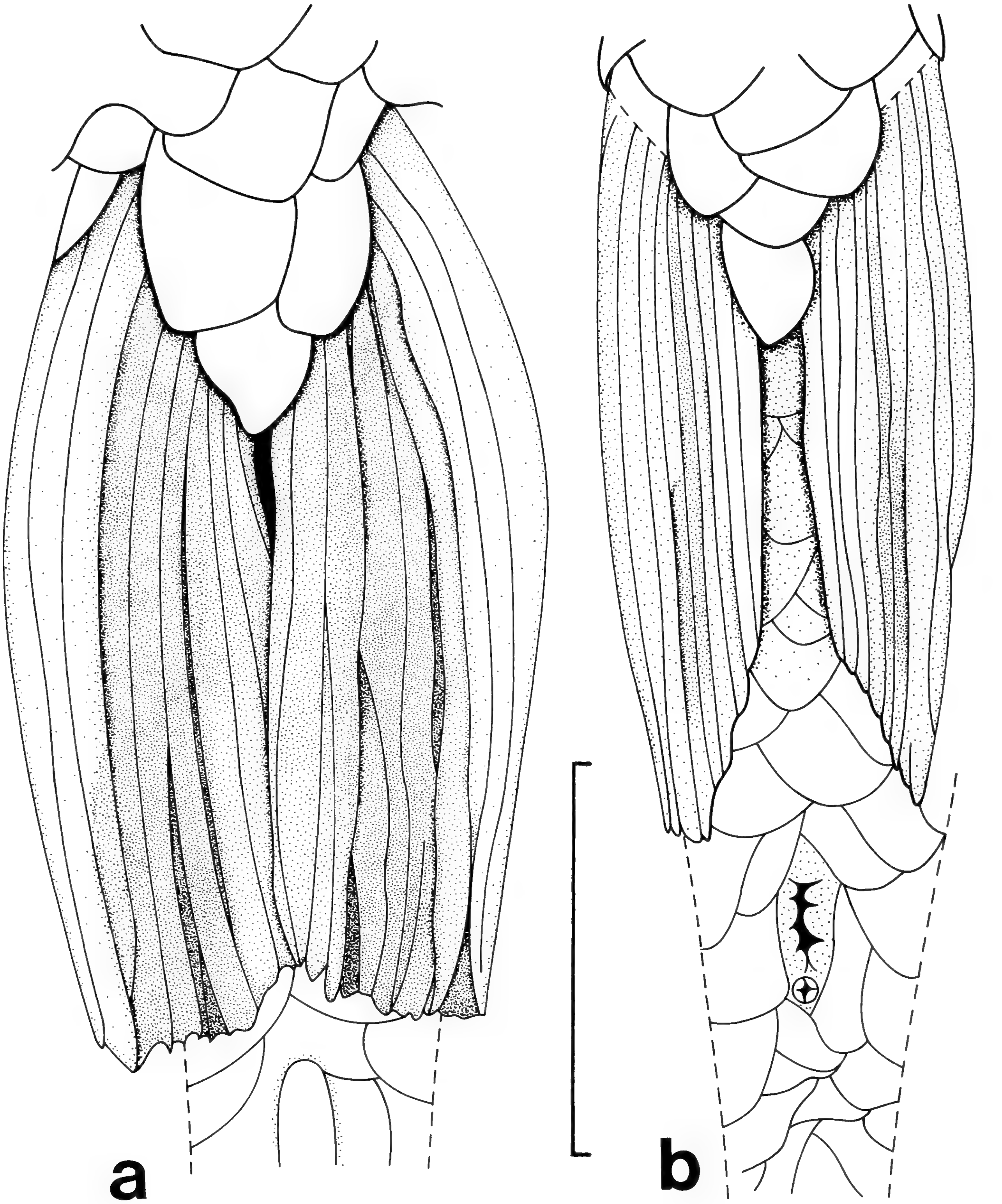

Fig. 3. Sexual dimorphism in ventral-fin shape of *Bryconamericus eigenmanni.* a, male; b, female. Scale bar: 5 mm.

cality of *B. eigenmanni* to be within the río Paraná basin, which implied overlapping geographical ranges between the two species. In actuality the type locality of *B. eigenmanni* is in an endorrheic drainage basin of central Argentina, separate from the Paraná/Plata basin.

The two type specimens of *B. eigenmanni* had been the only source of information on the species, leading to questions about its identity. The examination of more extensive samples of specimens from the type drainage of *B. eigenmanni* allows us to confirm the distinctiveness of the species and

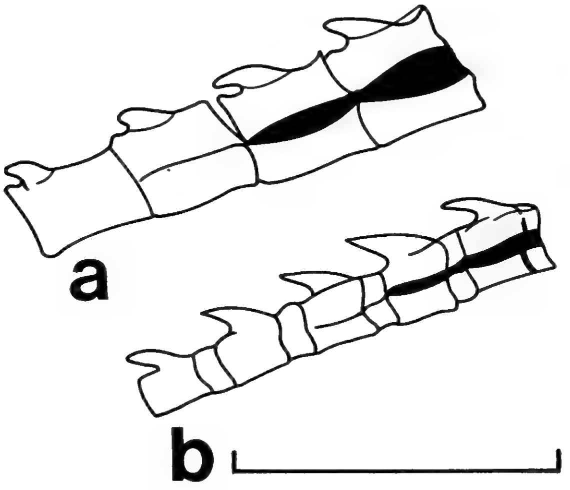

Fig. 4. Bony branched fin ray hooks in males of *Bryconamericus eigenmanni.* Left side, lateral view, tip of ray to the right. a, anal fin; b, ventral fin. Scale bar: 0.5 mm.

its restricted geographic distribution in central Argentina.

Bryconamericus eigenmanni differs from *B. iheringi* by the following combination of characters: higher number of maxilla teeth (3–6 vs. 2–4 in *B. iheringi*) (Fig. 2a) (Miquelarena & Aquino, 1995:567); premaxilla ascending process pointed and slightly curved (Fig. 2b); in *B. iheringi,* it is blunt and strongly curved (Miquelarena 1986: 30–32, Miquelarena & Aquino 1995:567); shallower body depth (28.7–33.0 (31.1) % SL; *n* = 20 vs. 33.7–38.3 (35.9) % SL; *n* = 19); shorter orbital diameter (21.9–30.7 (27.9) % HL; *n* = 20; 31.6–37.9 (34.9); *n* = 19); longer caudal-peduncle length (17.9–23.2 (20) % SL; *n* = 19 vs. 14.2–18.2 (15.9) % SL; *n* = 19); in males of *B. eigenmanni,* the fins are distinctly secondarily sexually dimorphic, with the first to fourth or fifth lateral branched rays curved to form a basket-like structure (Fig. 3a). In males of *B. iheringi,* the pelvic fins are almost flat, the same condition in females of both species.

According to the ichthyogeographical scheme proposed by Ringuelet (1975), the range of *B. eigenmanni* falls in the contact zone between the Andean and Paranensean domains, encompassing the so-called Sierras Grandes, which represents the main orographic system of the region. Based on the similarity in the composition of fish faunas to both slopes of the Sierras Grandes, Menni et al. (1984:28–29) proposed a demarcation between those domains west to these hills, a hypothesis which is also supported by the distribution range of *B. eigenmanni.*

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Caridina clinata, a new species of freshwater shrimp (Crustacea: Decapoda: Atyidae) from northern Vietnam

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Abstract.—*Caridina clinata,* a new species of atyid shrimp, is described from northern Vietnam. The new species is characterised by a short, sloping rostrum which reaches to or slightly exceeds the distal margin of the basal antennular segment, the shape of the sexual appendages, and its large egg size.

Eight species and subspecies of freshwater shrimps of the family Atyidae have been previously reported from Vietnam: *Caridina vietnamensis* Dang, 1967, *C. subnilotica* Dang, 1975, *C. acuticaudata* Dang, 1975, *C. flavilineata* Dang, 1975, *C. serrata serrata* Stimpson, 1860, *C. serrata cucphuongensis* Dang, 1980, *C. tonkinensis* Bouvier, 1919, and *C. cantonensis* Yu, 1938 (Dang 1967, 1975, 1980). Cai (1996) subsequently synonymized *Caridina vietnamensis* with *Neocaridina palmata palmata* (Shen, 1948). Recently, a revision of the *Caridina serrata* species group (Cai & Ng 1999) indicated that the specimens illustrated as "*C. serrata serrata*" by Dang (1980) probably represent an undescribed species and *C. serrata cucphuongensis* should be elevated to specific rank. *Caridina tonkinensis* and *C. cantonensis* have been shown to have a wide Chinese, Indo-Chinese and/or Southeast Asian distribution (Johnson 1961; Ng & Choy 1990a, 1990b; Cai & Ng, 1999). As a result of those studies, only four species: *C. subnilotica, C. acuticaudata, C. flavilineata* and *C. cucphuongensis* are known to be endemic to Vietnam.

Recently, we had an opportunity to examine several lots of specimens of *Caridina* collected from northern Vietnam. These specimens proved to belong to an undescribed species. Specimens are deposited in the Zoological Reference Collection of the Raffles Museum, National University of Singapore (ZRC); Zoological Museum of Hanoi University, Vietnam (ZMHU); Institute of Zoology, Academia Sinica, Beijing, China (IZAS); National Museum of Natural History, Leiden, The Netherlands (RMNH); National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM); and Muséum National d'Historie Naturelle, Paris, France (MNHN). The abbreviation cl is used for carapace length, measured from the postorbital margin to the posterior margin of the carapace.

Caridina clinata, new species
(Figs. 1, 2)

Material examined.—Holotype: male, cl 3.3 mm (ZRC 1998.550), ditch, Cuc Phuong National Park, Ninh Binh Province, northern Vietnam, 16 Sep 1997. Paratypes: 3 males, cl 3.0–3.4 mm, 7 females, cl 3.7–4.2 mm (ZRC 1998.551–560), 2 males, cl 3.0–3.2 mm, 2 females, cl 4.0–4.1 mm (IZAS), 1 male, cl 3.4 mm, 2 females, cl 3.4–3.6 mm (ZMHU), 1 male, cl 2.8 mm, 2 females, cl 3.2–4.0 mm (RMNH), 1 male, cl 2.8 mm, 2 females, cl 3.8–3.9 mm (USNM), same data as holotype. None-

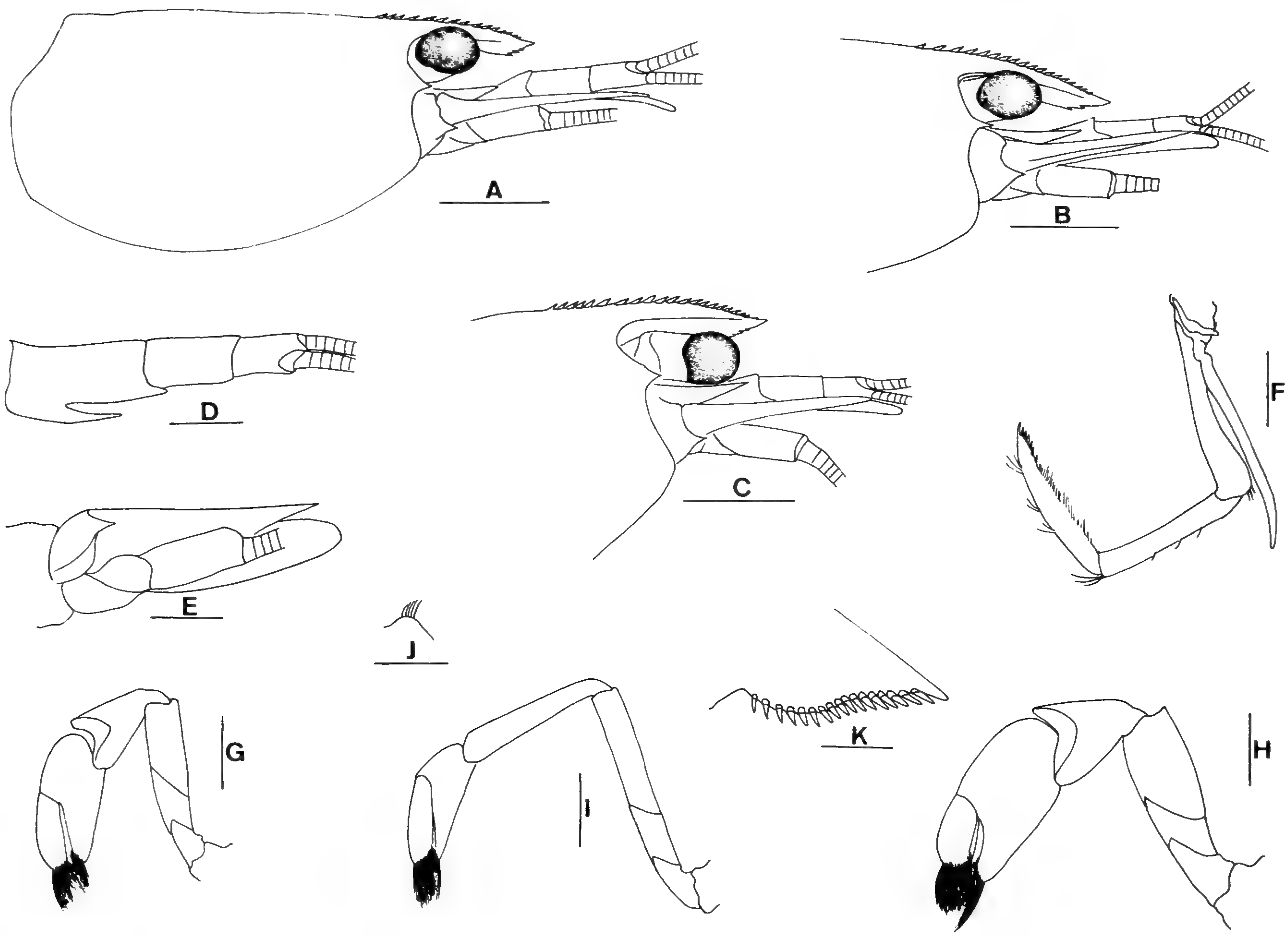

Fig. 1. *Caridina clinata,* new species, paratypes. A, cephalothorax; lateral view, male, cl 3.2 mm (ZRC 1998.551); B, anterior portion of cephalothorax, lateral view, female, cl 4.0 mm (ZRC 1998.552); C, anterior portion of cephalothorax, lateral view, female, cl 4.2 mm (ZRC 1998.553); D, right antennular peduncle; E, right scaphocerite; F, right third maxilliped; G, right first pereiopod of male; H, right first pereiopod of female; I, right second pereiopod; J, preanal carina, lateral view; K, uropodal diaeresis. Scales: A, B, C = 1 mm; D, E, F, G, H, I, J = 0.5 mm. K = 0.1 mm.

types: 1 ovigerous female, cl 4.2 mm (ZRC), approximately 8.7 km from Nho Quan on Phu Ly to Cucphuong Road, Ba Dien district, Ninh Binh Province, northern Vietnam, coll. H. H. Ng & D. C. J. Yeo (from fisherman), 16 Sep 1997.

Description.—Rostrum (Fig. 1A–C) short, reaching to or slightly exceeding distal margin of basal antennular segment, not reaching as far as middle of second segment, sloping ventrad anteriorly; armed dorsally with 13–21 (mode 14–16) teeth, including 3–5 (mode 4) teeth on carapace posterior to orbital margin; armed ventrally with 2–5 (mode 2–3) teeth. Suborbital angle acute, completely fused with antennal spine; pterygostomian margin rounded.

Abdomen with sixth somite 0.4 times as long as carapace, 1.5 times as long as fifth somite, slightly shorter than telson. Telson (Fig. 2A) (not including marginal spines) slightly longer than sixth somite, tapering posteriorly, lacking posteromedian projection; 1 pair of dorso-lateral spines near distal end, 5 pairs of spiniform setae on distal margin, lateral pair subequal to or slightly shorter than intermediate pairs; preanal angle rounded, symmetrical lacking spine.

Eyes well developed. Atennular peduncle (Fig. 1D) 0.6 times length of carapace; basal segment slightly shorter than half length of peduncle; second segment distinctively longer than third. Stylocerite not reaching distal margin of of basal antennular segment. Scaphocerite (Fig. 1E) ovate, reaching beyond distal end of antennular peduncle; 3.4 times as long as broad. Branchial formula as for genus. Epipods present on first 4 pereiopods. Third maxilliped (Fig. 1F) reaching slightly beyond distal end of antennular peduncle, ending in single terminal claw; exopod reaching to fourth of penultimate segment; ultimate segment as long as penultimate.

First pereiopod (Fig. 1G, H) short, robust, reaching slightly beyond distal margin of basal antennular segment; chela about 2.3 times as long as broad in male (Fig. 1G), 2.0 times in female (Fig. 1H); fingers as long as palm in male, 0.7 times as long as palm in female; carpus 1.5 times as long as high in male, 1.2 times as long as palm in female; merus slightly shorter than palm; merus 2.3 times in female and 1.3 times in male as long as broad. Second pereiopod (Fig. 1I) long, slender, reaching end of antennular peduncle; chela about 2.5 times as long as broad, fingers about 1.6 times as long as palm; carpus slightly longer than chela, about 4.7 times as long as high. Third pereiopod (Fig. 2B) reaching slightly beyond end of antennular peduncle; dactylus (Fig. 2C) terminating in 2 spines, bearing 5 spines on posterior margin; propodus 9 times as long as broad, about 3.6 times as long as dactylus, with numerous spinules on posterior margin. Fifth pereiopod (Fig. 1D) reaching slightly beyond distal margin of second antennular segment; dactylus (Fig. 1E) ending in curved claw, with row of 45–49 closely spaced spinules; propodus slender, 10 times as long as broad, about 3.3 times as long as dactylus (including terminal claw), with numerous spinules on posterior margin.

Endopod of male first pleopod (Fig. 2F) 2.8 times as long as broad, half as long as exopod, rounded distally; with appendix interna exceeding terminal margin of endopod by 0.3 its length; endopod with long plumose setae on outer and distal margins, with short simple setae on inner margin.

Appendix masculina of male second pleopod (Fig. 2G) extending to proximal 0.6 length of endopod, with some short spinules on outer surface and some long spinules on distal surface; appendix interna about 0.8 length of appendix masculina.

Uropodal diaeresis with 14–17 spinules.

Eggs large, ranging in dimensions from 0.60–0.75 to 1.10–1.15 mm.

Habitat.—This new species was found in a ditch with a sandy substratum and clear flowing water from the forest. Other decapods found in the ditch are the potamid crabs *Potamiscus cuphuongense* Dang, 1975 and *Potamiscus kimboiense* (Dang, 1975) (D. C. J. Yeo, pers. comm.). The latter species was originally placed in the genus *Ranguna* Bott, 1966, but is now regarded as a junior subjective synonym of *Potamiscus* Alcock, 1909 (Ng & Naiyanetr 1993).

Color (from a color photograph taken several hours after preservation in 10% formalin).—Body yellowish to grey and dark grey. There is one transverse black stripe which is irregularly broken at the lateral posterior margin of the carapace. Some irregular black spots are present on the ventrolateral parts of the carapace. The ventrolateral portion of the abdominal tergal pleura are mottled with black spots adjacent to the articular knobs at the posterior bases of the pleura. Black transverse stripes are present at the posteroventral ends of the first four pleura. The dorsum of the third abdominal somite has a black transverse stripe. The antenna, antennule and telson are yellowish to orange, and the pereiopods are translucent to yellowish.

Etymology.—The new species is named as 'clinata', Latin, meaning "sloping", alluding to the shape of rostrum.

Remarks.—*Caridina clinata* new species, is most similar to *C. flavilineata* from Namha, northern Vietnam, in the rostral formula and egg size. It differs from the latter, however, by the form of the rostrum which is short and sloping (vs. long and straight); the dactylus of fifth pereiopod has 45 to 49 denticulate spinules (vs. 20–30); the endopod of the male first pleopod reaching to half the length of the exopod (vs. 1/3 in *C. flavilineata*); the appendix masculina of the

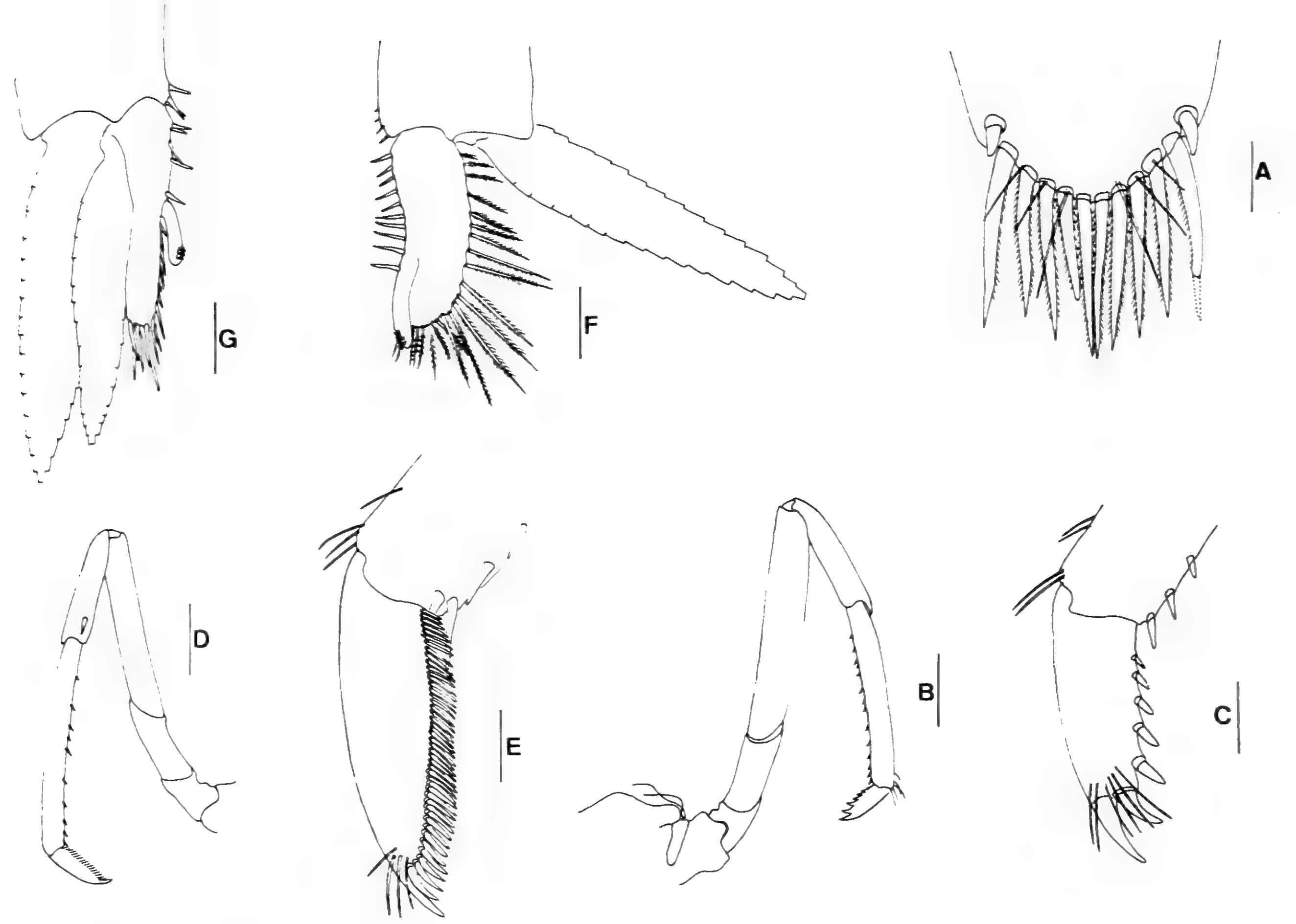

Fig. 2. *Caridina clinata,* new species, paratype, male, cl 3.2 mm (ZRC 1998.551). A, distal portion of telson; B, right third pereiopod; C, dactylus of right third pereiopod; D, right fifth pereiopod; E, dactylus of right fifth pereiopod; F, left male first pleopod; G, left male second pleopod. Scales. A, C, E, F, G = 0.2 mm, B, D = 0.5 mm.

male second pleopod reaching to 2/3 the length of the endopod (vs. reaching to half the length); and the appendix interna of the male second pleopod is 2/5 as long as the appendix masculina (vs. more than half the length) (cf. Dang 1975:70, fig. 5, Dang 1980:412, fig. 235). Dang (1980) had described *C. cucphuongensis* from the same area as *C. clinata,* although we did not manage to obtain fresh specimens from there. *Caridina clinata,* can easily be separated from *C. cucphuongensis* by the form of the rostrum and rostral formula [(2–5)13–21/2–5 vs. (1–3)5–9/0–2 in *C. cucphuongensis*]; the short stylocerite which does not reach the end of the basal segment of the antennular peduncle (vs. reaches beyond); and the symmetrical shape of the preanal carina (vs. asymmetrical) (cf. Dang 1980).

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Inclusion of the austral species *Pinnotheres politus* (Smith, 1869) and *Pinnotheres garthi* Fenucci, 1975 within the genus *Calyptraeotheres* Campos, 1990 (Crustacea: Brachyura: Pinnotheridae)

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Abstract.—The limpet crabs *Pinnotheres politus* (Smith, 1869) known from Perú to Chile, and *P. garthi* Fenucci, 1975 known from Brazil to Argentina, are transferred to the genus *Calyptraeotheres* Campos, 1990. As result, the diagnosis of the genus is emended in order to account for the presence or absence of the minute dactylus of the third maxilliped. Additional characters that remain diagnostics for *Calyptraeotheres* are, caparace with two longitudinal cervical depressions, anteriorly arcuate and sharp edged; walking legs 1–3 similar in shape, walking leg 4 slender and its dactylus longer than other walking legs; third maxilliped with a robust carpus, larger than the propodus; abdomen in both sexes with six abdominal somites and telson well separated. Species of *Calyptraeotheres* are obligatory symbionts of slipper shells (family Calyptraeidae).

The study of specimens and published descriptions and figures indicates that the austral limpet crabs *Pinnotheres garthi* Fenucci, 1975 and *P. politus* (Smith, 1869) should be included in the genus *Calyptraeotheres* Campos, 1990. As a result the original diagnosis of this genus needs to be emended. However, most of the characters provided by Campos (1990) to distinguish *Calyptraeotheres* remain valid. The following Institutions provided specimens for the present study: National Museum of Natural History, Smithsonian Institution (USNM); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" Washington D.C. (MACN); Laboratorio de Invertebrados, Facultad de Ciencias, Universidad Autónoma de Baja California, Ensenada (UABC). Other abbreviations used are: MXP3, third maxilliped; WL, walking legs.

Family Pinnotheridae de Haan, 1833
Calyptraeotheres Campos, 1990

Emended diagnosis (emendations underlined).—Female. Carapace arcuate anteriorly, sharp-edged; regions ill-defined, with 2 longitudinal cervical depressions from orbits to middle of carapace; front slightly projecting: MXP3 obliquely placed in buccal cavity; ischium and merus fused; palp 2- or 3-segmented, carpus larger than propodus, dactylus, when present, minute, inserted distoventrally on propodus; exopod with thin, unsegmented flagellum. WL1–3 similar in shape; WL4 more slender than others; propodus of WL1–2 with tuft of short stiff setae on distoventral margin; dactyli of WL1–3 similar in shape, acute and curved at tip, those of WL4 longest and sword-shaped. Abdomen covering sternum, with 6 abdominal somites and telson well separated.

Male: Carapace subpentagonal or suborbicular, regions ill-defined, dorsal region even, with short spaced setae; anterolateral margin with fringe of simple setae. MXP3 similar to that of female. Abdomen with 6 somites and telson well separated, widest at third somite, narrowing toward telson.

Distribution.—Northeast Pacific: Mexico, throughout Gulf of California, and west coast of Baja California Sur at Bahía Magdalena (*C. granti*). Southeast Pacific: Bahía Ancón, Perú to Castro, Isla Chilóe, Chile (*C. politus*). Southwest Atlantic: Brazil, Rio Grande do Sul; Argentina, Mar del Plata, Necochea, Golfo San Matías (*C. garthi*).

Type species.—By original designation, *Fabia granti* Glassell, 1933; host, *Crucibulum spinosum* (Sowerby).

Calyptraeotheres garthi (Fenucci, 1975), new combination

Figs. 1 E–F, 2B

Pinnotheres politus (not Smith, 1869).—Fenucci, 1971:355–367.

Pinnotheres garthi Fenucci, 1975:167, 169–171, 178, fig. 1A–B, 3D, I; Campos, 1990:365; Martins & D'Incao, 1996:11–13, fig. 7, 8 14F.

Material examined.—2 ovig. females (MACN 26315, 26316), S. SE Puerto Quequén, 8 Feb 1962, in *Crepidula* sp. on *Mytilus* sp., colls. M. Birabén & E. Martinez-Fontes; 3 females (MACN 29265, 26700), Necochea, Provincia de Buenos Aires, Apr 1978, coll. I. Pollites.

Distribution.—Southwest Atlantic: Brazil, Rio Grande do Sul; Argentina, Mar del Plata, Necochea, Golfo de San Matias.

Hosts.—Gastropoda: Calyptraeidae; in *Crepidula unguiformis* Lamark, *C. protea* Orbigny, and *Crepidula* sp.

Calyptraeotheres politus (Smith, 1869), new combination

Figs. 1C–D, 2C

Restricted synonymy:

Pinnotheres politus.—Schmitt et al., 1973: 81–82; Fenucci, 1975:166; Saelzer & Hapette, 1986:63–60; Campos, 1990: 365: Marquez & Pohle, 1995:349.

Material examined.—1 ovig. female, Bahía Ancón, Perú, coll. R. E. Coker (USNM 40448).

Distribution.—Southeast Pacific: Bahía Ancón, Perú to Castro, Isla Chilóe, Chile.

Hosts.—Gastropoda: Calyptraeidae: *Crepidula fecunda* Gallardo [= *C. dilatata* (not Lamark)] and *Calyptraea* sp (see Schmitt et al. 1973). Gallardo (1979) split *C. dilatata* Lamark in two species, *C. dilatata* from Africa and *C. fecunda* Gallardo from Chile (see Gallardo 1979, Hoagland 1983).

Taxonomic Remarks on the Genus *Calyptraeotheres*

Several characters support the inclusion of *Pinnotheres granti* and *P. politus* in the genus *Calyptraeotheres.* These include the presence of two longitudinal depressions on the carapace, front little projected, WL1–3 of similar shape, WL4 slender and its dactyl longer than the others, MXP3 with a carpus robust, larger than the propodus, and abdomen in both sexes of six somites and telson well separated. These features clearly distinguish this genus from others currently in the Pinnotheridae (Campos 1990). The species of *Calyptraeotheres* are obligatory symbionts of slipper shells (family Calyptraeidae). No other member of the Pinnotheridae is known to be symbiotic with slipper shells (Geiger & Martin 1999).

Marques & Pohle (1995) included of *C. politus* within the genus *Tumidotheres* Campos, 1989 based on presumably shared characters between *C. politus* and *Tumidotheres* spp; namely the narrowly spatulate dactylus of MXP3 that is inserted at an angular notch on the middle of the ventral margin of the propodus. As previously noted (Campos 1989), these characters are diagnostics for *Tumidotheres* (Fig. 2D); however, MXP3 of *C. politus* does not exhibit such characters. *Calyptraeotheres politus* and *C. garthi,* have the dactylus of the MXP3 rounded, minute and inserted subdistally on the ventral margin of the propodus (Fig. 2B–C). The genus *Tumidotheres* can be separated from *Calyptraeotheres* by the tumid and setose carapace, and by the above noted shape and insertion point of articles of the MXP3. In addition, species of *Tumidotheres* inhabit the mantle cavity

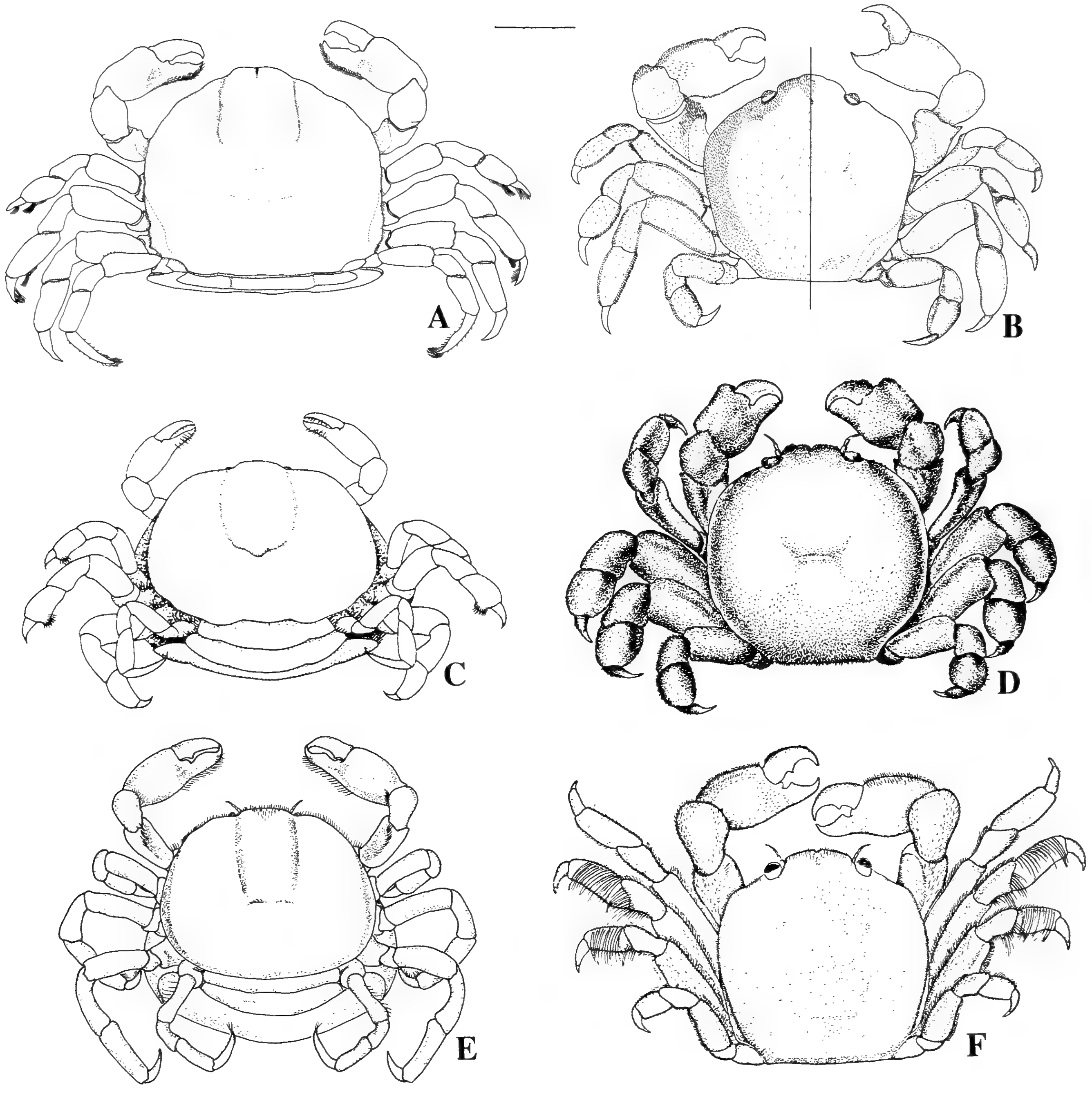

Fig. 1. Adult female and male respectively, A–B, *Calyptraeotheres granti* Glassell; C–D, *C. politus* (Smith); E–F, *C. garthi* (Fenucci). A–B from Campos, 1990; C modified from Retamal, 1981; D from Garth, 1957; E–F from Fenucci, 1975. Scale in mm, A = 2.5; B = 1.3; C = 2.6; D = 1.3; E = 3.1; F = 1.3.

of Bivalvia species, while species in *Calyptraeotheres* live between the shell and the head of slipper shells (family Calyptraeidae). Their different mode of life can be indicative of divergence and supports the separation of these genera.

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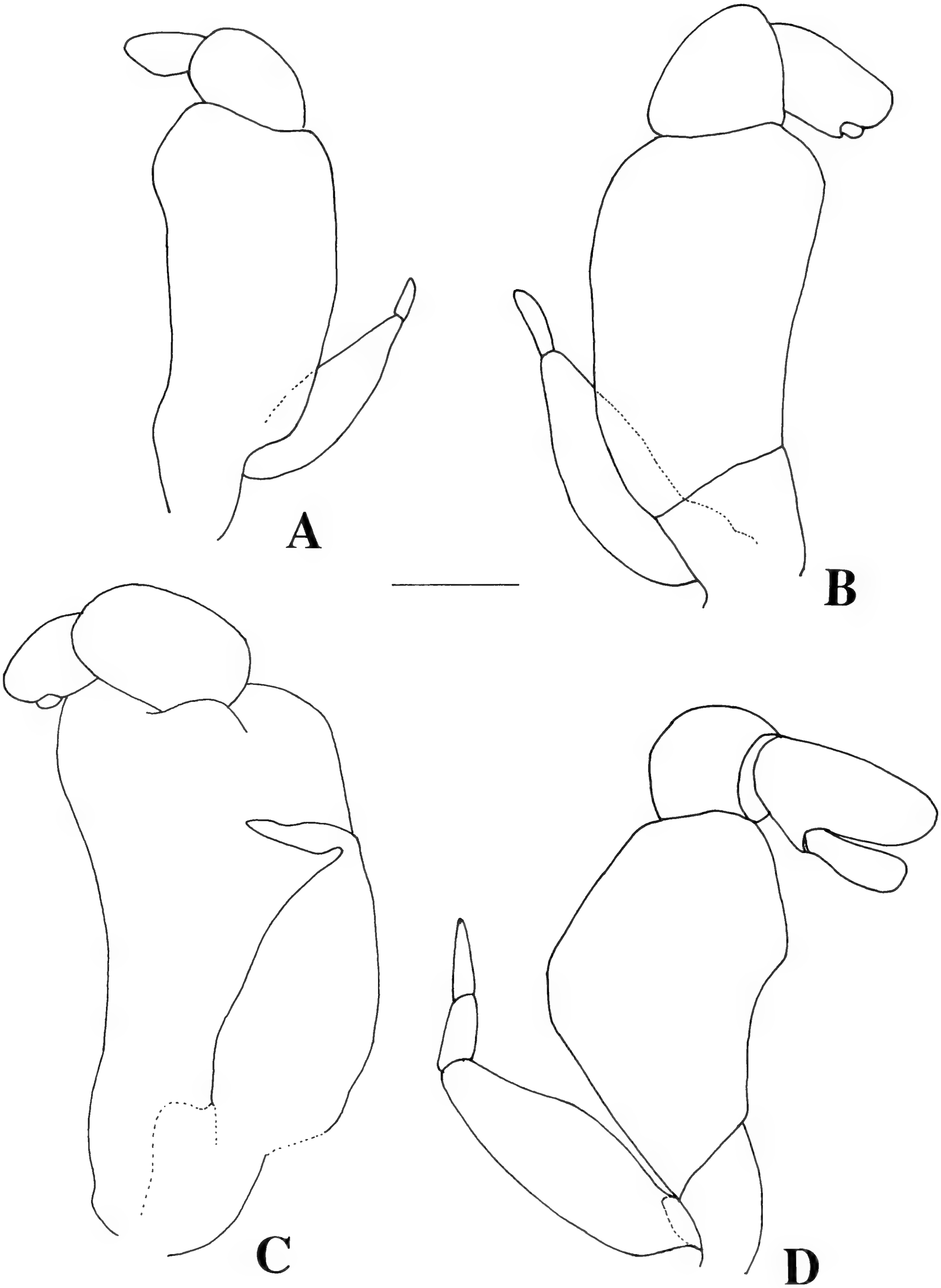

Fig. 2. Third maxilliped. A, *Calyptraeotheres granti* (Glassell); B, *C. garthi*; C, *C. politus* (Smith); D, *Tumidotheres margarita* (Smith). Scale in mm, A = 0.95; B = 0.43; C = 0.39; D = 0.70.

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Description of *Synalpheus williamsi,* a new species of sponge-dwelling shrimp (Crustacea: Decapoda: Alpheidae), with remarks on its first larval stage

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Abstract.—A new species of *Synalpheus* is described based on specimens collected from sponges in Belize and the Atlantic coast of Panamá. The new species, *S. williamsi,* is most similar morphologically to *S. goodei* Coutière, but the two species are consistently different in several morphological and larval features, and occupy distinct species of sponges. The shape of the major chela and of the uropodal exopods are the most reliable morphological characters that distinguish the two species. The first larval stage, a zoea I, was obtained from an ovigerous female of the new species. The zoea I is similar to that of *S. neomeris* (De Man), *S. triunguiculatus* (Paulson), *S. tumidomanus* (Paulson), and *S. scaphoceris* Coutière, in lacking pleopods and chelae, but can be distinguished by the presence of an acute projection on the pterygostomian corner.

Resumen.—Se describe una nueva especie de *Synalpheus* en base a especímenes recolectados dentro de esponjas en Belice y la costa Atlántica de Panamá. La nueva especie, *Synalpheus williamsi,* es muy parecida a *S. goodei* Coutière, pero posee distintas características ecológicas, morfológicas y larvarias. Estas dos especies de *Synalpheus* habitan distintas especies de esponjas. Los caracteres morfológicos más confiables para distinguirlas son la forma de la quela mayor y de los exópodos uropodales. De una hembra ovígera se obtuvo la primera fase larvaria, una zoea I desprovista de pleópodos y de quelas. La zoea I de la nueva especie es muy similar a la de *S. neomeris* (De Man), *S. triunguiculatus* (Paulson), *S. tumidomanus* (Paulson), y *S. scaphoceris* Coutière, pero se distingue de ellas por la presencia de una proyección pterigostomiana aguda en el caparazón.

During the course of collections made over several years in Belize and on the Atlantic coast of Panamá, we obtained a number of shrimps of a sponge-dwelling *Synalpheus* species morphologically similar to *S. goodei* Coutière, 1909. Specimens were collected from living sponges taken by SCUBA from various depths (1–15 m) on the outer reef ridge at the Smithsonian Institution's field station on Carrie Bow Cay, Belize (16°48′N, 88°05′W), and from Ulagsukun, Pico Feo, and Mamitupo reefs near the Smithsonian Tropical Research Institute's (STRI) field station in the San Blas Islands, on the Atlantic coast of Panamá (9°34′N, 78°58′W). Specimens from both areas were collected from the internal canals of the midnight-blue sponge *Hymeniacidon caerulea* Pulitzer-Finali, 1986, although one was associated with an unidentified orange encrusting sponge of tubular shape. Four specimens were collected free from any host, and had probably left their host sponges during sample handling. Usually, a heterosexual pair or a single adult was found in a same sponge. Here we describe these specimens. We also include a diagnosis of the first zoeal stage of this species hatched in the laboratory. Material is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Colección Nacional de Crustáceos from the Instituto de Biología UNAM, México (CNCR), the Muséum National d'Histoire Naturelle, Paris (MNHN), and in the Virginia Institute of Marine Science (VIMS). Measurements indicated are of carapace length including rostrum.

Synalpheus williamsi, new species
Figs. 1–6

Type specimens.—Holotype ♂, 3.6 mm (USNM 276158), allotype ovigerous ♀, 4.5 mm (USNM-276159), Carrie Bow Cay, Belize, 13 Jun 1996, from canals of same specimen of midnight-blue sponge *Hymeniacidon caerulea,* 18 m.—Paratypes: ♂, 4.4 mm, 2 ovigerous ♀♀, 4.3, 4.8 mm (USNM-276160), Carrie Bow Cay, Belize, 4 Apr 1993, from canals of same specimen of midnight-blue sponge *H. caerulea,* 13 m; Paratype ♂, 2.3 mm (CNCR 17987) Carrie Bow Cay, Belize, 12 Jun 1996, from canals of midnight-blue sponge *H. caerulea,* 18 m; Paratype ♂, 3.7 mm (MNHN-Na 13561) Ulagsukun Reef, Panamá, 17 Jan 1991, from canals of midnight-blue sponge *H. caerulea.*

Additional specimens examined (non paratypes).—Belize: Carrie Bow Cay, 5 Apr 1993, 2 ♂♂, 2.9, 3.8 mm (VIMS); 18 Aug 1994, ♂, 3.5 mm (VIMS); 26 Aug 1994, ♂, 4.7 mm (VIMS), zoea larvae (USNM-276161); in midnight-blue sponge *H. caerulea.* Panamá: Ulagsukun Reef, 18 Jan 1991 ovigerous ♀, 4.2 mm (VIMS); 10 Nov 1992, ♂, 3.7 mm (VIMS), in midnight-blue sponge *H. caerulea,* 1 m; Pico Feo Reef, 18 Jan 1991, ♂, 3.4 mm, ovigerous ♀, 4.2 mm (VIMS), in midnight-blue sponge *H. caerulea*; San Blas Islands: 1991, ♂, 4.3 mm (VIMS); Mamitupo Reef: 19 Jan 1991, ♂, 4.1 mm (VIMS), in orange tubular sponge.

Description of holotype.—Body form subcylindrical. Carapace smooth, with sparse short simple setae. Rostrum (Fig. 1a, d, e) slender, distally upturned, slightly overreaching orbital teeth, not reaching to distal margin of first segment of antennular peduncle; dorsally carinated; ventrally produced into small longitudinal keel, but without true orbitorostral process. Ocular hoods (Fig. 1a, d, e) dorsally convex, separated from rostral carina by broad depressions; triangular ocular teeth and rostrum with few apical setae; adrostral notches broadly rounded. Pterygostomian corner (Fig. 1b) produced into bluntly acute angle. Posterior margin (Fig. 2a, d) with distinct cardiac notch.

Abdomen with sparse simple setae; pleuron of first somite (Fig. 2d) with anterior corner almost in right angle, ventral margin sinuous and posteriorly bearing a blunt strongly hooked tooth directed anteriorly; second pleura broadly rounded anteriorly, with ventral margin slightly concave and posterior corner rounded, but with widely obtuse projection behind 3/4 of length; third to fifth pleura anteriorly and posteriorly obtuse, ventral margin triangular with apex progressively displaced posteriorly; sixth abdominal segment (Fig. 2a) with bluntly acute projection on posteroventral margin, shallow curved inferior concavity, triangular lateral lobe with convex sides, shallow obtuse upper emargination, and convex dorsal margin slightly overhanging telson. Telson (Fig. 1c) subtriangular, truncate, proximal margin slightly more than twice as wide as distal margin; lateral margins slightly convex just as far as distal pair of dorsal spines, then slightly concave; dorsal surface with mesial shallow depression and 2 pairs of dorsal spines, anterior pair situated slightly anterior to proximal third of length of telson, posterior pair of dorsal spines at second third of length of telson; distal margin arcuate, posterolateral corners not projected, 2 pairs of flanking distal

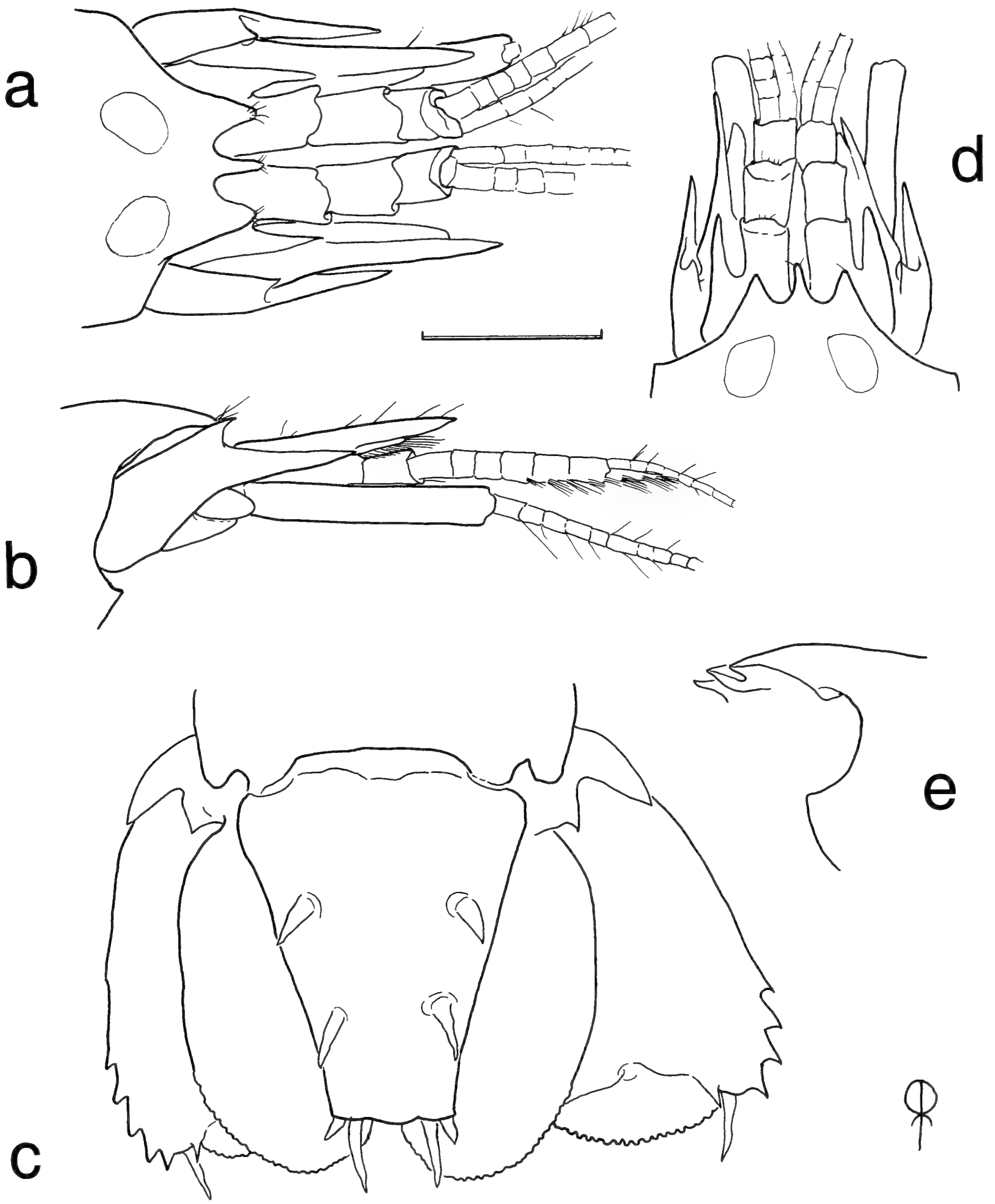
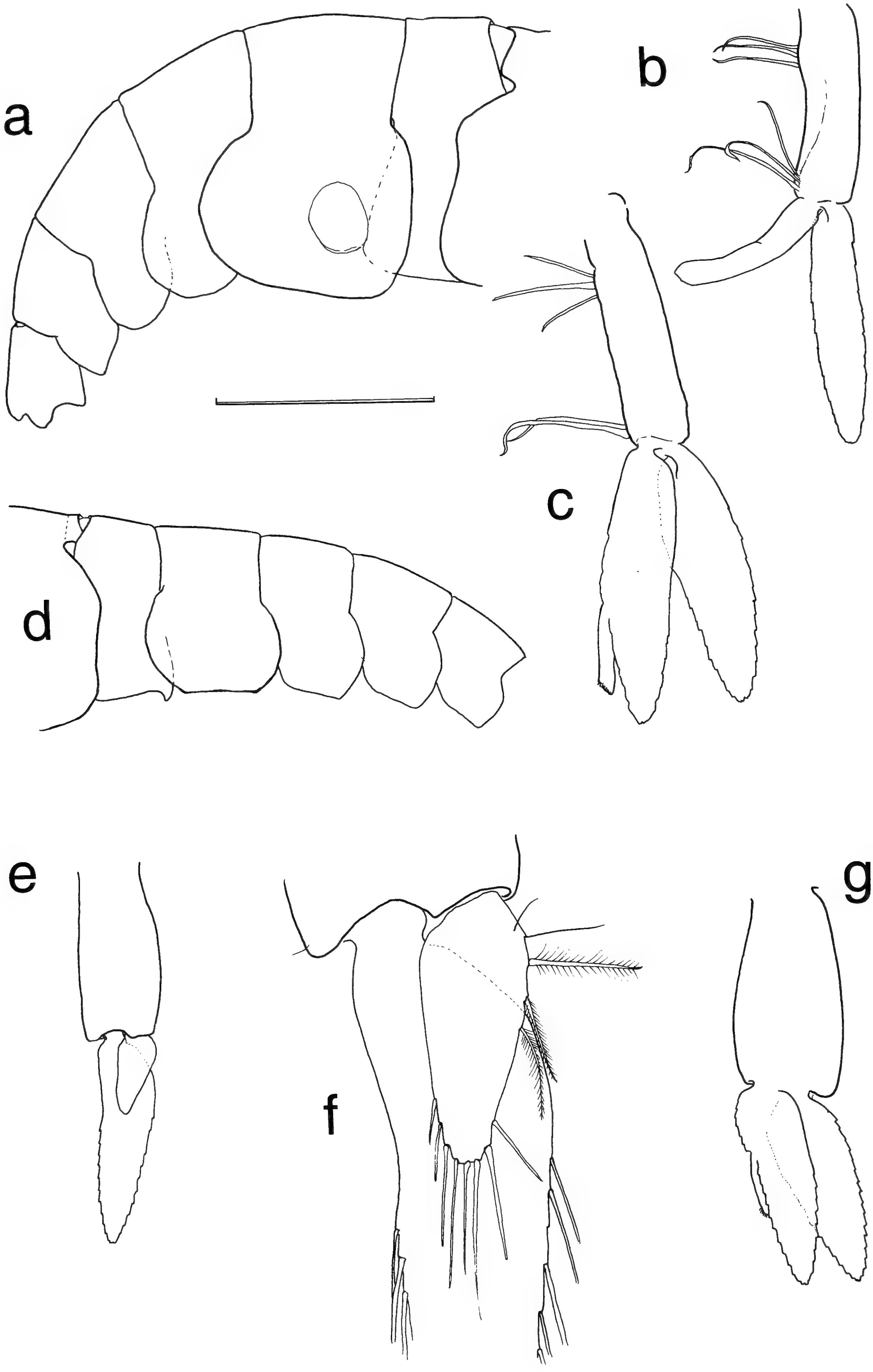


Fig. 1. *Synalpheus williamsi,* new species. Paratype male 4.4 mm (USNM 276160): a, anterior region of carapace and cephalic appendages, dorsal view; b, same, lateral view; c, telson and uropods, dorsal view. Paratype ovigerous female 4.3 mm (USNM 276160): d, anterior region of carapace and cephalic appendages, dorsal view; e, anterior region of carapace, lateroventral view. Scale bar = 1 mm for a, b, d, e and 0.72 mm for c.

movable spines, lateral pair shorter than innermost; mesial gap wider than combined bases of both pairs of spines, with 2 tufts of 3 erect setae on dorsal surface mesially adjacent to inner spines, and single row of 8 more conspicuous, posteriorly directed plumose setae of similar size, emerging from under mesial distal lobe.

Stylocerite (Fig. 1a, d) slender, with mesial side slightly concave, barely overreaching distal margin of basal article of antennular peduncle; this latter with lateral fan of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setae proximally on dorsal face; second and third segments of antennular peduncle decreasing in length. Upper flagellum (Fig. 1a, b) biramous, rami fused for 5 segments; lower ramus shorter, with 3 groups of aesthetascs on ventral face, and 4 and 5 additional groups posteriorly, upper ramus with 12 and 15 segments (left and right side, respectively). Lower flagellum normal, longer than upper.

Basicerite (Fig. 1a, b, d) with acute dorsolateral projection, and longer acute ventrolateral spine overreaching tip of stylocerite; scaphocerite with slightly reduced blade reaching to distal edge of antennular peduncle, narrower at base than lateral spine, which is robust, acute, with slightly concave lateral margin, and clearly overreaching antennular peduncle. Carpocerite (Fig. 1b, d) about 7 times as long as wide when viewed laterally, overreaching tip of lateral spine of scaphocerite.

Exopod of third maxilliped (Fig. 3f) not overreaching antepenultimate article, tip of ultimate segment (Fig. 3g) with circle of 7 strong blunt spines finely denticulate on proximal half of inner face. Remaining mouthparts as figured from paratypes (Fig. 3 a–e).

Major first pereiopod (Fig. 4a, b, c) massive, subcylindrical, with few sparse setae; palm about 1.75 times longer than wide, dorsodistal margin with blunt prominence overhanging insertion of dactyl, and bearing subterminal, ventrally directed, acute spine. Dactyl 0.3 times as long as palm, strongly compressed, dorsal margin broadly semicircular in lateral view (Fig. 4b), cutting edge almost flat with discrete blunt tip, internal face opposing outer face of pollex when closed. Pollex 0.7 times as long as dactyl, deeply excavated proximally to receive dactylar molar process, in ventral view (Fig. 4g), thick, triangular, with accessory subdistal obtuse projection on outer face, flanking outer face of dactyl when closed. Carpus cup-shaped, short and broad. Merus, about 0.8 times as long as height of palm, nearly triangular in cross section, inner edges slightly concave, outer convex, lower side flattened, with lamellar triangular projection on distal outer corner, upper side clearly convex.

Minor first pereiopod (Fig. 4d) slightly compressed. Palm about 1.7 times longer than high. Dactyl 0.7 times as long as palm, with several tufts of regular setae; extensor margin convex, with 2 longitudinal series of transverse parallel rows of setae distally curved towards tip of dactyl, inner series composed of about 12 rows, first row at start of second third of dactyl, last row at end of fourth fifth, shorter outer series, with first row opposing fifth row of inner series, setae similar in shape, length, and orientation, but slightly thinner; dactyl flexor margin excavated (Fig. 4e), tip with strong tooth flanked by two accessory blunt projections. Pollex with sinuous lower margin, sparse tufts of setae, strong apical tooth (Fig. 4f) continued backward into oblique widely convex blade. Carpus cup-shaped, about 0.5 times as long as palm; 1.2 times higher distally than mesial length in lateral view; upper and lower margins distally expanded over proximal portions of palm. Merus 1.5 times as long as palm, 2.5 times longer than maximum width; almost triangular in cross section; distal outer corner flared, without true spine.

Second pereiopod (Fig. 4h) more slender than all others. Fingers with strong tufts of setae, slightly more than 1.3 times as long as palm, latter 1.4 times longer than high.

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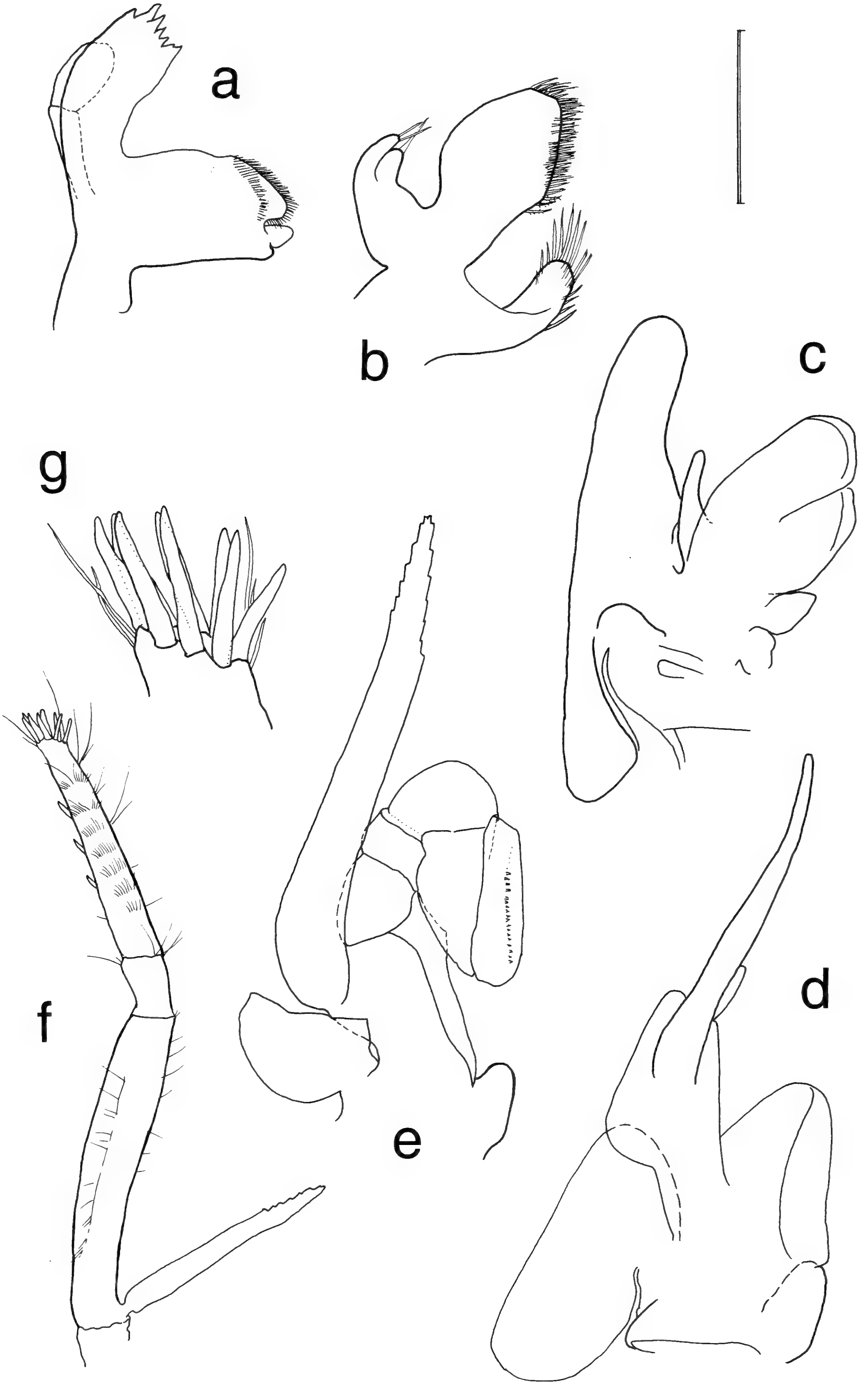
Fig. 2. *Synalpheus williamsi*, new species. Paratype ovigerous female 4.8 mm (USNM 276160): a, abdomen with one egg, lateral view; b, first pleopod; c, second pleopod. Paratype male 4.4 mm (USNM 276160): d, first 5 segments of abdomen, lateral view; e, first pleopod; f, same, detail of endopod; g, second pleopod. Scale bar = 2.2 mm for a, d, 1 mm for b, c, e, g, and 0.31 mm for f.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Carpus composed of 5 articles with ratio 4.5:1:1:1:2, second through fourth equally as long as high. Merus about 5.3 times longer than wide, and 0.9 times as long as carpus. Ischium four times longer than wide, and 0.7 times as long as merus.

Third pereiopod (Fig. 5a), strongest of posterior legs. Dactyl (Fig. 5d) biunguiculate, slightly longer than width of propodus, flexor margin concave. Propodus 6.3 times longer than wide, flexor margin with a longitudinal series of 7 strong movable spines and one terminal pair of movable spines flanking base of dactyl. Carpus 2.6 times longer than wide, extensor distal margin projected over propodus, strong movable spine on distal flexor margin. Merus 4.4 times longer than wide, unarmed. Ischium unarmed.

Fourth pereiopod (Fig. 5b, e) very similar to third, but slightly weaker.

Fifth pereiopod (Fig. 5c, f) weaker than fourth, with following slight differences, propodus with only two or three spines on flexor margin besides distal pair, and about five combs of stout setae transversely arranged on distal half of posterior face; carpus without spine.

Endopod of first pleopod (Fig. 2e) not as long as width of exopod, with few apical setae (Fig. 2f). Second pleopod (Fig. 2g) without appendix masculina. Pleopods 2–5 with appendix interna.

Uropodal exopod (Fig. 1c) with 5 strong distolateral teeth, longer movable spine and acute mesial tooth. Diaeresis present, distinct.

Color.—Live specimens were translucent faint gold to golden brown, with tip of chelae (fingers and distal part of palm included) of first pereiopods bright orange to red, second legs golden, third to fifth transparent, and traces of blue in the gut and in the branchiae. These traces were the same dark blue as the host sponge, and they still can be seen in some of the preserved specimens.

Variations.—The few discrepancies between the illustrations, from a male paratype, and the holotype are most probably due to the larger size of the figured paratype. The greater development of the endopod on the first pleopod (Fig. 2f) could be related to different stages of sexual maturity. Regarding sexual dimorphism, the most striking female characters are the broadly rounded shape of the first to fourth pleurae (Fig. 2a), the larger endopod of the first pleopod (Fig. 2b), and the insertion of

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Fig. 3. *Synalpheus williamsi,* new species. Mouthparts. Paratype male 4.4 mm (USNM 276160): a, mandible; b, first maxilla; c, second maxilla; d, first maxilliped; e, second maxilliped. Paratype ovigerous female 4.3 mm (USNM 276160): f, third maxilliped; g, same, detail of tip. Scale bar = 0.5 mm for a, b, c, d, e, 1 mm for f, and 0.25 mm for g.

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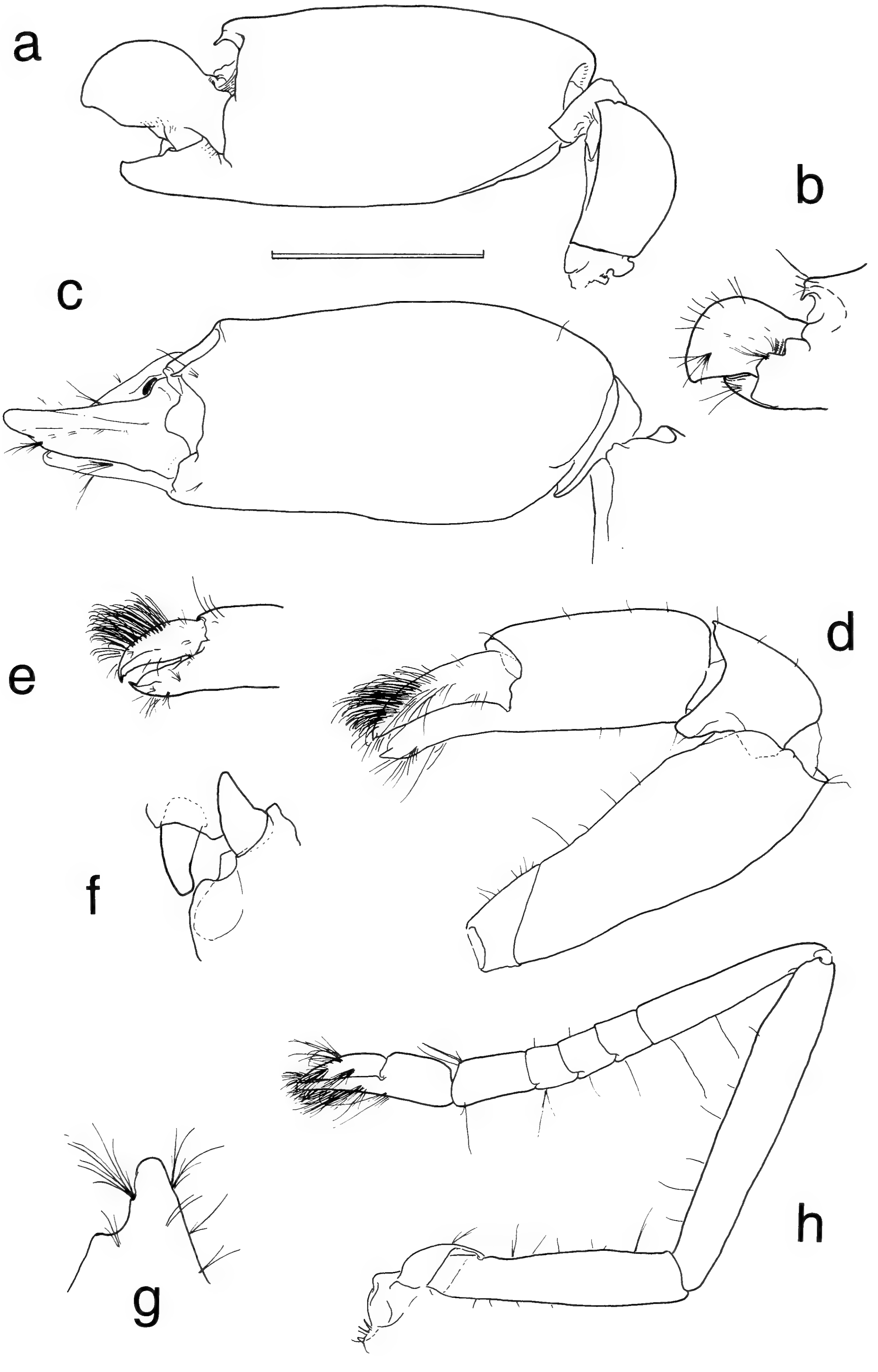
Fig. 4. *Synalpheus williamsi,* new species. Paratype male 4.4 mm (USNM 276160): a, major first pereiopod in lateral view; c, chela of same, dorsal view; g, same, tip of pollex, ventral view; h, second pereiopod. Paratype ovigerous female 4.3 mm (USNM 276160): b, anterior portion of major first pereiopod, external face, lateral view; d, minor first pereiopod, lateral view; e, distal portion of same, lateroventral view; f, same, detail of tip, frontolateral view. Scale bar = 2.5 mm for a, 2.2 mm for b, c, 1 mm for d, 1.4 mm for e, g, 0.2 mm for f, and 2 mm for h.

Fig. 5. *Synalpheus williamsi,* new species. Paratype male 4.4 mm (USNM 276160): a, third pereiopod; b, fourth pereiopod; c, fifth pereiopod; d, detail of distal portion of third pereiopod; e, detail of distal portion of fourth pereiopod; f, detail of distal portion of fifth pereiopod. Scale bar = 1 mm for a, b, c, and 0.31 mm for d, e, f.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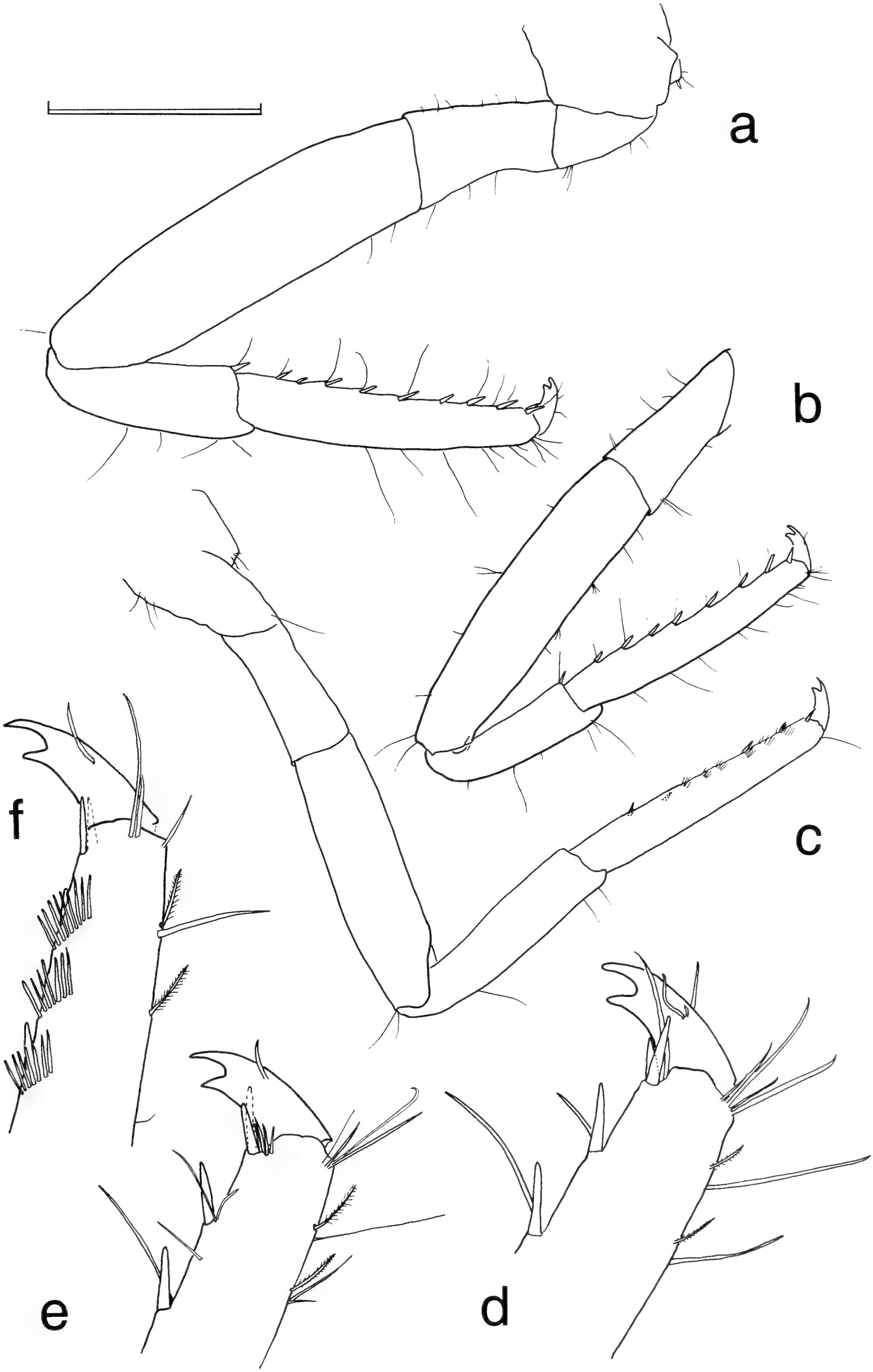
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the appendix interna beyond the midpoint in the remaining pleopods (Fig. 2c).

On the tip of third maxilliped, eight or seven spines is the most frequent formula (as in the holotype), but the allotype has nine spines on one side and ten on the other. The number of immovable teeth on the lateral margin of the uropodal exopod varies from three to six, with a mode of four; this variation apparently relates to size and perhaps sex, considering that the smaller specimens have fewer teeth, and that the only two specimens with six teeth were males.

Eggs and larva.—Eggs measure 0.9–1.0 mm long, and about 0.6 mm wide. One ovigerous female released larvae in the laboratory. Seven larvae were recovered swimming freely, but no attempts were made to raise them beyond the first stage. They were both preserved and stored in ethanol along with two eggs and another larva with half its body still in the egg case.

Description of zoea I.—Carapace subcylindrical (Fig. 6a), pterygostomian corner projected into acute spine, low bump on middorsal line, and angular projection proximal to depression at base of rostrum; latter, broadly triangular, pointed, directed downwards, shorter than, and somewhat hidden by ocular peduncles; eyes not covered by carapace.

Antennular peduncle with 3 segments. Antennal scale with 2 outer plumose setae, outer apical spine, and 9 plumose setae on inner and distal margins; endopod reaching to first inner seta on scale, entire, with one strong and one small apical seta. Maxillae and mandible buds present. All maxillipeds with well developed endopods and strong exopods, but setae present only on exopods.

First to fourth pairs of pereiopods biramous, without apparent segmentation, exopods without setae. Third and fourth pereiopods rudimentary, folded anteriorly against thorax. Fifth pair, long, turned forwards, uniramous, without setae.

Abdomen with sixth segment not clearly separated from telson. Pleopods absent. Uropods fused with telson. Telson (Fig. 6b), broad, bilobate, with 7 + 7 setae, outer 2 pairs feathered on inner side only, remaining 5 pairs plumose on both sides, innermost pair less than 0.25 as long as adjacent.

Ecology.—Most specimens of the new species, *S. williamsi,* came from internal canals of the midnight-blue sponge *Hymeniacidon caerulea.* In a few cases (<25%) we were not able to record the exact origin of our specimens, since they were found among debris in sampling containers. Only once did we collect a specimen (male) of *S. williamsi,* new species, from an unidentified orange encrusting sponge of tubular shape that was clearly different from *H. caerulea.*

Traces of blue in the gut of some specimens, and the anecdotal record in our field notes of a voided fecal pellet containing sponge spicules, are suggestive of a parasitic relation between the shrimp and the sponge.

Etymology.—It is an honor and pleasure to name this species after Dr. Austin B. Williams, National Oceanic and Atmospheric Administration, National Marine Fisheries Service Systematics Laboratory, National Museum of Natural History, Smithsonian Institution, Washington, D.C. This is in appreciation for his many important contributions to the knowledge of decapod crustaceans, and in recognition of his personal generosity and integrity.

Remarks.—Synalpheus williamsi, new species, is morphologically similar to *S. goodei* Coutière, but the following characteristics of the latter serve to distinguish the two species: the blade on the scaphocerite is more reduced, the pollex on the large chela is longer and without an accessory lateral emargination (best seen in ventral view), the small chela is more elongate, the distal margin of the telson is narrower, the lateral margin of the uropodal exopod has more fixed spines and has a noticeably stronger inner spine, adjacent to the movable one (see Coutière 1909, and Dardeau 1984). Also, unlike the new species, the first larva of *S. goodei* hatches at a more

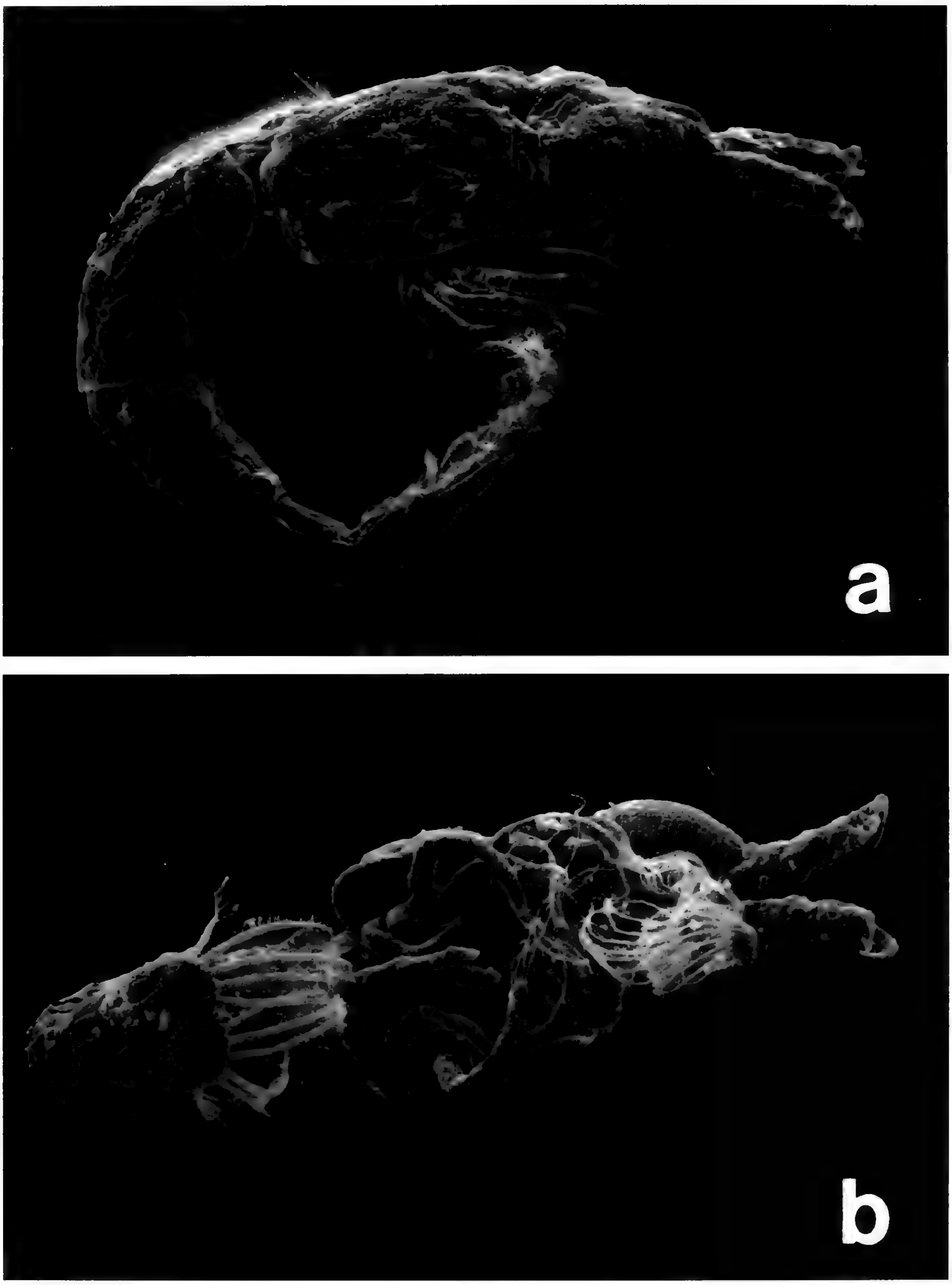

Fig. 6. *Synalpheus williamsi,* new species. Scanning electron micrographs of first zoea stage: a, lateral view; b, ventral view. Magnification = 71×.

advanced stage with both pairs of chelae and pleopods present (Gurney 1949).

Among the 12 species of *Synalpheus* whose first larva has been described or figured, the zoea I from the new species, *S. williamsi,* is most similar to that of *S. neomeris* (De Man, 1888), *S. triunguiculatus* (Paulson, 1875), *S. tumidomanus* (Paulson, 1875), and *S. scaphoceris* Coutière, 1910, but it can be readily distinguished by the acute projection of the pterygostomian corner; additionally, the first zoea of *S. scaphoceris* has the sixth abdominal somite clearly distinct (Dardeau 1986: fig. 3b). Lack of pleopods and chelae on the first pair of pereiopods is suggestive of a normal development pattern, i.e., not abbreviated nor direct as has been documented for other species of *Synalpheus* (see Knowlton 1973, and Bhuti et al. 1977).

As in the case of *S. gambarelloides* (Nardo, 1847), and probably *S. longicarpus* (Herrick, 1891), recorded by Rüetzler (1976) and Erdman & Blake (1987) respectively, the new species, *S. williamsi,* appears to be a parasitic endobiont of sponges; more careful observations on live specimens might provide conclusive evidence on its diet.

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Two new freshwater crabs of the genus *Ptychophallus* Smalley, 1964 (Crustacea: Decapoda: Brachyura: Pseudothelphusidae) from Panamá, with notes on the distribution of the genus

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Abstract.—Two new species of freshwater crabs of the genus *Ptychophallus* Smalley, from Panamá, *P. uncinatus* and *P. kuna,* are described and illustrated. The addition of these two species means the genus now includes 13 species, all of which are distributed in Panamá and Costa Rica. The species are distinguished primarily by differences in characters of the male first gonopod. A summary of the geographic distribution of the species in the genus is presented.

The systematics of the genus *Ptychophallus* Smalley, 1964a, were reviewed by Rodríguez (1982, 1994) who found that a number of characters of the male first gonopod in species of this genus were homologous with those of *Hypolobocera* Ortmann, 1897 and *Neostrengeria* Pretzmann, 1965. These characters are the presence of a caudal crest, a lateral lobe, and a central papilla on the spermatic channel. Rodríguez (1982) considered *Ptychophallus* to be transitional between Andean and Central American Pseudothelphusidae because species of this genus present a fusion of the cephalic and caudal borders forming a mesial process, a morphological characteristic present in all pseudothelphusids species from Central America (including Mexico), but absent in species of *Hypolobocera* and *Neostrengeria* from South America.

Species of *Ptychophallus* are distinguished primarily by characteristics of the third maxilliped and male first gonopod. The exognath of the third maxilliped is 0.6 to 0.7 as long as the ischium. The male first gonopod has a prominent apex that is bent cephalically and is joined to the gonopod by a narrow peduncle; the lateral projection is large, and usually divided into two lobes; and the caudal ridge extends longitudinally on the distal half of the caudal surface.

A study of freshwater crabs in the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM), revealed two new species of *Ptychophallus* from Panamá, bringing to 13 the total number of species currently recognized in this genus. This number excludes *P. campylos* Pretzmann, 1965, a species that was originally briefly described, without illustrations (Pretzmann 1965). This species was listed by Pretzmann (1971), and he (Pretzmann 1972) subsequently added details with illustrations and photographs. Rodríguez (1982:80) indicated in a footnote that based on the information provided by Pretzmann (1965, 1971, 1972), *P. campylos* could not be separated from *P. tristani* (Rathbun, 1896); however, Rodríguez did not formally synonymize Pretzmann's taxon with Rathbun's and excluded *P. campylos* from his treatment of *Ptychophallus* species. The type of *P. campylos,* deposited in the Naturhistorisches Museum, Vienna, needs to be examined in order to properly evaluate the validity of Pretzmann's taxon.

The terminology used for the morphology of the male first gonopod follows that of Smalley (1964b) and Rodríguez (1982). The abbreviations cb and cl stand for carapace breadth (measured at the widest point) and carapace length (measured along the midline), respectively. Color nomenclature used follows Smithe (1975).

Family Pseudothelphusidae Rathbun, 1893
Tribe Hypolobocerini Pretzmann, 1971
Genus *Ptychophallus* Smalley, 1964a
Ptychophallus uncinatus, new species
Figs. 1, 2, 5

Material.—Holotype: ♂, cl 16.4 mm, cb 26.5 mm, Rio San Pedro, Bocas del Toro, Panamá, Jan 1978, leg. B. L. Gordon (USNM 276164). Paratype: ♂ (juvenile) cl 9.5 mm, cb 15.2 mm, same locality as holotype (USNM 276165).

Type locality.—Rio San Pedro, Bocas del Toro, Panamá.

Diagnosis.—First male gonopod with very broad lateral projection divided into 2 subequal lobes by deep depression on caudal surface and lateral notch; distal lobe with crest-like flange; distocaudal ridge short and narrow, with lateral crest; subapical mesial process with triangular base and hook-like projection; central papilla of spermatic channel robust, swollen.

Description of holotype.—Carapace (Fig. 1) with narrow, deep cervical groove curving posteriorly and not reaching lateral margin. Anterolateral margin with shallow sinus just posterior to anteroexternal orbital angle; rest of margin with papillae. Postfrontal lobes wide, delimited anteriorly by transverse depression; median groove narrow, deep, with incision on upper margin of front. Surface of carapace in front of postfrontal lobes flat and inclined anteriorly. Upper border of front thin, marked with row of tubercles; lower margin sinuous in frontal view. Surface of front between upper and lower borders high and slightly excavated. Upper and lower orbital margins each with row of tubercles. Surface of carapace covered with small papillae; limits between regions demarcated. Third maxilliped (Fig. 2E) with merus of endognath regularly curved, with shallow depression on distal part of external margin; exognath approximately 0.6 times length of ischium of third maxilliped.

First pereiopods absent in holotype. In paratype, right cheliped slightly larger than left. Merus with 3 crests as follows: upper crest with rows of tubercles, internal lower crest with rows of teeth, and external lower crest with few tubercles. Carpus with 4 tubercles on internal crest and prominent blunt spine distally. Palm of both chelipeds smooth, moderately swollen. Fingers of chelae not gaping when closed, tips crossing, with rows of tubercles on dorsal side.

Surface of walking legs (pereiopods 2–5; Fig. 1) with rows of minute setae. Dactyls each with 5 rows of large spines slightly diminishing in size proximally, rows arranged as follows: anterolateral and anteroventral rows each with 5 spines, external row with 5 spines plus 2 proximal papillae, posteroventral row with 4 spines, and posterolateral row with 5 spines.

First male gonopod (Fig. 2A–C) wide in caudal view. Lateral projection very wide, divided in 2 subequal lobes by deep depression on caudal surface and lateral notch; distal lobe with crest-like flange directed distally; proximal lobe almost rounded; margins with minute setae; distocaudal ridge short and narrow, with lateral crest, reaching only to middle of deep depression dividing lateral projection. Subapical mesial process with triangular base and hook-like projection; apical mesial process triangular (Fig. 2C, D). Apex bent cephalolaterally, with field of spines directed cephalolaterally; caudal border of apex with shallow notch near middle, and deep notch near lateral side; central papillae of spermatic channel robust, swollen (Fig. 2B, C, D).

Color.—In alcohol, the dorsal side of the carapace is light brown (near 239, Ground Cinnamon). The walking legs are Buff (124). The chelae are True Cinnamon (139)

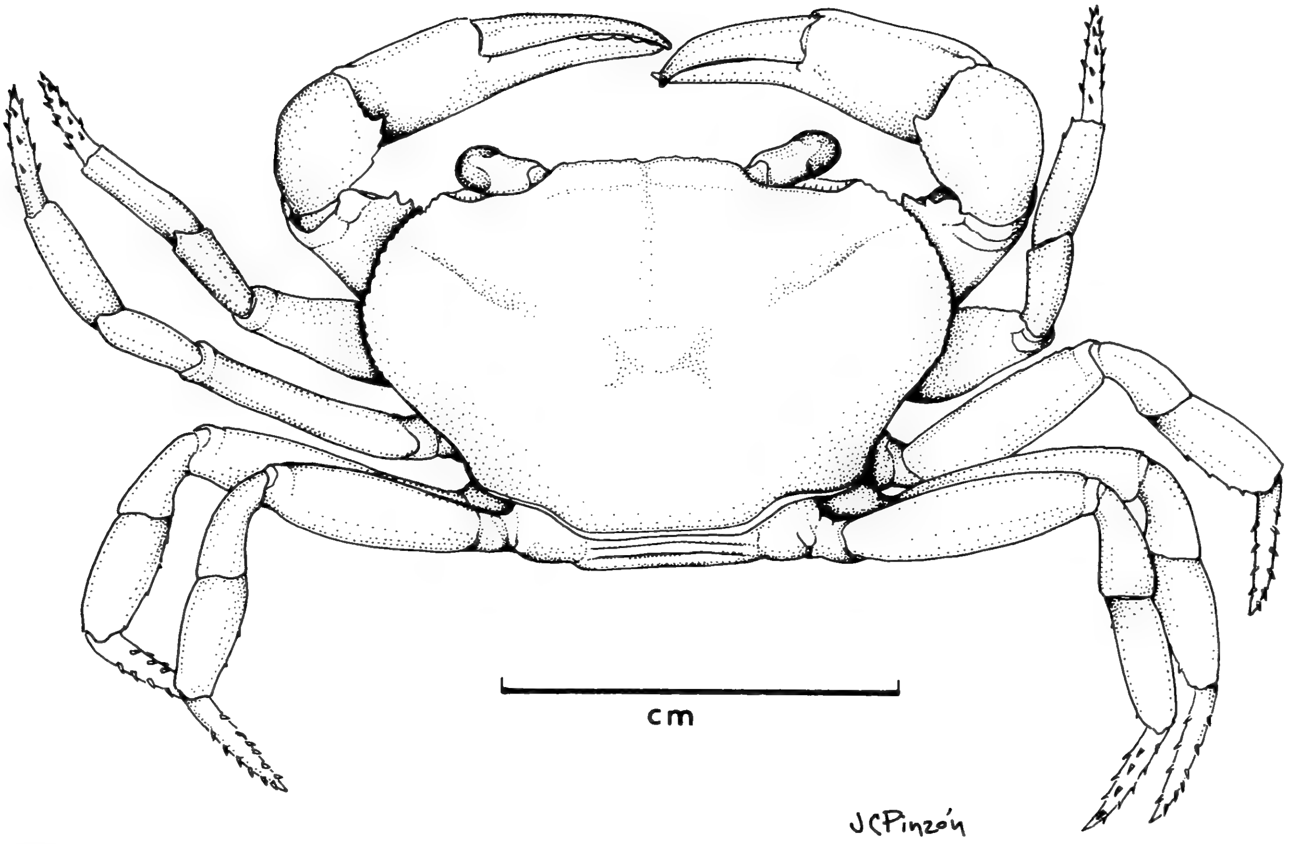

Fig. 1. *Ptychophallus uncinatus,* new species, male paratype, cl 9.5 mm, cb 15.2 mm, dorsal view (USNM 276165).

dorsally, and Buff (124) ventrally. The ventral surface of the carapace is Buff (124).

Etymology.—The specific name is from the Latin *uncinatus,* meaning hooked, and is given in reference to the form of the subapical mesial process of the first gonopod.

Remarks.—This new species is most similar to *Ptychophallus tumimanus* (Rathbun, 1898). The two can be distinguished by differences in the male first gonopod. In the new species the distal lobe of the lateral projection is a crest-like flange directed distally, and the lateral border of the proximal lobe has minute setae (not shown in Fig. 2A–C); in *P. tumimanus* the distal lobe is rounded, and the lateral border of the proximal lobe has rows of long setae. In the new species the distocaudal ridge has a lateral crest, and the subapical mesial process has a triangular base and hook-like projection; in *P. tumimanus* the distocaudal ridge has a rounded surface, the subapical mesial process is subtriangular, almost rounded.

Ptychophallus uncinatus, new species, is also similar to *P. montanus* (Rathbun, 1898). The male first gonopod of the new species differs markedly from that of *P. montanus* in the shape of the apex. In the new species the apex is wide, the caudal border has a notch near the middle, and the central papilla of the spermatic channel is robust and swollen (Fig. 2D); in *P. montanus* the apex is narrow, the caudal border is entire and lacks a median notch, and the central papilla of the spermatic channel is thin and curved. In addition, the male first gonopod of the new species has lateral projections that extend laterally beyond the distal end of the laterocaudal expansion. (Fig. 2A), whereas the lateral projections do not exceed the laterocaudal expansion in *P. montanus.*

Ptychophallus kuna, new species
Figs. 3–5

Material.—Holotype: ♂, cl 15.6 mm, cb 24.9 mm, Portobelo, Panamá, 25 Feb 1973: (USNM 184340).

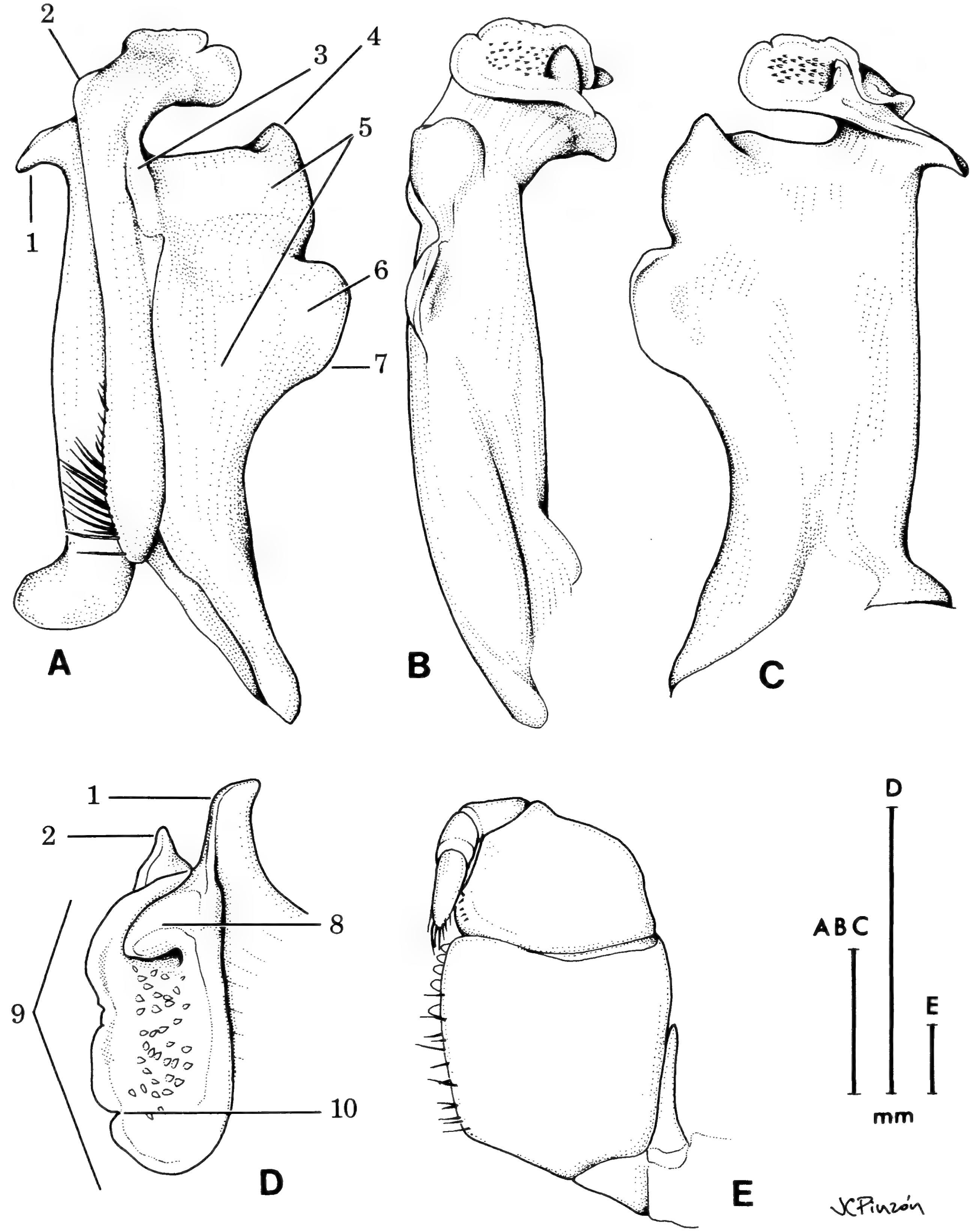

Fig. 2. *Ptychophallus uncinatus,* new species, male holotype, cl 16.4 mm, cb 26.5 mm (USNM 276164). A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, apex of same, distal view; E, left third maxilliped, external view. 1, subapical mesial process; 2, apical mesial process; 3, distocaudal ridge; 4, distal lobe of lateral projection; 5, lateral projection; 6, proximal lobe of lateral projection; 7, lateral border of proximal lobe; 8, central papilla of spermatic channel; 9, caudal border of apex; 10, notch of caudal border.

Diagnosis.—First male gonopod with lateral projection narrow, divided into 2 subequal lobes by shallow notch; distal lobe small, subtriangular and with distal surface close to gonopod axis; proximal lobe subtriangular; distocaudal ridge short, weakly defined, almost continuous with distal lobe of lateral projection; subapical mesial process robust, flange-like; central papilla of spermatic channel thin, delicate.

Description of holotype.—Carapace (Fig. 3A) with narrow, shallow cervical groove curved posteriorly and not reaching lateral margin. Anterolateral margin with shallow sinus just posterior to anteroexternal orbital angle; remaining margin with papillae. Postfrontal lobes wide, delimited anteriorly by transverse depression; median groove narrow. Surface of carapace in front of postfrontal lobes flat, inclined anteriorly. Upper border of front thin, marked with row of tubercles; lower margin visible in dorsal view, sinuous in frontal view. Surface of front between upper and lower borders high, slightly excavated. Upper and lower orbital margins each with row of conspicuous tubercles. Surface of carapace covered with small papillae; limits between regions well demarcated. Third maxilliped (Fig. 3D) with merus of endognath strongly curved and with deep depression on distal part of external margin; exognath approximately 0.6 times length of ischium of third maxilliped.

First pereiopods heterochelous; right cheliped larger than left. Merus with 3 crests as follows: upper crest with rows of tubercles, internal lower crest with rows of teeth, and external lower crest with rows of tubercles. Carpus with 4 tubercles on internal crest, and prominent blunt spine distally. Palm smooth, swollen. Fingers of chelae (Fig. 3B) not gaping when closed, tips crossing and with rows of tubercles on dorsal surface.

Walking legs (pereiopods 2–5; Fig. 3C) strong. Dactyls each with 5 rows of large spines diminishing in size proximally, rows arranged as follows: anterolateral and anteroventral rows each with 5 spines, external row with 5 spines and 2 proximal papillae, and posteroventral and posterolateral rows each with 3 spines.

First male gonopod (Fig. 4) narrow in caudal and cephalic views. Lateral projection narrow, divided in 2 subequal lobes by shallow notch; distal lobe small, subtriangular, distal surface close to gonopod axis; proximal lobe subtriangular, lateral border sinuous and with proximal papilla; distocaudal ridge very short, weakly defined and almost continuous with distal lobe of lateral projection. Subapical mesial process robust, flange-like (Fig. 4C, D); apical mesial process subtriangular, almost rounded. Apex bent cephalolaterally, with field of spines directed cephalolaterally; caudal border of apex with deep incision near lateral side; central papilla of spermatic channel thin, delicate (Fig. 4B, C, D).

Color.—In alcohol, dorsal surface of the carapace brown (near Kingfisher Rufous, 240). Walking legs Raw Sienna (136) dorsally, and True Cinnamon (139) ventrally. Chelae Kingfisher Rufous (240) dorsally, and True Cinnamon (139) with Olive-Brown specks (28) ventrally. Ventral surface of carapace Robin Rufous (340).

Etymology.—The species is named in honor of the Kuna Indians, in whose territory this new species was found.

Remarks.—This new species can be differentiated from other congenerics by the first male gonopod. The gonopod is distinct in that it has a short, weakly defined caudal ridge which is almost continuous with the distal lobe of the lateral projection.

Distribution of *Ptychophallus* Species

Distribution records of species of *Ptychophallus* can be found in the original descriptions as well as in various freshwater crab reports from central America (Pretzmann 1965, 1968, 1971, 1972, 1980; Rodríguez 1982, 1994; Smalley 1964a; Villalobos 1974). The species of this genus are known exclusively from Central America between

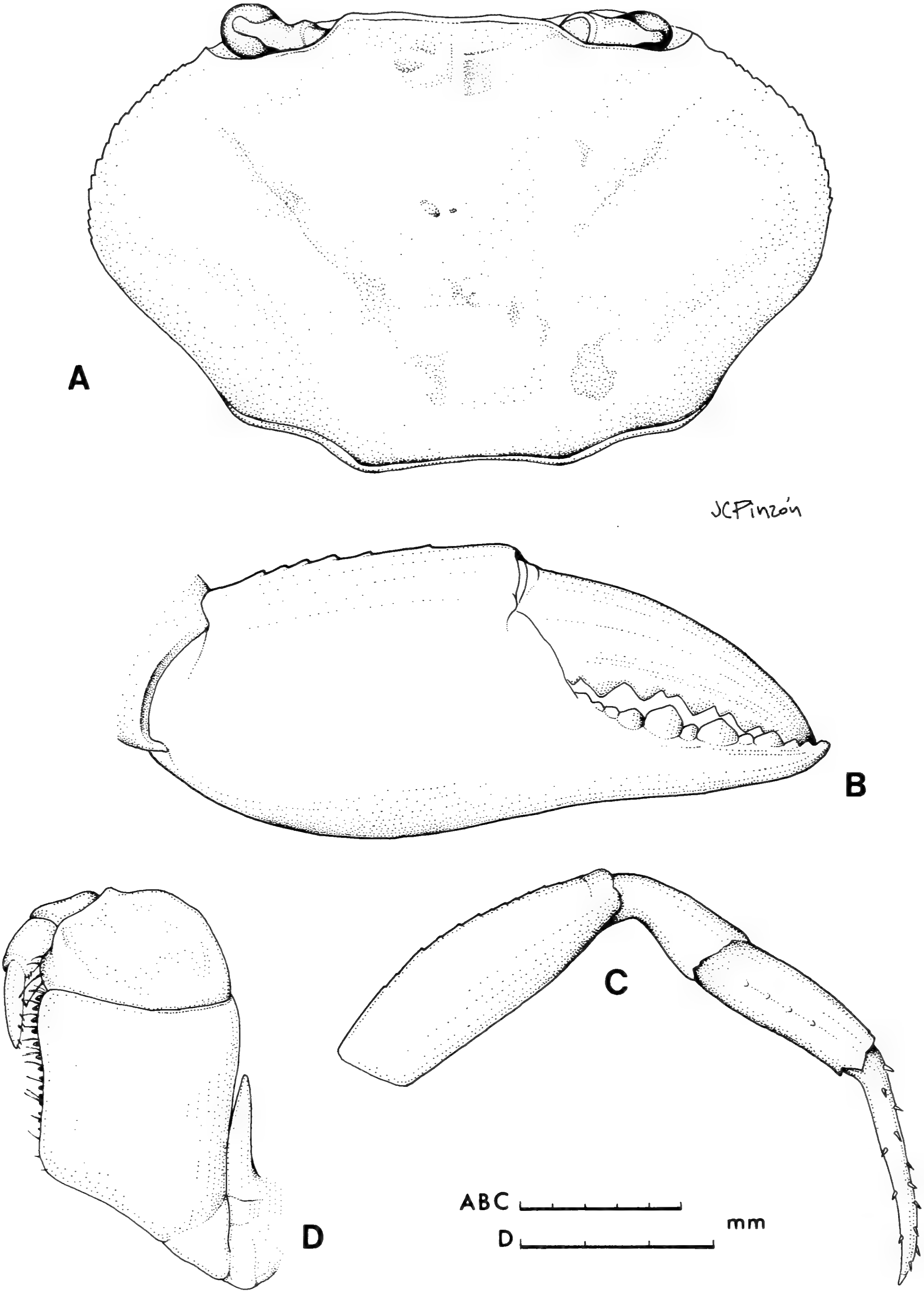

Fig. 3. *Ptychophallus kuna,* new species, male holotype, cl 15.6 mm, cb 24.9 mm (USNM 184340). A, carapace, dorsal view; B, chela of large cheliped, external view; C, left third pereiopod, lateral view; D, third maxilliped, external view.

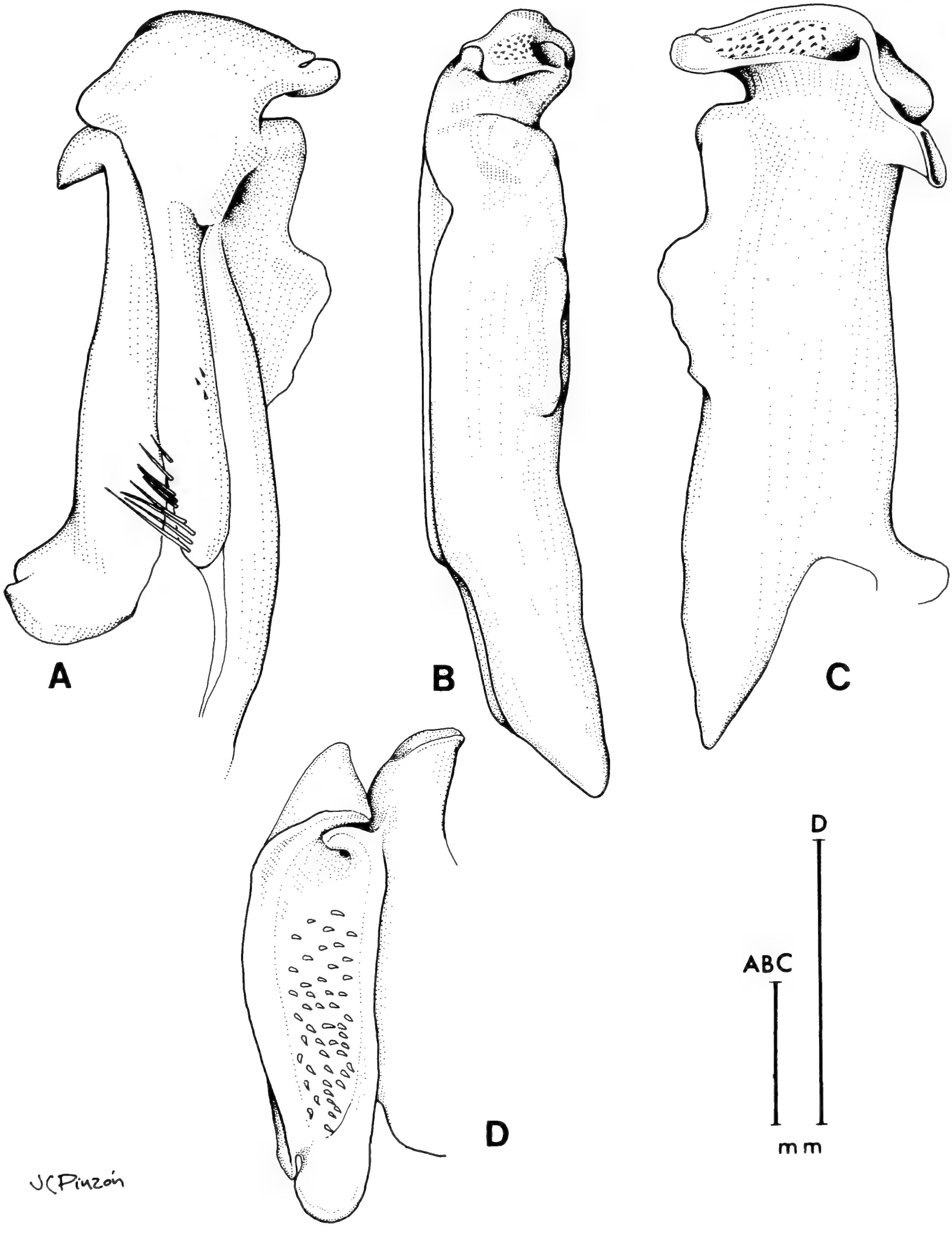

Fig. 4. *Ptychophallus kuna,* new species, male holotype, cl 15.6 mm, cb 24.9 mm (USNM 184340), left first gonopod: A, caudal view; B, lateral view; C, cephalic view; D, apex, distal view.

Cana Mount, Darién Province, Panamá, and Monteverde, Puntarenas Province, Costa Rica (Fig. 5). Six species occur in localities of the Atlantic drainage: *P. cocleensis* Pretzmann, 1965, *P. exilipes* (Rathbun, 1898), *P. lavallensis* Pretzmann, 1978, *P. tumimanus, P. kuna,* new species, and *P. uncinatus,* new species. Six species occur

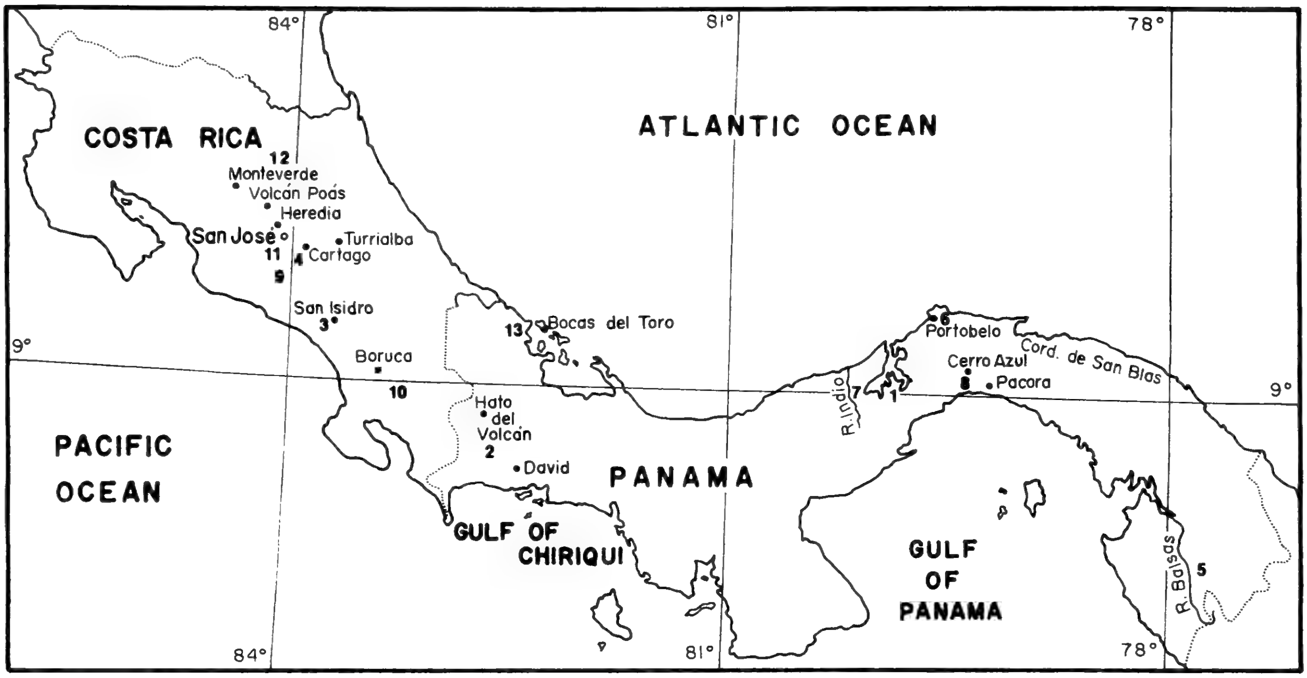

Fig. 5. Distribution of species of *Ptychophallus* Smalley, 1964: 1, *P. cocleensis* Pretzmann, 1965; 2, *P. colombianus* (Rathbun, 1893); 3, *P. costaricensis* Villalobos, 1974; 4, *P. exilipes* (Rathbun, 1898); 5, *P. goldmanni* Pretzmann, 1965; 6, *P. kuna*, new species; 7, *P. lavallensis* Pretzmann, 1978; 8, *P. micracanthus* Rodríguez, 1994; 9, *P. montanus* (Rathbun, 1898); 10, *P. paraxanthusi* Bott, 1968; 11, *P. tristani* (Rathbun, 1896); 12, *P. tumimanus* (Rathbun, 1898); 13, *P. uncinatus*, new species.

in localities of the Pacific drainage: *P. colombianus* (Rathbun, 1893); *P. costaricensis* Villalobos, 1974, *P. goldmanni* Pretzmann, 1965, *P. micracanthus* Rodríguez, 1994, *P. paraxanthusi* Bott, 1968, and *P. tristani.* One species, *P. montanus,* has been found in both Atlantic and Pacific drainages.

Species of Pseudothelphusidae are usually found at altitudes ranging from 100 to 3000 m. However, when they occur in coastal mountain ranges such as those found along the Pacific or Atlantic coasts of Panamá and Colombia, some species can reach sea level. Species of *Ptychophallus,* for example, range from 0 to 2000 m above sea level.

Acknowledgments

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A new species of *Chevalia* (Crustacea: Amphipoda: Corophiidae) from the Indian Ocean with remarks on *Chevalia carpenteri* and the *C. aviculae* superspecies complex

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Abstract.—A new amphipod, *Chevalia hirsuta,* is described and figured from material collected in the Indian Ocean by the Yale Seychelles Expedition. The relationship of this species to all known *Chevalia* is discussed, along with a review of several morphological characters of potential diagnostic value.

The genus *Chevalia* was reviewed by Barnard & Thomas (1987), who described a new species, *Chevalia carpenteri* from Belize, adding to a genus previously regarded as monotypic. Their review also re-established the validity of *C. mexicana* Pearse, 1913, and *C. inequalis* (Stout, 1913), which were previously synonymized with *Chevalia aviculae* Walker, 1904 (Shoemaker 1942; Barnard 1962, 1970). Furthermore, Barnard & Thomas (1987) showed that a *Chevalia* superspecies complex exists, with variants known from the Galapagos (Barnard 1979), Fiji (Myers 1985) and Hawaii (Barnard 1970), in addition to *C. inaequalis* and *C. mexicana.* Clearly, *Chevalia aviculae* has been a convenient taxonomic assignment for what is actually a complex of sibling species.

Another new species is herein described from the Seychelles Archipelago in the Indian Ocean, collected during the Yale Seychelles Expedition (YSE), 1957–1958. The relationship of this new species to other *Chevalia* (in particular to *C. aviculae* and *C. carpenteri*), a discussion of diagnostic characters and an emendment of the key provided by Barnard & Thomas (1987) are presented.

Chevalia hirsuta new species
Figs. 1–6

Diagnosis.—Article 2 of pereopods 5–7 ovate, broadly expanded, posterodistal corner not produced. Pereopods densely setose; dense bundles of long setae on posterior margin of article 2 pereopods 5–7, anterodistal and posterodistal margin of article 4, pereopods 3–7, uropod 1 peduncle and uropod 3 rami. Pleonal epimera rounded.

Description of holotype female.—Head nearly twice as long as first pereon segment; coxae small, separated from each other. Mandible, palp article 1 short, article 2 slightly longer than article 3, articles 2 and 3 setose. Lower lip, inner lobes and outer lobes separated, distal margins broadly convex, setose. Maxilla 1, inner plate small, lightly setose, outer plate with 11 distal spines, palp 2-articulate, first article short. Maxilla 2, inner plate with oblique row of facial setae and setose inner margin, outer plate distally setose. Maxilliped, inner plate setose along inner margin, outer plate with 7 spines along inner margin, palp 4-articulate, second article long, article 3 with oblique row of long facial setae, article 4 tapered, distally setose. Antenna 1 longer than antenna 2, densely setose, accessory flagellum 3-articulate, third article minute, length of article 1 of flagellum nearly 300% that of article 2, and 2 densely setose. Antenna 2, length of article 1 of flagellum nearly 300% that of article 2. Gnathopod 1 much smaller than gnathopod 2, coxa produced, anterior margin weakly concave, posterior margin broadly rounded, article 2 with dense posterodistal bundle of very long setae, article 5 linear, longer than article 6, densely setose, article 6 subchelate, ovate, palm oblique, convex. Gnathopod 2, ventral margin of coxa excavate, anterodistal corner rounded, article 2 shorter than article 6, article 5 short with small posterior lobe, article 6 broad, palm oblique, sinusoidal, proximoposterior tooth strong, pointed, posterior margin lined with fascicles of setae and smaller curly facial setae. Pereopod 3, length of gill and oostegite subequal to that of article 2, article 2, anterior margin setose, article 4 expanded, distal margin armed with many long setae, article 5 short, dactyl simple. Pereopod 4, gill 80% length of article 2, oostegite 125% length of article 2, article 2, anterior margin setose, article 4 expanded, article 5 short, dactyl simple. Pereopod 5, gill 30% longer than article 2, oostegite longer than entire appendage, article 2 posterior margin expanded, with dense medial bundle of long setae, article 5, posterodistal corner with 4 stout submarginal spines. Pereopods 6 and 7 similar, basis expanded, posterior margin setose, article 4, anterodistal and posterodistal corners each with bundles of very long setae, article 5, posterodistal corner with 4 stout submarginal spines; pereopod 6, gill nearly as long as basis. Uropod 1, peduncle with dense distal bundle of long setae, outer ramus shorter than inner, opposing inner margins (viewed dorsally) with complexly serrate teeth. Uropod 2, outer ramus shorter than inner ramus, posterior margin setose, apically spinose, inner ramus lanceolate, margins naked. Uropod 3, distal margin of inner and outer ramus with dense bundles of extremely long setae. Telson subquadrate, distal corners weakly produced, with scale-like plates, posterior margin with two sparse bundles of long and short setae, lateral margins lightly setose.

Male.—The males are smaller, but very similar to the females in the major diagnostic features. However, in the largest male (YPM 9741) the setal bundles are generally denser and the setae slightly longer than in the largest females.

Variation.—In the smallest individuals of both sexes, article 2 of pereopods 5–7 is only slightly expanded, and the posterior margin is nearly straight and parallel to the anterior margin. In these smaller individuals the diagnostic long setae are present but relatively shorter and fewer in number than in larger specimens; smaller specimens, however, typically bear longer setae on the posterior margin of the antennae than those exhibited by the holotype female.

Etymology.—The specific epithet is derived from the Latin *hirsutus,* meaning hairy, and alludes to the extremely long and dense setae of the pereopods, urosome, and telson.

Material examined.—Female holotype, YPM 9206, 10.1 mm. Seychelles: Maliki Pate, off Cerf Island, 4°33′N, 55°30′E, under algae on dead coral. Yale Seychelles Expedition Station 29. Collector, A. J. Kohn, 2 November 1957. Male allotype, YPM 9741, 9.1 mm. 7 female paratypes, YPM 9742. 6 male paratypes, YPM 9743. Female paratype, 7.0 mm, YPM 9744. 20 male and female paratypes, YPM 9828. Female paratype, 6.1 mm, YPM 9829. Allotype and paratypes with same data as holotype. All specimens deposited in the Yale Peabody Museum.

Remarks.—Barnard & Thomas (1987) subdivided the genus *Chevalia* into two groups, based primarily on diagnostic features of the oostegites and pereopods 5–7. One group, represented by the *C. aviculae* superspecies complex, was defined by having three pairs of oostegites (pereopods 3–5) and a produced posterodistal corner on the basis of pereopods 5–7. *Chevalia carpenteri* was placed as the sole member of a

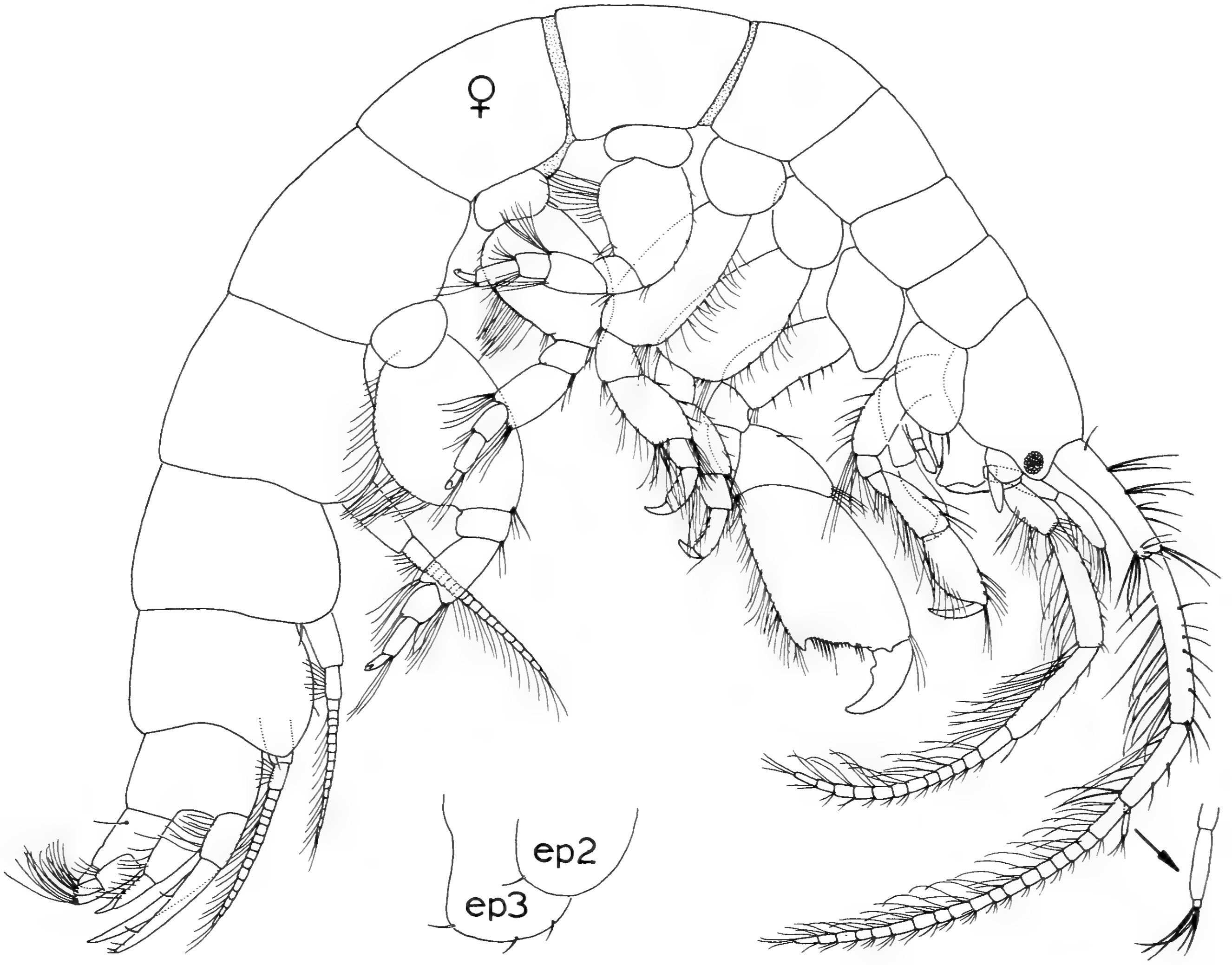

Fig. 1. A: YPM 9206, *Chevalia hirsuta* new species, female holotype, 10.1 mm. Abbreviations are: A, antenna; Md, mandible; Ll, lower lip; Mx, maxilla; Mxpd, maxilliped; Gn, gnathopod; P, pereopod; Pl, pleopod; U, uropod; T, telson; ep, epimeron; in, incisor; mlr, molar; plp, palp. Gnathopods are numbered Gn1 and Gn2; pereopods are numbered P3–P7.

second group because it possesses only 2 pairs of oostegites (on pereopods 4 and 5), and the basis of pereopods 5–7 is ovate, the posterodistal corner not produced. The new species described herein, *C. hirsuta,* has broadly rounded posterodistal corners of the basis of pereopods 5–7 and three pairs of oostegites; as such, it represents an intermediate form with characters overlapping both groups.

Based upon the ovoid condition of article 2 pereopods 5–7, *C. hirsuta* is morphologically allied to *C. carpenteri* of the Caribbean. However, based upon its possession of three pairs of oostegites, and rounded (i.e., not produced) epimeral plates, *C. hirsuta* is similar to all forms of the *C. aviculae* complex as defined by Barnard & Thomas (1987). Aside from the apparently unique combination of oostegite and basis characteristics of pereopods 5–7, *C. hirsuta* clearly differs from all known species of *Chevalia* in its possession of dense bundles of exceptionally long setae on various parts of the pereopods and uropods.

The type species of *Chevalia, C. aviculae,* was described from Sri Lanka [formerly Ceylon] by Walker (1904) and has also been reported from Madagascar by Ledoyer (1982), although the latter record is now provisionally attributed to *C. mexicana* Pearse 1913 (Barnard & Thomas 1987). Walker's figures are not very detailed, and the form he described is not easily distin-

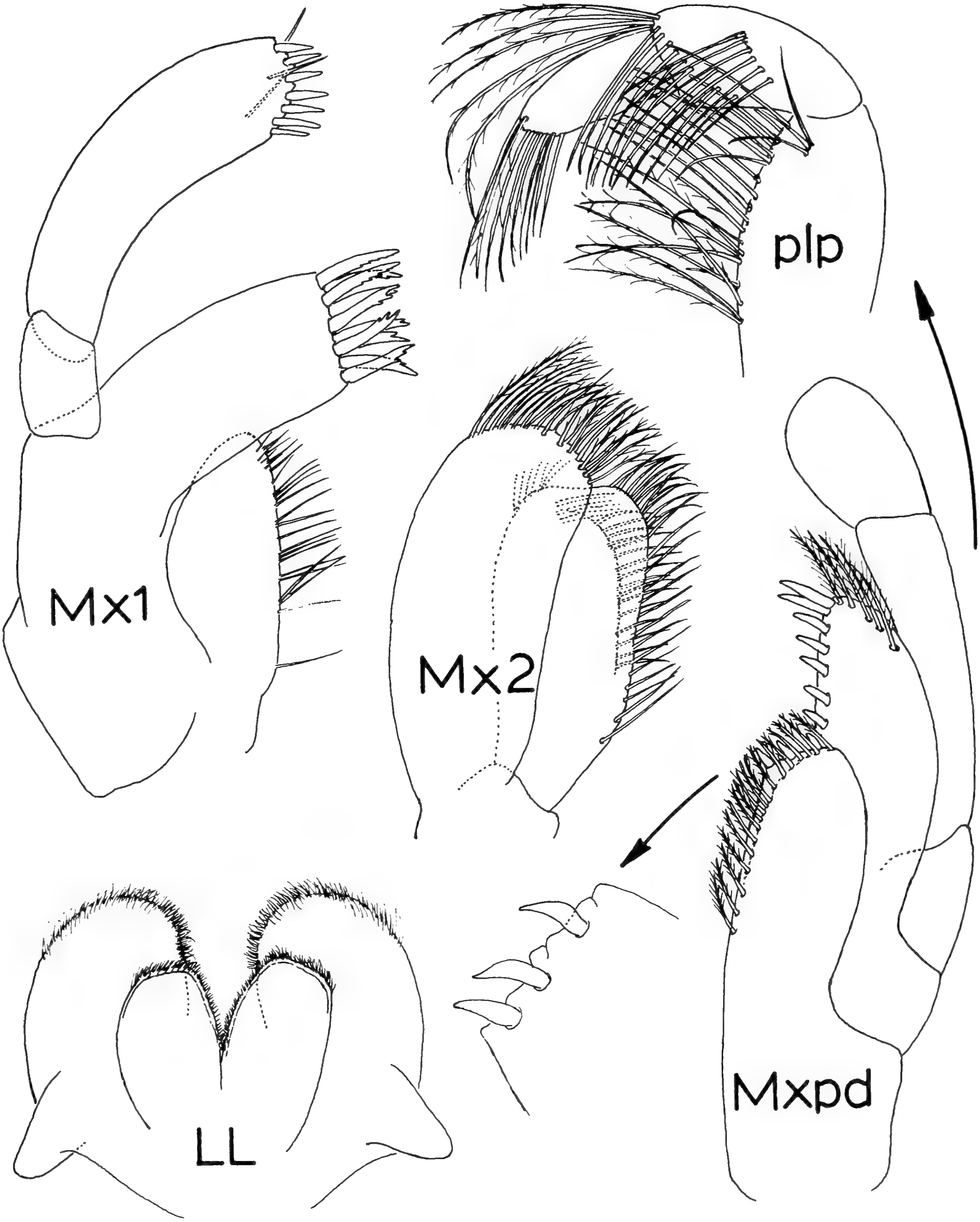

Fig. 2. YPM 9206, *Chevalia hirsuta,* new species, female holotype, 10.1 mm. For abbreviations, see Fig. 1.

guishable from other members of the *C. aviculae* superspecies complex (Barnard & Thomas 1987). The diagnostic posterodistally produced article 2 of pereopod 7 (= Walker's pereopod 5, plate VII, figure 50), is clearly figured, however, and serves to distinguish that form from *C. hirsuta.* These two variant forms of *Chevalia* (i.e., from Madagascar and Sri Lanka), although collected from areas relatively near the type locality of *C. hirsuta,* are both easily distinguished from the latter by the diagnostic condition of pereopods 5–7. Additionally, although the examination of additional

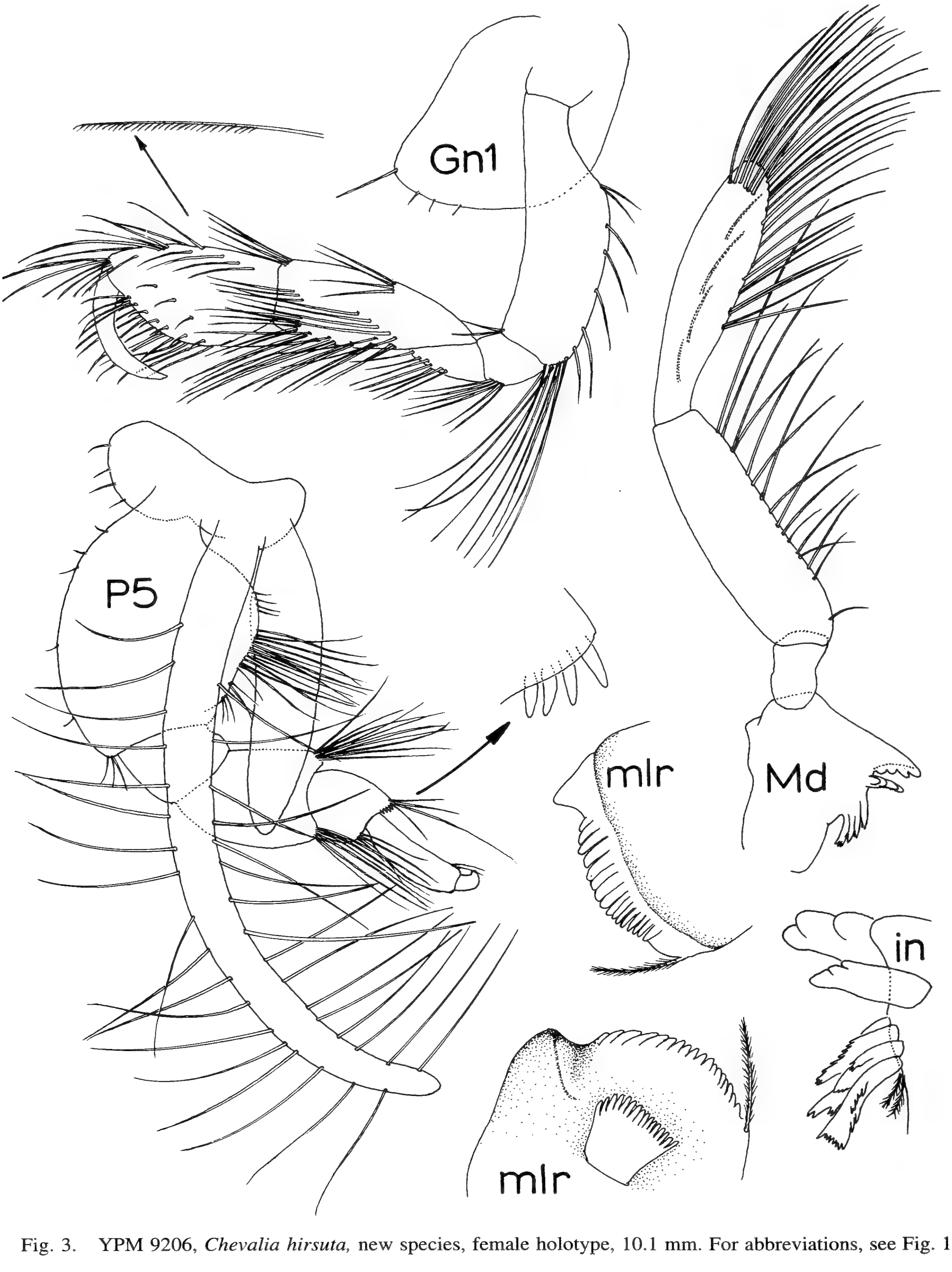

Fig. 3. YPM 9206, *Chevalia hirsuta,* new species, female holotype, 10.1 mm. For abbreviations, see Fig. 1.

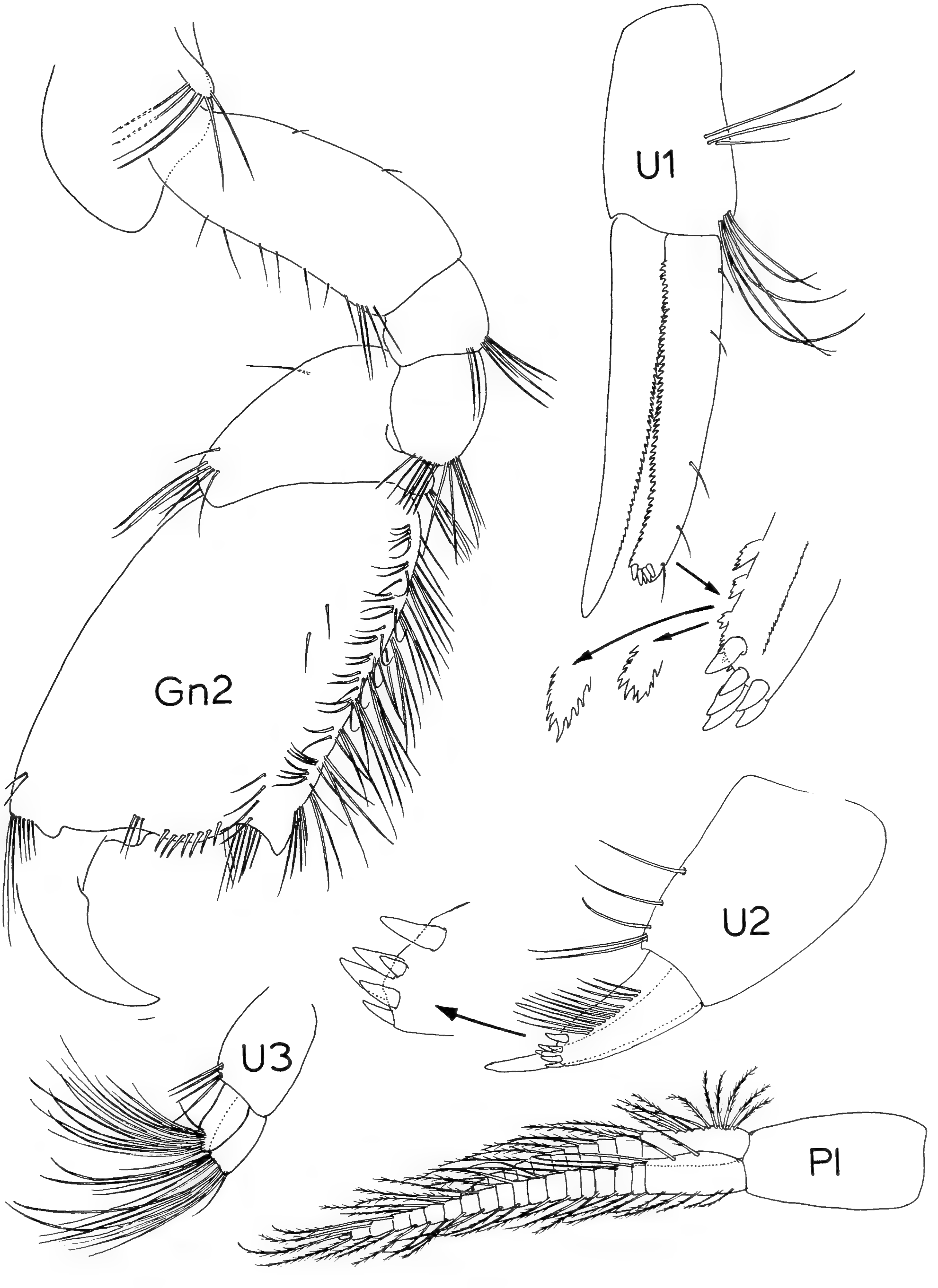

Fig. 4. YPM 9206, *Chevalia hirsuta*, new species, female holotype, 10.1 mm. For abbreviations, see Fig. 1.

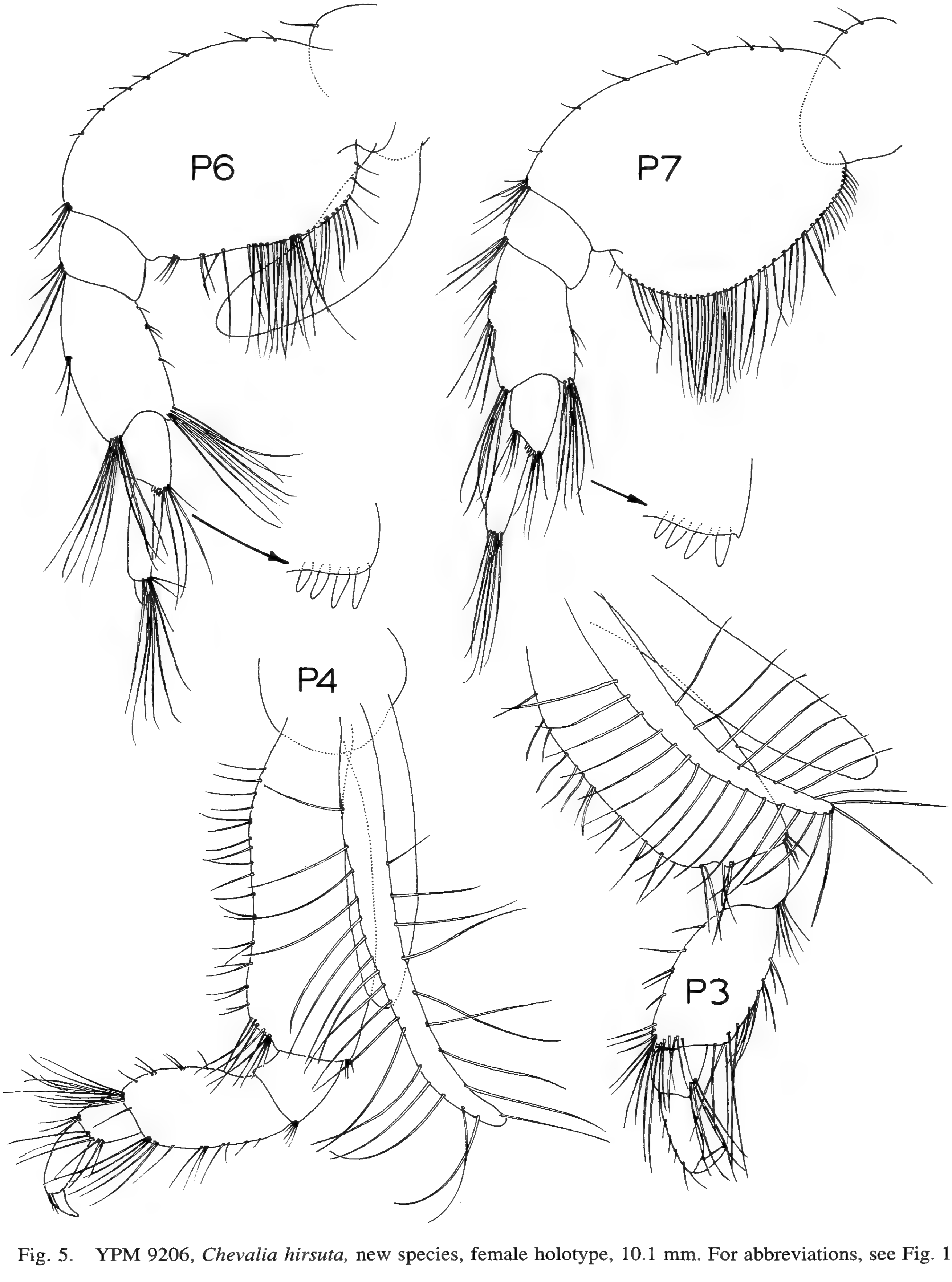

Fig. 5. YPM 9206, *Chevalia hirsuta,* new species, female holotype, 10.1 mm. For abbreviations, see Fig. 1.

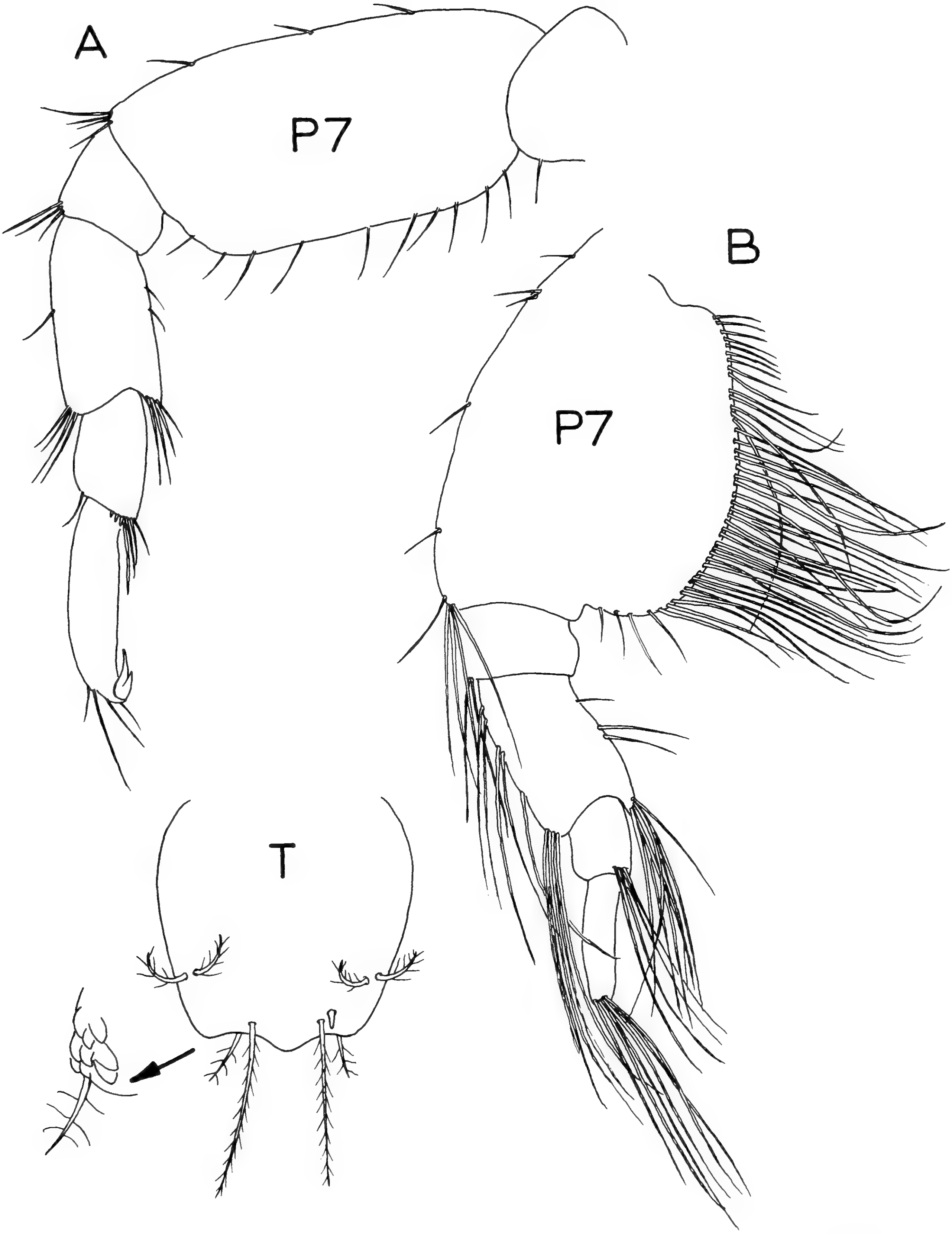

Fig. 6. *Chevalia hirsuta,* new species. Telson, YPM 9744, female paratype, 7.0 mm. A: YPM 9829, female paratype, 6.1 mm; B: YPM 9741 male allotype, 9.0 mm.

specimens may prove otherwise, *C. hirsuta* is very large compared to all other species of *Chevalia* (adults); the largest specimen of *C. hirsuta* examined (YPM 9206) is nearly 2.5 times larger than any other known species of the genus.

There is some similarity between small specimens of *C. hirsuta* and *C. pacifica,* recently described from Madang Lagoon, Papua, New Guinea (Myers 1995); in both species, article 2 of pereopod 7 is ovate, and not produced posteroventrally. *Chevalia hirsuta* differs from *C. pacifica* in having a prominent palmar tooth on gnathopod 2, which is distinct even in the smallest specimens (4–5 mm); a palmar tooth is lacking in *C. pacifica* as figured by Myers (1995). Furthermore, in small specimens of *C. hirsuta* the rami of uropod 1 are subequal in length, whereas in the figured specimen of *C. pacifica* the inner ramus is nearly 30% longer than the outer ramus.

Barnard & Thomas (1987) defined a variant of the *C. aviculae* complex, based upon a description of *C. aviculae* from Fiji by Myers (1985). Subsequently, Myers (1995) erected *C. pacifica* to attribute full species status to the Fijian variant; however, he based this new taxon upon specimens collected from New Guinea, rather than Fiji. Myers' (1995) figure of pereopod 7 of *C. pacifica* from New Guinea differs from what he had figured previously for the Fiji specimens (Myers 1985). The Fiji specimens, therefore, probably represent a different, and as yet undescribed, species.

Two characters are of potential future value in evaluating the species assignments of *Chevalia*: the number of submarginal spines at the anterodistal corner, article 5, pereopods 5–7; and the basic morphology of the subserrations of the teeth on the inner margin of the outer ramus, uropod 1. In *C. hirsuta* there are 4 anterodistal submarginal spines on article 5, pereopods 5–7. On the holotype of *C. carpenteri* (USNM 195157) there are only two spines. Furthermore, these spines are bifid on the type specimen, compared to simple on *C. hirsuta.* An examination of several of the specimens of *Chevalia* spp. described by Barnard & Thomas (1987) has confirmed different patterns of this character, depending on specimen provenance. Strong differences were also noted between the micromorphology of the subserrations of the teeth on the inner margin of the outer ramus of uropod 1. In *C. hirsuta,* the marginal subserrations are large and very irregular, whereas in *C. carpenteri* the subserrations are small and very regular. These two characters should prove useful in helping to distinguish, perhaps as new species, several of the morphs referred to by Barnard & Thomas (1987) from various localities around the world.

Key to the taxa of *Chevalia* (modified from Barnard & Thomas 1987)

1. Article 2 of pereopods 5–7 ovate, not produced posteroventrally 2
   Article 2 of pereopod 7 subquadrate, produced or squared posteroventrally ... . *aviculae* complex and *pacifica*
2. Oostegites 2 pairs, article 2 of pereopods 5–7 in fully developed adults moderately expanded, length more than twice width, pereopods 3–7, urosome and telson with normal setae .... *carpenteri*
   Oostegites 3 pairs, article 2 of pereopods 5–7 in fully developed adults greatly expanded, width 90% length; pereopods 3–7, urosome and telson with dense bundles of exceptionally long setae ... *hirsuta*

Acknowledgments

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Megagidiella azul, a new genus and species of cavernicolous amphipod crustacean (Bogidiellidae) from Brazil, with remarks on its biogeographic and phylogenetic relationships

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Abstract.—*Megagidiella azul,* a new genus and species, is described from Gruta do Lago Azul, a cave in central-western Brazil. With a body length of more than 16 mm, this species is the largest bogidiellid recorded to date. In addition to its large size, the absence of a mandibular palp is a unique diagnostic character for the family Bogidiellidae and alone merits recognition of a new genus. The occurrence of *Megagidiella azul* in an isolated, inland cave habitat marks another exceptional biogeographic record of a bogidiellid amphipod from South America.

Recent biological exploration of caves by speleologists in several karst areas in Brazil has revealed many new localities for gammaridean amphipod crustaceans and other subterranean organisms (Pinto-da-Rocha 1995). One such investigation in the Serra da Bodoquena Karst of central-western Brazil resulted in the discovery of a new stygobiont amphipod genus of the family Bogidiellidae, described below. The specimens were collected from a deep, subterranean lake in Gruta do Lago Azul (Blue Lake Cave).

Megagidiella, new genus

Diagnosis.—Eyes absent. Body smooth, unpigmented. Uronites not fused. Coxal plates longer than wide, not overlapping. Coxal gills occurring on pereopods 4–6; sternal gills absent. Oostegites on pereopods 2–5, sublinear. No sexual dimorphism. Interantennal (lateral) lobe of head narrowly rounded anteriorly. Mandibular palp absent. Maxilla 1: palp 2-segmented; outer plate with 7 serrate spines; inner plate with 3 apical plumose setae. Gnathopod 1 propodus much larger than gnathopod 2 propodus. Pereopods 5–7 with narrow bases. Pleopods and uropods unmodified. Pleopods biramous; outer ramus 3-segmented; inner ramus reduced, 1-segmented. Uropods biramous; peduncle of uropod 1 with several ventrolateral (basofacial) spines; uropod 3 relatively long. Telson about as long as broad, with shallow excavation.

Type species.—*Megagidiella azul,* new species by monotypy; gender feminine.

Etymology.—The generic name, referring to the relatively large size of the type species, is a combination of the Greek prefix "mega" (= large) and part of the family name.

Remarks and relationships.—Bogidiellids are relatively small amphipods, their body lengths generally range between 1–3 mm, occasionally exceeding 5 mm. With adult specimens reaching a body length of 16.2 mm, *Megagidiella* is an extraordinary exception. The more significant diagnostic character, however, is the absence of a mandibular palp, a morphological reduction to date not reported in the family Bogidiellidae (sensu Stock 1981). Apart from its size and absence of a mandibular palp, *Megagidiella* closely resembles the typical morphology of *Bogidiella,* s. str., e.g., gnatho-

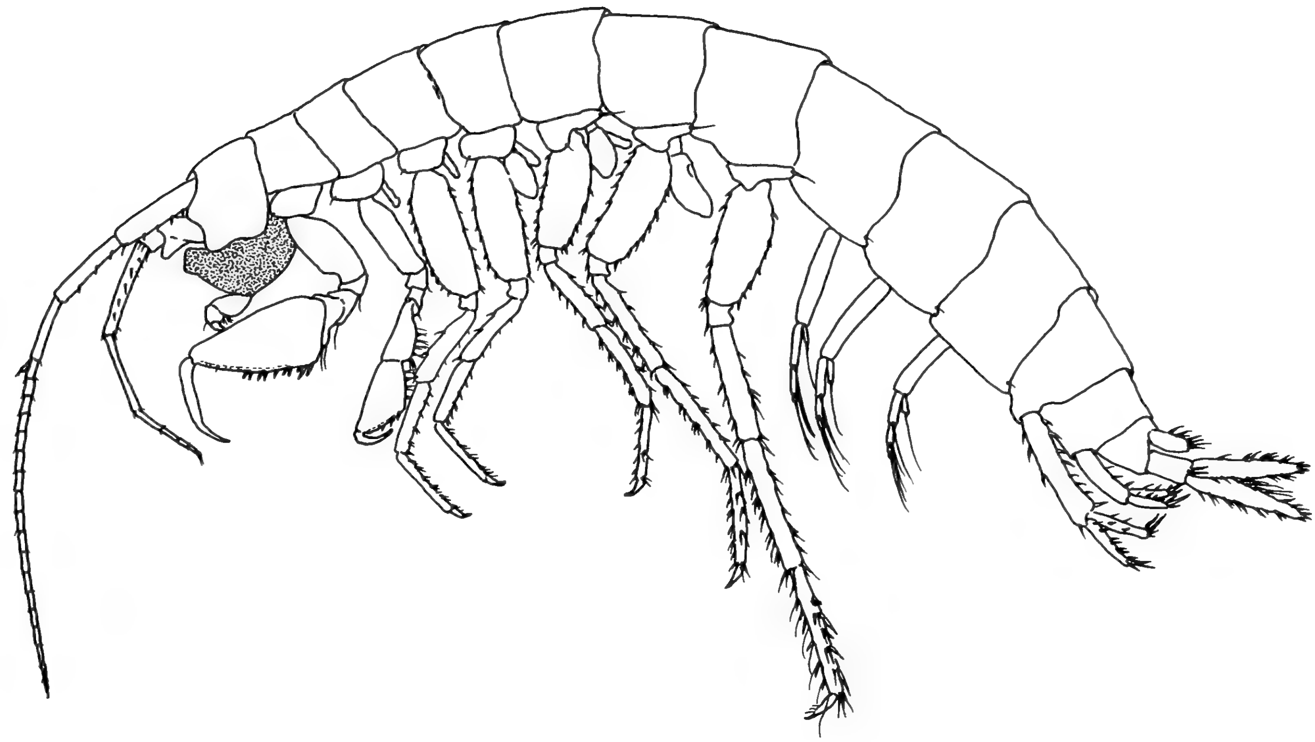

Fig. 1. *Megagidiella azul,* n. sp., holotype female (16.2 mm) from Lago Azul Cave, Bonito, Estado Mato Grosso do Sul, Brazil. Note: buccal mass is shaded.

pod 1 larger than gnathopod 2; pereopods 3–7 with narrow bases; coxal plates not overlapping, wider than long; 3-segmented pleopodal outer ramus; reduced, 1-segmented pleopodal inner rami. Minor exceptions from the general bogidiellid model are a 1-segmented accessory flagellum and the armature of the telson. Of all described bogidiellid species, a 1-segmented accessory flagellum is known only in 4 genera: *Artesia* Holsinger (*in* Holsinger & Longley 1980), *Kergueleniola* Ruffo, 1970, *Marigidiella* Stock, 1981, and *Parabogidiella* Holsinger (*in* Holsinger & Longley 1980).

The armature of the telson shows a remarkable resemblance to that of *Spelaeogammarus* da Silva Brum, 1975, from caves in eastern Brazil: *Megagidiella* has 2–3 apical and 3–5 subapical (lateral) spines per telsonic lobe in comparison with 2 apical and 3–4 subapical spines in *Spelaeogammarus.* The combination of 2 apical spines with more than 2 subapical spines is exceptional for bogidiellids. Moreover, the armature and shape of uropods 1–3 show noteworthy similarities in both genera, for example, a row of long setae on the medial margin of the outer ramus of uropod 3. Along with *Artesia,* from an Artesian Well in Texas, these are the only bogidiellids known with setae on the rami of uropod 3.

Megagidiella azul, new species
Figs. 1–4

Material examined.—Holotype female (16.2 mm), allotype male (15 mm), and 3 paratypes (1 male, 1 female, 1 juvenile), collected by Adrian Boller, 1 July 1991.

Type locality.—Gruta do Lago Azul, northwest of Bonito, Estado Mato Grosso do Sul, Brazil.

The holotype is dissected and mounted on microscope slides in Faure's medium. It is deposited in the Museu Nacional (UFRJ) in Rio de Janeiro, Brazil (MNRJ 13339). The allotype and paratypes are preserved in alcohol and will be retained in the research collection of JRH under the catalog no. H-3487.

Diagnosis.—With the characters of the genus. Largest male 15 mm, largest female 16.2 mm (Fig. 1).

Description.—Antenna 1 (Fig. 2a) about

50% length of body. Peduncular segments 1–3 gradually decreasing in length distally. Primary flagellum longer than peduncle, with up to 19 articles in adult specimens, without aesthetascs. Accessory flagellum 1-segmented.

Antenna 2 (Fig. 2b) about half as long as antenna 1. Peduncular segment 4 longer than segment 5. Flagellum as long as peduncular segment 5, with 5 articles.

Upper lip (Fig. 2c) rounded apically, with setules along distal margin.

Mandible (Fig. 2h, i): palp absent; molar prominent, rounded, weakly triturative, bearing 1 long, finely serrate seta; left lacinia mobilis 5-dentate, right lacinia 2-dentate, with serrate upper margin; left and right mandible with 4–6, variably plumose accessory spines.

Lower lip (Fig. 2d) bearing setules on outer lobes and on distal margins of inner lobes; inner lobes small but distinct; lateral processes short with bluntly rounded corners.

Maxilla 1 (Fig. 2e): Palp 2-segmented, with 3 apical setae. Outer plate with 7 comblike spines (Fig. 2f), bearing loosely inserted setules on surface and in row along medial margin. Inner plate with marginal setules and 3 apical plumose setae.

Maxilla 2 (Fig. 2g): Outer plate with approximately 24 naked apical setae; apical margin of inner plate bearing about 17 naked setae and 3 plumose setae; both plates with fine setules.

Maxilliped (Fig. 2j): Palp 4-segmented; 3 blunt spines along apical margin of outer plate; apical margin of inner plate with 2 bifid (y-shaped) spines, 4 plumose setae, and 1 naked seta.

Gnathopod 1 (Fig. 3a): Basis naked, bearing only 1 short seta at distoposterior corner. Carpus short, triangular shaped, with 2 setae on pointed posterior lobe. Propodus almost twice as long as broad, approximately twice the size of gnathopod 2 propodus. Palmar margin oblique and even, finely serrate along whole margin, with 5 medial and 5–6 lateral spines; medial margin with about 27 short setae and 4 angular spines of unequal length. Dactyl about 80% length of propodus.

Gnathopod 2 (Fig. 3b): Basis naked, bearing only 1 short seta at distoposterior corner. Propodus bearing 18–20 short setae (12–13 laterally and 6–7 medially), 5 spines near corner, and a single lateral spine at mid-palmer margin. Palm with distinctly oblique, finely serrate margin. Dactyl about 60% length of propodus.

Pereopods 3 and 4 subequal (Fig. 4a, b). Bases narrow, anterior margins little expanded. Dactyls 24–27% length of propods.

Pereopods 5–7 (Fig. 4c–e) increasing in length posteriorly. Bases narrow, posterior margins very weakly expanded. Dactyls about 22, 26, and 28% length of propods, respectively.

All pereopod bases apparently without lenticular organs.

Coxal plates small, wider than long; plates 1–4 rectangular, plates 5–7 at least 2 times wider than long.

Coxal gills (Fig. 4a, d) present in 3 pairs, ovate on pereopods 4 and 5 and sack-shaped on pereopod 6.

Oostegites (Fig. 3b, 4a, c) small, sublinear, occurring on pereopods 2–5 (not setose in material examined).

Epimeral plates (Fig. 3c) with small, but distinct distoposterior corners, bearing 1 setule each in groove immediately above corner.

Pleopods 1–3 (Fig. 4f) similar. Inner ramus reduced, 1-segmented, with terminal plumose seta. Outer ramus 3-segmented, with 2 terminal plumose setae per segment.

Uropod 1 (Fig. 4g) biramous, outer ramus slightly shorter than inner ramus; rami about 64% length of peduncle. Peduncle bearing 14–15 spines, 3 of which inserted along ventrolateral (basofacial) margin. Outer ramus with 12 lateral spines and 4 apical spines. Inner ramus with 4–5 apical and 5 dorsomedial spines.

Uropod 2 (Fig. 4h): Inner and outer rami subequal, slightly longer than peduncle. Peduncle with 6 spines. Outer ramus bearing

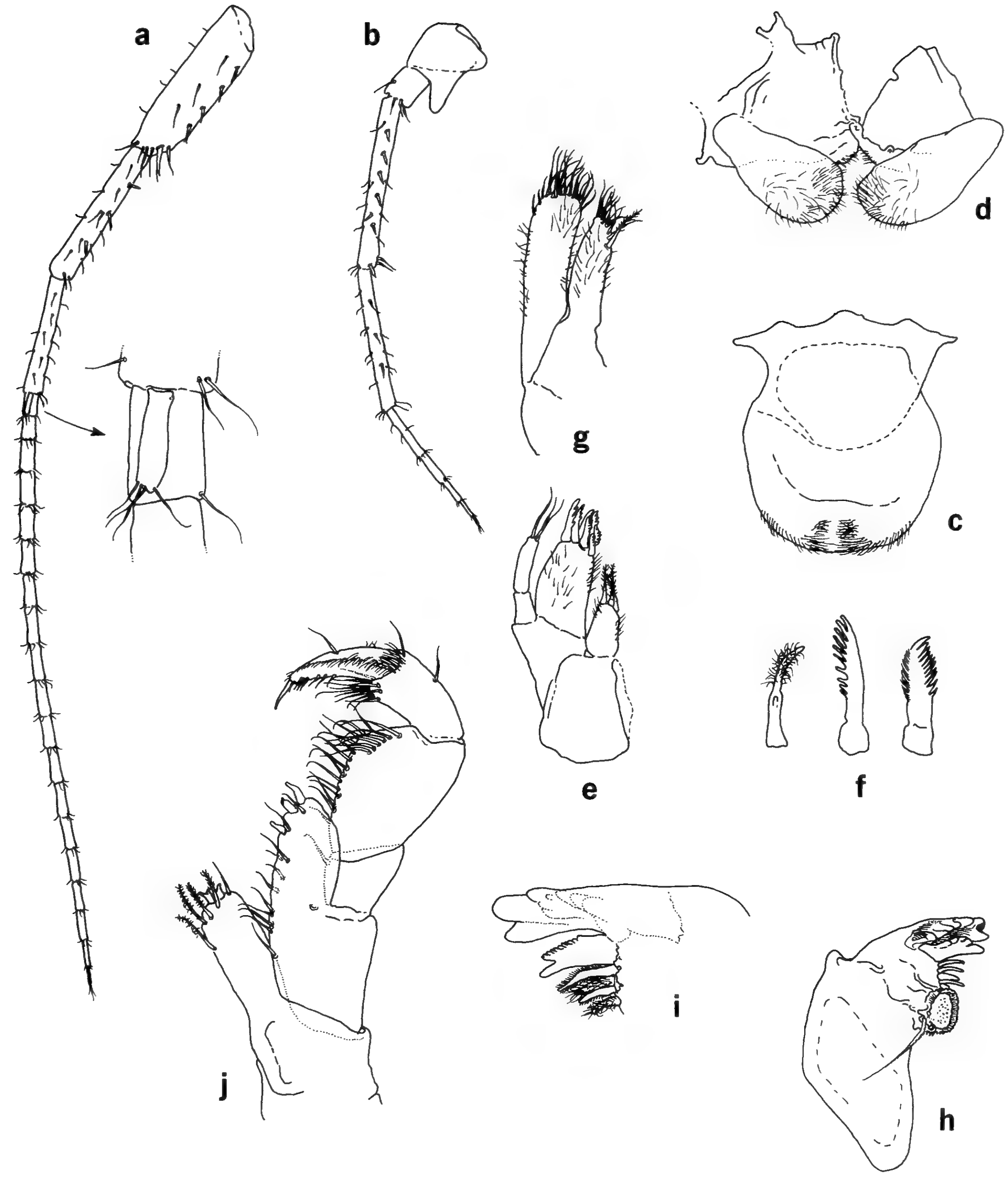

Fig. 2. *Megagidiella azul,* n. sp., holotype female (16.2 mm): a) antenna 1 (accessory flagellum enlarged), b) antenna 2, c) upper lip, d) lower lip, e) maxilla 1, f) enlarged spine and seta types of maxilla 1, g) maxilla 2, h) left mandible, i) incisor, lacinia mobilis, and spine row of right mandible, j) maxilliped.

8 lateral spines and 4 apical spines (2 long ones and 2 short ones). Inner ramus bearing 5 spines along medial and lateral margins and 5 apical spines (3 long ones and 2 short ones).

Uropod 3 (Fig. 4i) long, with subequal, 1-segmented rami. Peduncle about 48% length of rami, with 2–4 spines. Outer ramus with 6 apical spines and 6 sets of spines along lateral margin (with 1–5 spines per set); medial margin bearing 4–5 long plumose setae. Inner ramus with 6–7 apical spines and about 19 medial and lateral spines (some doubly inserted).

Telson (Fig. 3d, e) about as broad as long; apex with shallow excavation (8% length of telson); each half bearing 2 plumose setae, 2 (sometimes 3) apical and 3–5 subapical spines.

Variation.—Morphological variation, apart from usual differences between juveniles and adults (e.g., number of spines on

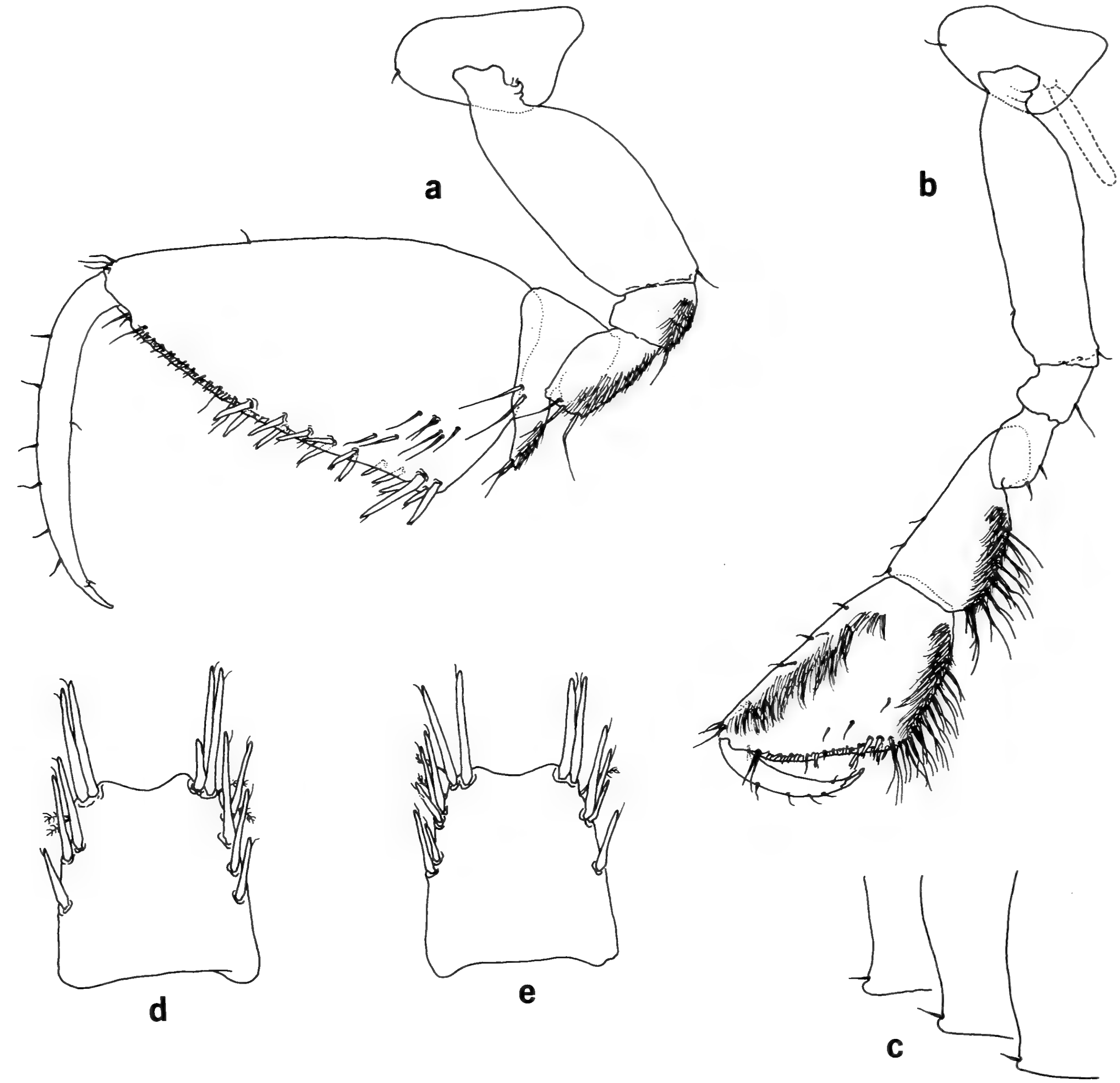

Fig. 3. *Megagidiella azul,* n. sp., holotype female (16.2 mm): a) gnathopod 1, b) gnathopod 2, c) epimeral plates, d) telson, e) telson, allotype male (15 mm).

appendages, flagellum articles, etc.), was observed most obviously in the armature of the telson. The number of subapical spines in the adult females (16 mm in length) varied from 2 to 5 per side, whereas both adult males (15 and 11 mm in length) had a constant number of 3 subapical spines. In the holotype female, a short third apical spine was inserted on the left telsonic apex (Fig. 3d).

Etymology.—The epithet *azul* is based on the name of the type locality and is used as a noun in apposition.

Discussion

The type material was collected at a depth between 6 and 12 m from a deep, turquoise-blue lake inside Blue Lake Cave. The cave is located at the southern edge of the world's largest wetland area along the Serra da Bodoquena in central-western Brazil (Pinto-da-Rocha 1995). Because of the large cave entrance, the lake, about 50 m inside the cave, receives light during some hours of the day (Pires 1987). The water in the lake presumably marks the upper portion of a subterranean aquifer.

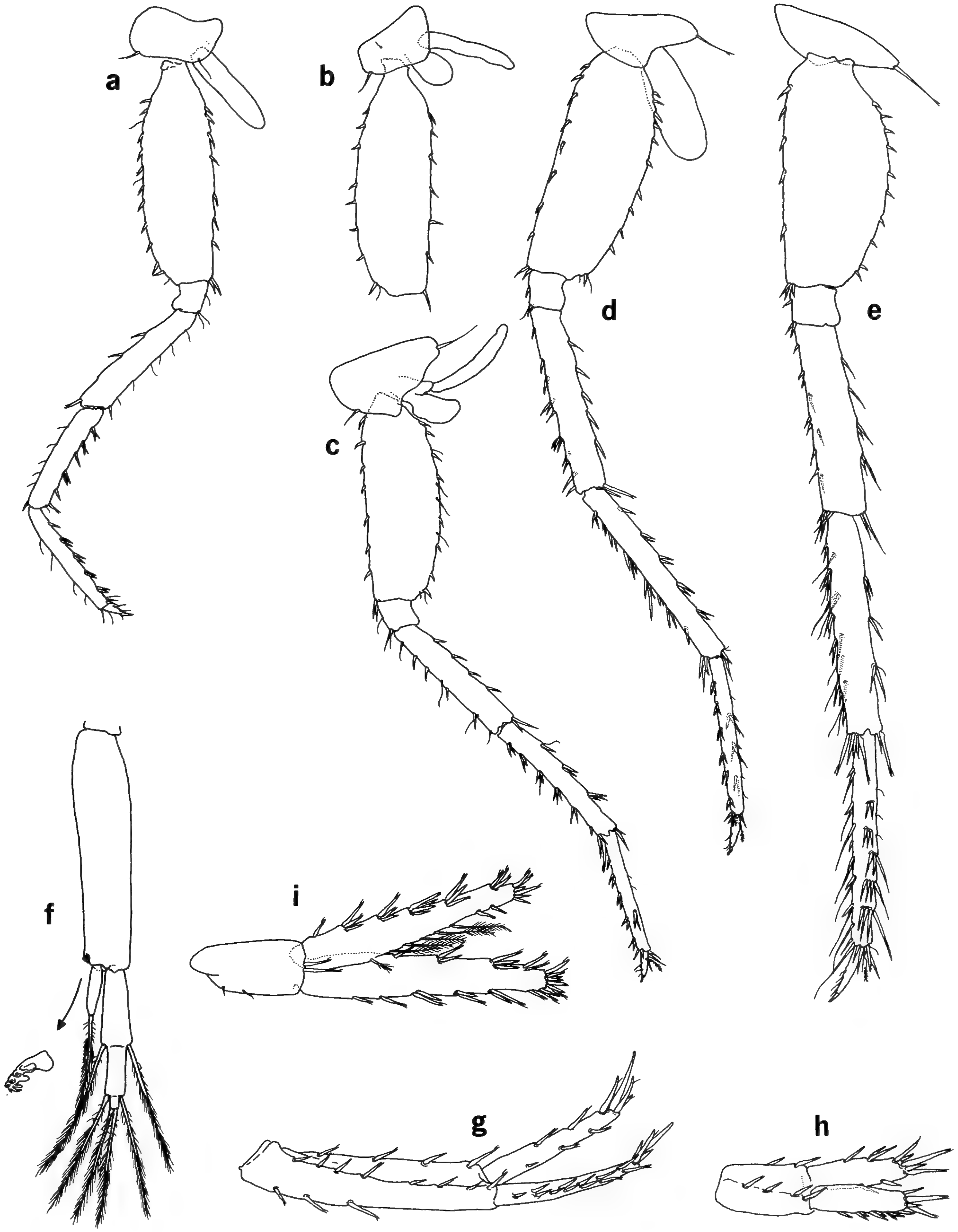

Fig. 4. *Megagidiella azul,* n. sp., holotype female (16.2 mm): a) pereopod 3, b) pereopod 4, c) pereopod 5, d) pereopod 6, e) pereopod 7, f) pleopod 2, g) left uropod 1, h) left uropod 2, i) left uropod 3.

Blue Lake Cave was already biogeographically significant prior to the discovery of *Megagidiella azul,* inasmuch as it is the only known locality in the western hemisphere for the extremely rare crustacean order Spelaeogriphacea. Prior to the discovery of *Potiicoara brasiliensis* Pires, 1987 in Blue Lake Cave, the only other spelaeogriphacean known to science was *Spelaeogriphus lepidopus* Gordon 1957 from caves on Table Mountain in South Africa. One explanation for the occurrence of freshwater stygobiont spelaeogriphaceans in caves on opposite sides of the Atlantic Ocean is that these species are derived from a common ancestor which inhabited Gondwana prior to the separation of Africa and South America in the Early Cretaceous. Although it is tempting to speculate that bogidiellids and spelaeogriphaceans share a similar evolutionary history affected by continental drift, there is to date no evidence that the ranges of these groups form a generalized distribution track. Bogidiellids are recorded only from a few localities near coastal regions in northeastern and northern Africa, whereas the freshwater amphipod fauna in central and southern Africa is composed primarily of epigean paramelitids, and stygobiont ingolfiellids and sternophysingids.

From an ecological perspective, it is important to note that *M. azul* dwells in a large lake of phreatic water. The extraordinary size of this species might imply a correlation of body size and available habitat space. An interesting parallel example of this phenomenon can be observed in the amphipod family Ingolfiellidae. Most ingolfiellids, like many bogidiellid taxa, are less than 3 mm long and live in interstitial habitats. In contrast to the norm, however, species of the ingolfiellid genus *Trogloleleupia* live in large "open" cave lakes in central and southern Africa and may reach 23 mm in length (Griffiths 1989).

Bogidiellid amphipods have a near world-wide distribution pattern, occuring exclusively in subterranean habitats. Their distribution pattern is characterized by several regions with relatively dense concentrations of species. For example, the South American continent shows the highest generic diversity as opposed to the Mediterranean region where species richness is higher but generic diversity is lower. To date, 18 species, distributed among 10 genera and subgenera, are known from South America (Fig. 5).

The discovery of *Megagidiella azul* in the interior of South America, approximately 1000 km from the nearest coast, is biogeographically significant because the vast majority of bogidiellids occupy ranges between 100–200 km from marine coastal regions. South America shows a remarkable pattern of isolated aquatic habitats, and has promise for the future study of stygobiont organisms and their environments.

Subsequent to the completion of the manuscript, we received additional megagidiellids from several new localities in the state Mato Grosso do Sul, Brazil. These specimens match the description given in this paper and show the same morphological variation as observed in the type species.

New localities.—2 juveniles (6 and 7 mm) from Gruta do Mimoso, Bonito, collected by E. P. Costa, Jr., Feb and Jun, 1998; 1 female (12.5 mm) from Abismo do Poço, Jardin, collected by N. Moracchioli, Jun, 1998; 2 females (13 mm) from Buraco dos Abelhas, Jardin, collected by E. P. Costa, Jr., Apr and Jun, 1998.

Comments.—According to Dr. Eleonora Trajano (pers. comm.), all specimens were found in large cave lakes. They occurred in the water column at depths of 20–52 meters. Spelaeogriphaceans were also present in Gruta do Mimoso, but they inhabited only the benthic sediments of the lake.

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We are grateful to Dr. Eleonora Trajano, University of São Paulo, Brazil, for providing us with the specimens of the new bog-

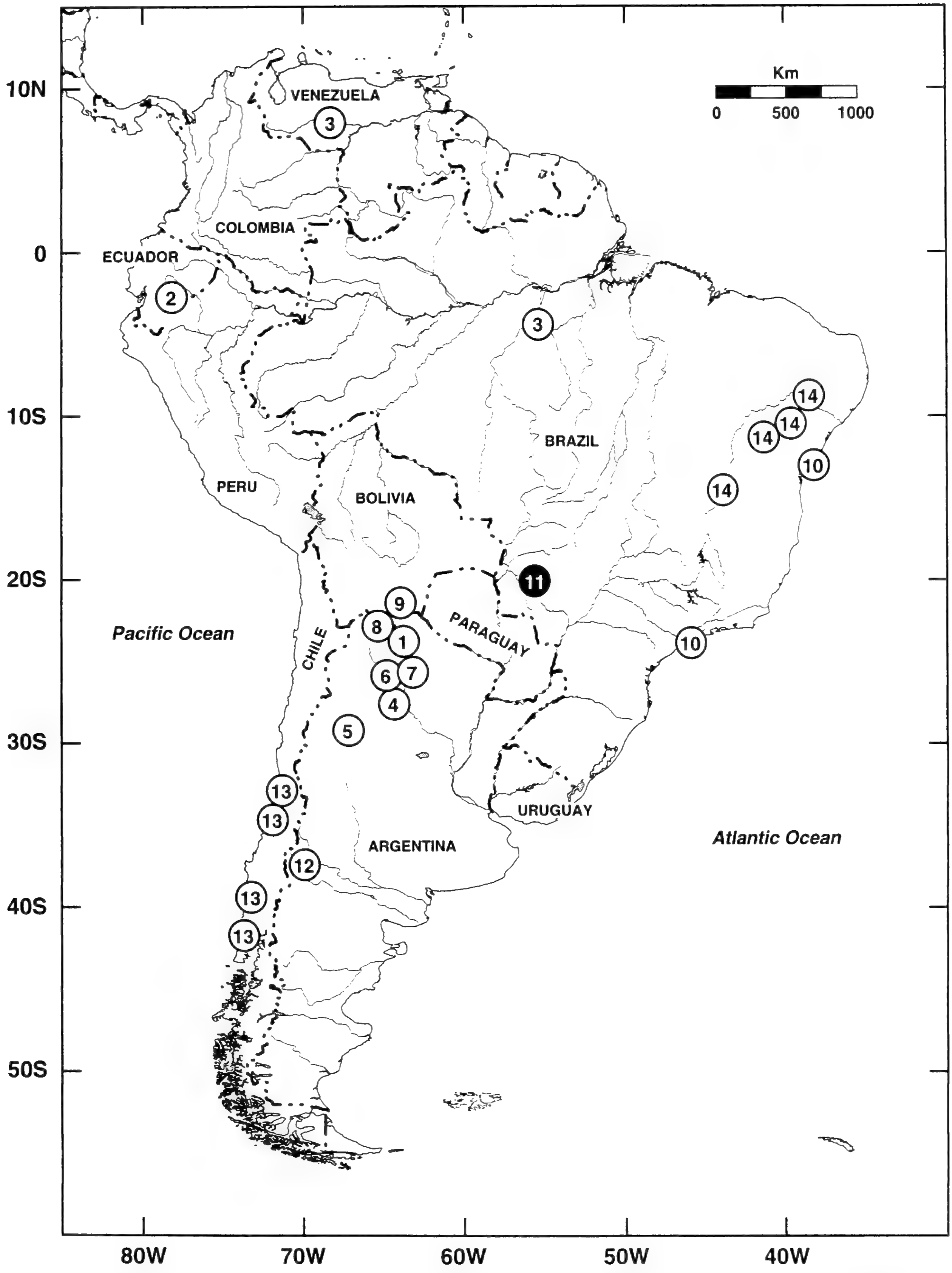

Fig. 5. Geographic distribution of bogidiellid amphipods in continental South America: (1) *Bogidiella cooki* Grosso & Ringuelet (1979); (2) *B. gammariformis* Sket (1985); (3) *B. neotropica* Ruffo (1952); (4) *B.* (*Dycticogidiella*) *ringueleti* Grosso & Fernández (1988); (5) *B.* (*Dyct.*) *talampayensis* Grosso & Claps (1985); (6) *B.* (*Mesochthongidiella*) *tucumanensis* Grosso & Fernández (1985); (7) *B.* (*Stygogidiella*) *hormocollensis* Grosso & Fernández (1988); (8) *B.* (*Styg.*) *lavillai* Grosso & Claps (1984); (9) *Eobogidiella purmamarcensis* Karaman (1982); (10) *Marigidiella brasiliensis* Stock (1981; see also Siewing, 1953); (11) *Megagidiella azul*, n. gen., n. sp. (background darkened for emphasis); (12) *Patagongidiella danieli* Grosso & Fernández (1993) and *P. mauryi* Grosso & Fernández (1993) (both in same locality); (13) *Pseudingolfiella chilensis* Noodt (1965); (14) *Spelaeogammarus bahiensis* da Silva Brum (1975) and *S.* spp.

idiellid amphipod for identification and study, and to Adrian Boller for collecting the bogidiellids from Blue Lake Cave. We also thank the Graphics Office at Old Dominion University for generating of the distribution map. This study was supported by a PEET grant from the National Science Foundation to JRH (DEB-9521752).

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The western and southern distribution of *Mesocyclops edax* (S. A. Forbes) (Crustacea: Copepoda: Cyclopoida)

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Abstract.—A review of published records and material of the cyclopoid copepod *Mesocyclops edax* (S. A. Forbes) established its presence in the drainage basins of the Colorado and Columbia Rivers in the western U.S.A., and verified published records from Cuba, Guatemala, and Mexico. *Mesocyclops nicaraguensis* Herbst is a junior synonym of *M. edax.* We provide supplementary morphological observations and describe certain morphological variations observed in some populations of *M. edax.*

The cyclopoid copepod *Mesocyclops edax* (S. A. Forbes, 1891) is a common and often numerous plankter in surface waterbodies of North America, and its biology and genetics have been the subject of many reports (e.g., Williamson 1986; Wyngaard 1991; Wyngaard et al. 1985, 1995). *Mesocyclops edax* is widespread in south-central and eastern Canada (Patalas 1986) and in the conterminous U.S.A. east of the Rocky Mountains; the animals undergo diapause in winter in colder latitudes. The western and southern limits of *M. edax* are less well documented. Patalas (1986) failed to find it in his own collections or in published records west of the Canadian Pacific continental divide. Published records of *M. edax* from the western U.S.A. are few, and confirmed records from Mexico and Central America even fewer. We review western and southern records of *M. edax,* confirming those records where possible through examination of available specimens.

The question of the synonymy of *Mesocyclops nicaraguensis* Herbst, 1960 with *M. edax,* first raised by Cole (1976), has continued unresolved. We compared specimens from the type-locality of *M. nicaraguensis* in Lake Nicaragua, and from other waterbodies in Nicaragua to populations of *M. edax* from across North America.

Dussart (1985) and Dahms & Fernando (1995a) redescribed adult *M. edax.* We add observations on certain morphological features of interest for the systematics of the genus, and note some morphological variations observed during the course of this study.

Specimens were deposited in the collections of the National Museum of Natural History (USNM), and the Centro para la Investigación en Recursos Acuáticos de Nicaragua, Universidad Nacional Autónoma de Nicaragua (CIRA/UNAN).

Order Cyclopoida G. O. Sars, 1886
Family Cyclopidae Burmeister, 1834
Subfamily Cyclopinae Dana, 1853
Genus *Mesocyclops* G. O. Sars, 1914
Mesocyclops edax (S. A. Forbes, 1891)
Figs. 1–3

Cyclops edax S. A. Forbes, 1891:709–710, 715, 717, 718, pl. III fig. 15, pl. IV figs. 16–19.

Cyclops leuckarti Claus, 1857 (partim).—Marsh 1893:191, 193, 209–211, 224, pl. IV fig. 17, pl. V figs. 2–6.

Mesocyclops edax.—G. O. Sars 1914:58.
Cyclops leuckharti.—Coker 1926:230–234, 247–248, 257, pl. 40 figs. 5–7.
Mesocyclops Leuckarti edax.—Kiefer 1929a:306–307, figs. 4, 5.
Mesocyclops obsoletus (Koch, 1838).—C. B. Wilson 1929:129.
Mesocyclops nicaraguensis Herbst, 1960: 27, 42–45, figs. 33–41.
Non *Cyclops simplex* Poggenpol, 1874.—Herrick, 1887:14, 17–18, pl. VII fig. 1.
?Non *Cyclops tenuissimus* Herrick, 1883: 499–500, pl. V figs. 24, 25, pl. VI, figs. 20, 21.

Material examined.—Canada: USNM 79773, 10 ♀♀, Lake-of-the-Woods, Ontario, 17 Jul 1909. USNM 251908, 6 ♀♀, 8 ♂♂, Red Bridge Pond, Halifax, Nova Scotia, 8 Jul 1992, leg. G. A. Wyngaard. U.S.A.: USNM Acc. No. 120079 (Marsh Collection), 1 ♀, slide, Hutchins, Texas, C. D. Marsh prep. no. 3101. USNM 62590, 10 ♀♀, Lake Erie, 12 Jul 1928, don. Buffalo Society of Natural Science. USNM 78730, 10 ♀♀, Welaka, Florida, 1 Apr 1938, leg. L. Cable. USNM 216873, 10 ♀♀, Crane's Pond, Newport, North Carolina, 24 Aug 1984, leg. M. C. Swift. USNM 235221, 7 ♀♀, Lake Powell, Utah, 17 Jan 1985, leg. L. Haury. USNM 251156, 60+ ♀♀ ♂♂ and copepodids, Lake Union, Seattle, State of Washington, 47°39′12″N, 122°19′24″W, 10 Oct 1991, leg. Parametrix Inc. for Municipality of Metropolitan Seattle (METRO), gift of J. R. Cordell. USNM 264309, 13 ♀♀, Hueco Spring I, near New Braunfels, Cornal Co., Texas, 8–10 Aug 1992, leg. C. B. Barr. USNM 278133, 1 ♀ 2 ♂♂ 2 copepodids, San Joaquin River, Fresno, California, 10 Sep 1995, leg. S. Callison. Mikropräparate 2993 and 2994, 1 ♀, partly dissected on 2 slides, Lake Otay, San Diego, California, 29 Feb 1936, leg. Light, prep. F. Kiefer, Kiefer Collection, Staatliches Museum für Naturkunde Karlsruhe. 20 ♀♀ ♂♂, culture, New Orleans, Louisiana, 1989, collection of G. G. Marten. Mexico: USNM 251674, 1 CV ♂, Lake Pátzcuaro, Michoacán, 19°30′N, 101°38′W, 17 Oct 1991, leg. A. Orbe-Mendoza and P. Aguilar. USNM 259699, 1 ♀, Cenote Viejo, Quintana Roo, Mexico, 21 Jul 1987, leg. E. Suárez-Morales. Guatemala: USNM 250931, 6 ♀♀ 4 ♂♂ 1 copepodid stage V (CV) ♀, all mounted on 2 slides, 16 Mar 1972, and 3 ♀♀ 1 ♂, all mounted on 3 slides, 19 Aug 1972, Lake Izabál, leg. L. G. Brinson, prep. det. H. C. Yeatman. Nicaragua: USNM 259614, 1 ♀ (dissected on slide), 1 ♂ 5 copepodids, Lake Nicaragua (Lake Cocibolca), Managua, 1991. USNM 259616, 6 ♀♀ 1 ♂ 57 copepodids, Lake Nicaragua, 1993. USNM 243696, 10 ♀♀, Lake Asososca, Managua, 22 Oct 1991. USNM 243700, 10 ♀♀ 10 ♂♂, Lake Las Canoas, 21 Jan 1993. USNM 243701, 8 ♀♀ 3 ♂♂, Lake Nicaragua, Sample 97-11, 13 Jun 1997. USNM 243707, 200+, Lake Nicaragua, Samples N97-09 and N97-11, 13 Jun 1997. USNM 243710, 100+, Lake Asososca, Managua, 22 Oct 1991. USNM 243713, 500+, Lake Managua, Point 7, 23 Mar 1995. USNM 243715, 100+, Lake Las Canoas, 21 Jan 1993. Legs. L. Moreno. Additional material deposited in the Plankton Collection, CIRA/UNAN. Cuba: 1 ♀, partly dissected on slide, Sabanilla Reservoir, 15 May 1965, collection of C. H. Fernando.

Supplementary description of female.—We describe certain morphological features of the adult female, to supplement previous redescriptions (Dussart 1985, Dahms & Fernando 1995a).

Medians (ranges, *n*) of lengths, excluding caudal setae, in mm: Canada: Ontario (USNM 79773), 1.41 (1.24–1.48, *n* = 10); Nova Scotia (USNM 251908), 1.43 (1.38–1.49, *n* = 6). U.S.A.: Lake Erie (USNM 62590), 1.23 (1.06–1.33, *n* = 10); Florida (USNM 78730), 1.27 (1.09–1.35; *n* = 10); North Carolina (USNM 216873), 1.31 (1.22–1.38, *n* = 10); Utah (USNM 235221), 1.17 (1.11–1.18, *n* = 7); Louisiana (Marten collection), 1.40 (1.26–1.53, *n* = 10); Texas (USNM 264309), 1.30 (1.28–1.36, *n* = 10). Mexico: Quintana Roo (USNM 259699), 1.08 (*n* = 1). Guatemala: Lake Izabál

(USNM 250931), 1.26 (1.23–1.40, $n = 9$). Nicaragua: Lake Nicaragua (Lake Cocibolca) (USNM 259614), 1.18 ($n = 1$); Lake Nicaragua (USNM 259616), 1.38 (1.26–1.45, $n = 6$); Lake Asososca (USNM 243696), 1.02 (0.96–1.15, $n = 10$); Lake Las Canoas (USNM 243700), 1.17 (1.09–1.31, $n = 10$).

Habitus (Fig. 1A) typically cyclopiform; occasional individuals with circular pits on prosomites. Pediger 5 (Fig. 1B–E) usually without ornament except normal hair-sensilla, except group of hairs on lateral surfaces in one female from Nicaragua. Genital double somite (Fig. 1B–D) with group of 6 tiny pores posterior to leg 6, pore pattern otherwise as in figures. Pore-canal usually single as in Fig. 1D, but sometimes appearing divided (Fig. 1F, G). Posterior pore-canal usually represented as stout and posteriorly directed, but strongly recurved in oblique view (in direction of arrows, Fig. 1G). Anal somite (Fig. 1H) with continuous row of spines along posterior margin; caudal ramus usually divergent in preserved specimens, with 4–5 irregular groups of hairs on medial surface.

Hyaline membrane of antennule terminal segment beginning at lateral seta, usually with several large notches (Fig. 2A). Specimen from Cuba with this condition exaggerated on one side, giving impression of single deep notch (Fig. 2B).

Antenna basis (Fig. 2C–F) in most populations with secondary curved row of small spines (Fig. 2E, arrow; Dahms & Fernando 1995a), row absent in some populations (Fig. 2C).

Maxilla (Fig. 2G) with group of tiny spines on frontal side.

Maxilliped (Fig. 2H, I) usually with more complex surface spine pattern than indicated by Dahms & Fernando (1995a).

Legs 1–4, caudal surfaces of coxa-bases ornamented as in Fig. 3A–D. Medial spine of leg 1 basipodite with slender spinules in North American populations (Fig. 3A), with more and stouter spinules in some southern populations, e.g., Cuba (Fig. 3E). Couplers (intercoxal sclerites) of legs 1–3 always with small submarginal spinules (Fig. 3F–H, J–L), number of spinules on leg 1 coupler varying from 1 to 5 in North American populations and from 7 to 10 on specimen from Cuba, with similar, but fewer spines on couplers of legs 2 and 3. These spines usually stout, but slightly longer and slimmer in specimens from Guatemala and Nicaragua. Two projections on margin of leg 4 coupler usually rounded (Fig. 3M), but sometimes acute and inward- or outward-directed (Fig. 3D, I). Both terminal spines of leg 4 endopodite 3 with spinulate margins, spinules of lateral terminal spine fewer and coarser than spinules of medial terminal spine in all specimens examined (Fig. 3N).

Discussion

Balcer et al. (1984), Coker (1943), Cole (1960), and Patalas (1986) traced the changing descriptions and taxonomy of *Mesocyclops edax*. These changes are a story of advances in understanding the taxonomy of the genus *Mesocyclops* and the morphologically similar genus *Thermocyclops* (see also comments by Dahms & Fernando 1995a, 1995b). In spite of much previous discussion, three points remain to be resolved.

The synonymy of Mesocyclops nicaraguensis *Herbst, 1960.*—The question of the possible synonymy of *M. nicaraguensis* Herbst, 1960, which was described from Lake Nicaragua, was first raised by Cole (1976). Yeatman, who determined Cole's Nicaraguan copepods, affirmed Cole's opinion (H. C. Yeatman, in litt. to JWR, 1991). Reid (1990) also proposed the synonymy. Absent formal examination, however, *M. nicaraguensis* has continued to be treated as a distinct taxon (e.g., Cisneros & Mangas 1991, Collado, 1984, Dussart & Fernando 1986). The type specimens of *M. nicaraguensis* cannot be located (H.-V. Herbst, in litt. to JWR, 1991), and there is no non-type material from the original collection

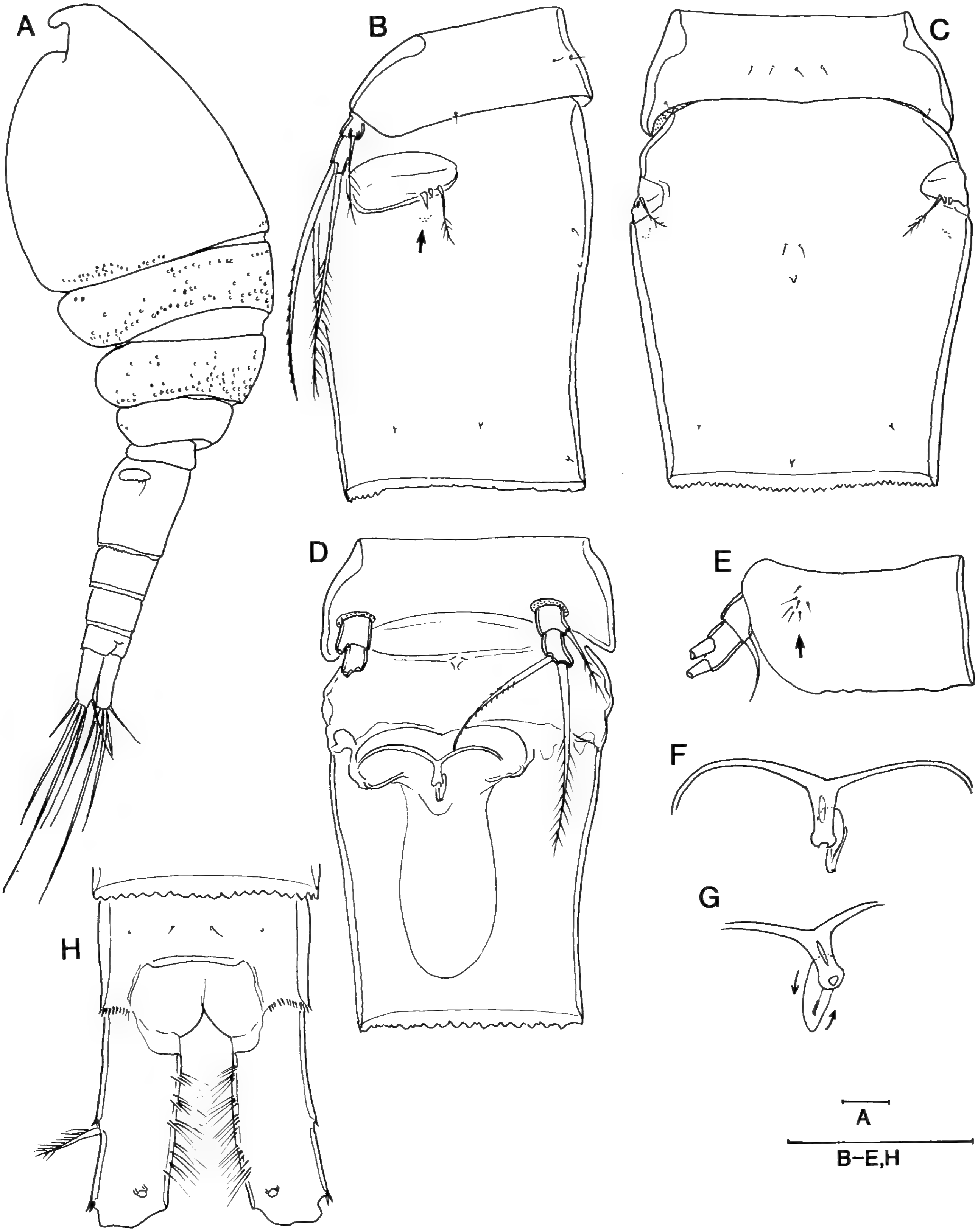

Fig. 1. *Mesocyclops edax,* female. A–C, F–H, specimens from North Carolina, U.S.A. (USNM 216873); D, Louisiana, U.S.A. (Marten Collection); E, Lake Nicaragua (USNM 259614). A, Habitus, lateral; B, Pediger 5 and genital double somite, left lateral; C, Pediger 5 and genital double somite, dorsal; D, Pediger 5 and genital double somite, ventral (leg 5 setae foreshortened); E, Pediger 5, left lateral; F, Copulatory pore and pore-canal, ventral, enlarged; G, Copulatory pore and pore-canal, ventral-oblique, enlarged; H, Anal somite and caudal rami, dorsal. Scales equal 100 μm.

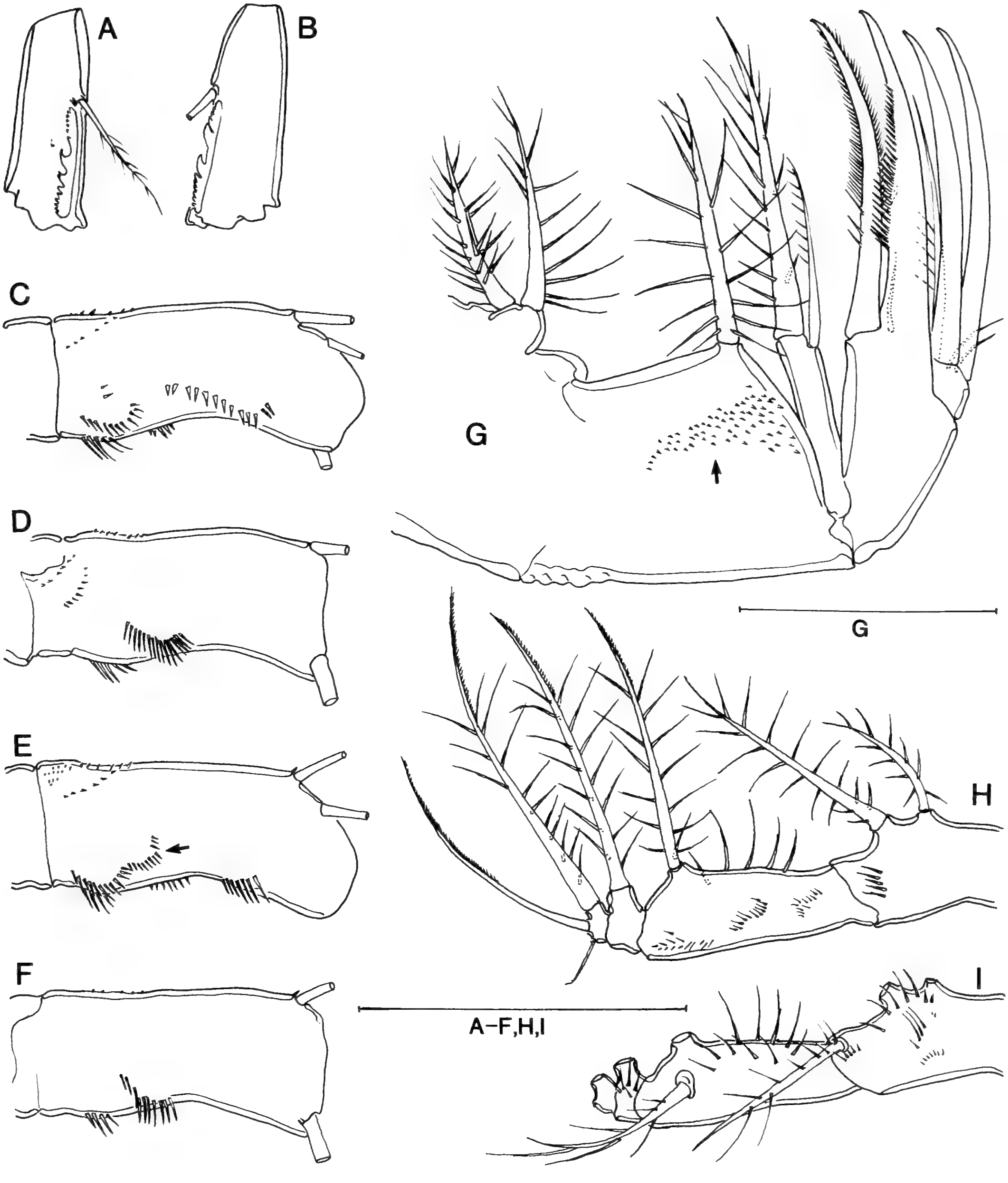

Fig. 2. *Mesocyclops edax,* female. A, C, D, G–I, specimens from North Carolina (USNM 216873); B, E, F, Specimen from Cuba (Fernando Collection). A, B, Antennule terminal segment; C, E, Antenna basis, caudal side; D, F, Antenna basis, frontal side; G, Maxilla, frontal side; H, I, Maxilliped. Scales equal 100 μm.

(G. Hartmann, in litt. to JWR, 1991). No material remains from Cole's (1976) study of Lake Nicaragua (H. C. Yeatman, in litt. to JWR, 1991).

There are a few differences between published descriptions of *M. edax* and *M. nicaraguensis.* The most obvious is the lengths of adult females, 0.83–1.1 mm for *M. edax* (Dahms & Fernando 1995a, Dussart 1985) and about 1.45 mm for *M. nicaraguensis* (Herbst 1960). This difference in lengths was the only discriminator used by Dussart (1987) and Petkovski (1986) in their keys to American *Mesocyclops.* How-

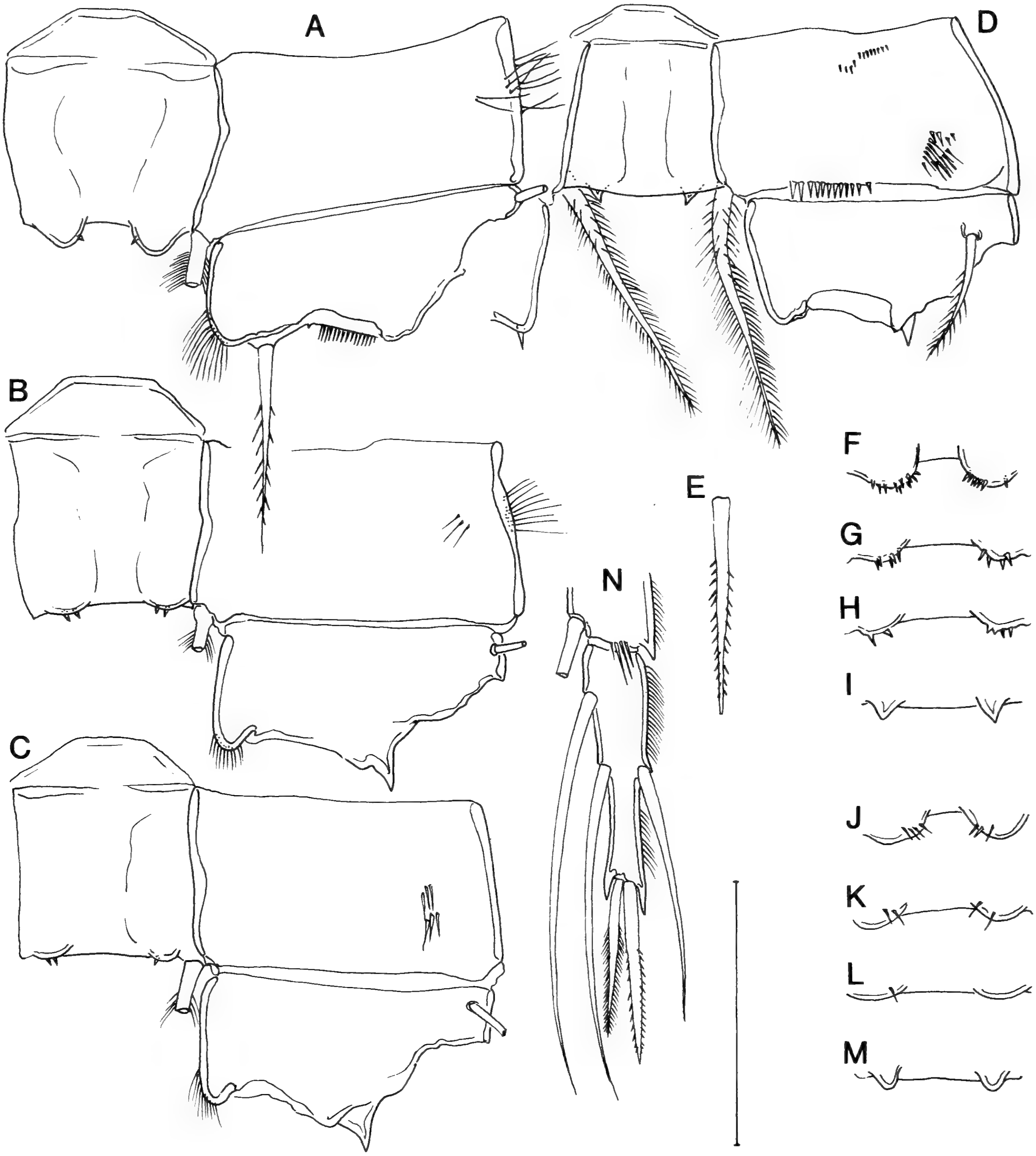

Fig. 3. *Mesocyclops edax,* female. A–D, N, specimens from North Carolina (USNM 216873); E–I, Cuba (Fernando Collection); J-M, Guatemala (USNM 250931). Scale equals 100 μm.

ever, we report populations of *M. edax* from Ontario, Nova Scotia, and Louisiana with individuals longer than 1.45 mm. Lengths of females from lakes in Nicaragua varied from 0.96 to 1.45 mm. There is then no meaningful difference in the lengths of northern and southern populations, nor is there any correlation between length and latitude.

The remaining apparent difference consists of the presence of submarginal spines on the leg 1 coupler in *M. edax,* while Herbst (1960: fig. 37) indicated no ornament on the leg 1 coupler in *M. nicaraguensis.* However, all specimens from Lake Nicaragua examined by us had such spines. A single female from Nicaragua bore small spines on the lateral surface of pediger 5

(Fig. 1E). The presence or absence of spines at this location is a much used character in the genus systematics. However, the facts that this condition is apparently extremely rare and found only in one Nicaraguan population, and that all females from Nicaragua were otherwise congruent in all respects with the diagnosis of *M. edax,* persuaded us to consider *M. nicaraguensis* synonymous with the former taxon.

Habitat as well as genetic factors may account for some variation. Barwick & Hudson (1985) reported that individuals of *M. edax* in the tailwater of a reservoir were small and the posterior edges of the urosomes were sculptured, in contrast to a "reservoir form" that averaged larger and had smooth urosomal edges. Specimens were, however, unavailable (P. L. Hudson, in litt. to JWR, 1998). Wyngaard et al. (1985) noted differences in body size, clutch size, and egg size among wild populations from Michigan and Florida.

The taxon Cyclops tenuissimus *(Herrick, 1883).*—Cole (1960) suggested that *Cyclops tenuissimus,* described by Herrick (1883) from Kentucky, U.S.A., is a senior synonym of *M. edax.* Cole pointed out that the combination of several characters, the relationships of the lengths of the leg 5 terminal seta and subterminal spine, the antennular hyaline membrane with several small notches, and the caudal rami hairs possessed by *C. tenuissimus* matches only *M. edax* among North American cyclopoids. However, Herrick showed the genital segment of *C. tenuissimus* as very slender and the seminal receptacle with narrow lateral and posterior extensions, and in his text described (and named) this species as "the most slender cyclops known to me". Cole's argument might easily be accepted if not for the contradictions between Herrick's description and the relative robustness of *M. edax* and the broad lateral and posterior expansions of its seminal receptacle. Since Herrick's description matches no presently known American cyclopoid species in all respects, in our opinion the identity of Herrick's specimens remains in question.

The western and southern distribution of M. edax.—The published records from Pacific drainage basins in the U.S.A. and Canada are few and relatively recent. Several were confirmed by material made available for this report, and we consider all of them entirely reliable. Simenstad & Cordell (1985) listed *M. edax* from the Columbia River basin in Washington State. The previously unpublished record herein from Lake Union, Washington, also comes from the Columbia River basin. The few records from the Colorado River basin include those of Soto & Hurlbert (1991a, 1991b) from California, and of Maddux et al. (1987) and Sollberger & Paulson (1992) from the Colorado River in Arizona and Nevada. The records reported herein from San Diego and Fresno, California are new. In western Canada, *M. edax* was recently reported from British Columbia (Chengalath & Shih 1994, Shih & Chengalath 1994).

Only recent reports of *M. edax* from Mexico, Central America, and the Antilles are reliable. As noted by Cole (1960), prior to and even following the revision of Coker (1943) which established the distinction between *M. edax* and populations in the Americas referred to as *M. leuckarti, M. edax* was likely to be reported as *M. leuckarti* (e.g., Comita 1950). In the Americas, records of *M. leuckarti* may refer to other members of the *leuckarti*-group, such as *M. americanus* Dussart, 1985, *M. aspericornis* (Daday, 1906), or *M. ruttneri* Kiefer, 1981, or even to any of several species of *Thermocyclops* now known to be present in the region (Dussart 1985, Dussart & Fernando 1990, Reid 1993, Reid & Reed 1994). Cole (1960) pointed out inconsistencies in Marsh's (1910) description of *M. leuckarti* which apparently led Marsh to synonymize *M. edax* with the former species. Examples of Marsh's confusion can be found among the slide-mounted specimens labeled "*M. leuckarti*" in the Marsh Collection at the

National Museum of Natural History. Among these specimens one of us (JWR) has identified *M. longisetus* (Thiébaud, 1912), *M. reidae* Petkovski, 1986, *M. venezolanus* Dussart, 1987, and *Thermocyclops decipiens* Kiefer, 1929b, but neither *M. leuckarti* nor *M. edax*. The extensive Marsh Collection contains no unequivocal specimen of *M. edax* from any locality south of Texas. Pearse's (1921) record of *M. leuckarti* var. *edax* from Lake Valencia, Venezuela, may refer to *M. brasilianus* Kiefer, 1933, as suggested by Infante et al. (1979), or to some other congener with haired caudal rami, such as *M. aspericornis* which also occurs in Lake Valencia (Reid & Saunders 1986). Pearse's (1915) record of *M. leuckarti* var. *edax* from Colombia is similarly suspect.

Additional problems are the sparsity of general collections of plankton from Central America and the Antilles, and the presence of *M. edax* and *M. leuckarti,* but not other congeners, in the widely used key of Yeatman (1959). Before publication of the keys to American *Mesocyclops* by Petkovski (1986) and Dussart (1987) and a local checklist by Reid (1990), any of the many congeners in the region was likely to be identified as one of those two species. Similar doubts as to the validity of Central American records were implied in the summary by Collado, Fernando, & Sephton (1984) of the distribution of zooplankters from this area, since those authors included no records of *M. edax* other than those from Cuba by Smith & Fernando (1978, 1980).

Smith & Fernando's record from Cuba is the only report of *M. edax* from the Antilles, and is supported by preserved material.

Most of the few Mexican and Central American records of *M. edax* can be likewise verified. Coker (1943) and Osorio-Tafall (1944) reported *M. edax* from Lake Pátzcuaro, Mexico. Copepodids of *Mesocyclops,* including one stage V copepodid referable to *M. edax* from Lake Pátzcuaro examined for this report substantiate their records. *Mesocyclops edax* was reported from the Yucatán Peninsula (and specimens archived) by Suárez-Morales et al. (1996). The reports by Brinson & Nordlie (1975) and Deevey et al. (1980) from eight or more lakes including Lake Izabál in the Guatemalan lake district were substantiated by the specimens furnished by H. C. Yeatman.

The scarcity of reports of *M. edax* south of the U.S.A. may correctly reflect its distribution. General collections, mainly from shallow waterbodies in Costa Rica (Collado & Fernando 1984) and Honduras (Marten et al. 1994) failed to record this species. The presence of *M. edax* in several large Central American lakes and its apparent absence from smaller waterbodies might imply some direct temperature effect. On the other hand, it was collected from Laguna Sabanilla near Havana, Cuba, which is shallow (maximum depth 1.3 m) and near sea level (Straskraba et al. 1969). Some of the Guatemalan lakes are also shallow, such as Petenxil (4 m maximum; Deevey et al. 1980). Better adapted neotropical cyclopoids may outcompete *M. edax* in most conditions. One candidate might be *Thermocyclops decipiens,* which is a pantropical facultatively omnivorous plankter that is frequently successful in the mesotrophic to eutrophic conditions in which *M. edax* also thrives (Reid 1989). It is usual for *M. edax* and the much smaller *Thermocyclops inversus* Kiefer, 1936 to co-occur (Coker 1943, Cole 1976, Deevey et al. 1980, Osorio-Tafall 1944, and our samples from Nicaragua). In Guatemala, *T. decipiens* (reported by Deevey et al. [1980] as *Mesocyclops hyalinus* [Rehberg, 1880], a synonym) occurred with *M. edax* in only one lake. *Thermocyclops decipiens* was also numerous in the sample from Laguna Sabanilla examined for this report. *Thermocyclops decipiens* ranges from 0.75–0.99 mm in length, thus approaching the length of *M. edax*. It is common in the Antilles including Cuba and in Central America (Reid 1985, 1989), but does not extend northwards past southern Mexico (Suárez-Morales & Reid 1998).

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A new species of *Orbiniella* (Orbiniidae: Polychaeta) from Marion Island, Indian Ocean

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Abstract.—After the Marion Dufresnes MD/03 Expedition in 1974, a new expedition Marion Dufresnes MD/08 was undertaken to study benthic invertebrates from the South West Indian Ocean. *Orbiniella marionensis,* a new species of Orbiniidae, Polychaeta from Marion Island, Indian Ocean is described. This species was collected during the Marion Dufresnes BENTHOS Expedition around subantarctic Islands. *Orbiniella marionensis* is compared with other species of the genus Orbiniella Day, 1954 and differs in having only one preanal segment and by the absence of modified setae in the posterior region.

Materials and Methods

Polychaetes collected during the Marion Dufresnes BENTHOS Expedition from Marion and Prince Edward Islands were described by Gillet (1991). A description of the sampling site of the MD/08 BENTHOS Expedition is provided by Arnaud & Hureau (1979). Different sampling methods were used: Charcot dredge, Okean grab, Lithods nets and Trawl. Specimens were conserved in 70% ethanol and observed by light microscopy with an Olympus CHT2 and by scanning electron microscopy with an Olympus JSM 5200.

Material has been deposited at the Institut de Recherche Fondamentale et Appliquée, Angers-France and a duplicate collection in the Museum National d'Histoire Naturelle de Paris, France and in the South African Museum, Cape Town, South Africa.

Family Orbiniidae Hartman, 1942

The name Orbiniidae was used by Hartman (1942) in place of Ariciidae with the type genus *Orbinia,* Quatrefages, 1865.

The orbiniids have been studied by Hartman (1957), Pettibone (1957) and more recently reviewed by Day (1973). The orbiniids have lateral parapodia in the thoracic region and dorsal parapodia in the abdominal region. The prostomium is without appendages and is followed usually by one or two asetigerous segments. The setae are simple capillaries and simple hooks, sometimes with furcate or crenulate setae. Hartman (1957) divided the family in two subfamilies: Orbiniinae, including the larger orbiniids with one achaetous segment behind the prostomium and, Protoariciniinae with two achaetous segments behind the prostomium. The Protoariciniinae was revised by Solis-Weiss & Fauchald (1989).

Genus *Orbiniella* Day, 1954

Type species.—*Orbiniella minuta* Day, 1954: 22–23, fig. 3 g–k.

Prostomium round. First two segments without setae. Setigerous segments without gills or appendages. Setae include crenulate capillaries and simple acicular. In Fauchald (1977) the genus *Orbiniella* lacks branchiae. Buzhinskaja (1992) suggested that *Falklandiella annulata* Hartman (1967) be transferred to *Orbiniella.* Buzhinskaja (1992) suggested that *Orbiniella branchiata* be referred elsewhere. Blake (1996) suggests that some species of *Orbiniella* might be juveniles of other orbiniids such as *Naineris.* In the natural world, 10 species of *Orbiniella* are known.

Orbiniella marionensis new species

Figs. 1A–D, 2A–D; Table I

Material examined.—Holotype: Marion Island 26.03.1976; station 18 (BB 108) 46°49.8′S, 37°56.2′E, complete, 29 setigers, 7 mm long, 1.3 mm wide with parapodia and 1.0 mm wide without parapodia. Paratypes: Marion Island station 12 (BB 79), 46°55.7′S, 37°54.1′E, 6 exemplars; station 15 (BB 88), 46°57.7′S, 37°59.9′E, 1 exemplar; station 18 (BB 108) 46°49.8′S, 37°56.2′E, 12 exemplars; station 34 (BB 168), 46°50.2′S, 37°51.2′E, 4 exemplars Material deposited IRFA Angers IRFA-ORB.015.

Description.—Holotype colorless in ethanol, with one preanal achaetous segment. The prostomium is rounded, 0.2 mm long and 0.4 mm wide, large and eyeless. The second and third segments are achaetous and without parapodium (Figs. 1A, 2A, B). The following segments are setigerous, without gills and ventral cirri and with dorsal cirri (Figs. 1D, 2D). Setae include crenulate capillaries (Fig. 1B) and from the first setiger 2 to 4 simple acicular spines (Fig. 1C). The pygidium is round with one preanal segment (Fig. 2C).

The paratype material generally ressembles the holotype closely. The number of setigers varies between 14 (4 mm long) and 29 (7 mm long) and width varies from 1.3 mm with parapodia to 1.0 mm without parapodia.

Discussion.—*Orbiniella marionensis* differs from *Orbiniella minuta* Day, 1954, described from Tristan da Cunha (Day 1954) and from Marion and Prince Edward Islands (Day 1971) by the presence of dorsal cirri (Table I). *Orbiniella marionensis* has two to four acicular setae from the first setiger. It differs by the absence of modified crenulate setae in the posterior region and by having only one preanal achaetous segment. *Orbiniella uniformis* Hartman, 1967 lacks dorsal cirri and has only one falcate acicular spine from setiger 15. *Orbiniella drakei* Hartman, 1967 has ventral and dorsal cirri and a modified posterior region with very long segments. *Orbiniella marionensis* also differs from *O. dayi* Branch, 1998 which has no preanal segments and cirri are absent. For the same reasons, it differs from *O. hobsonae* Blake & Hilbig, 1990. These two species differ by the kind of setae, simple acicular and crenulate capillaries in *O. dayi* but barbed acicular and bristled capillaries in *O. hobsonae. Orbiniella aciculata* Blake, 1985 has an unsegmented posterior region. *O. annulata* Hartman (1967) *O. nuda* Hobson, 1974 and *O. plumisetosa* Buzhinskaja, 1992 have eyes in the anterior region and have different setae: *O. plumisetosa* has plumose cirrate setae, *O. nuda* has spinous capillaries and *O. annulata* has crenulate capillaries.

Habitat.—Infralittoral from 95 to 210 meters depth on sand, clay-sand or mud.

Subantarctic distribution.—Marion Islands.

Etymology.—The specific name *marionensis* refers to Marion Islands and is a Latin adjective.

Key to the genera *Orbiniella* Day, 1954

1. Eyes present 2
   Eyes absent 4
2. Body colored, plumate cirrate setae present .... *O. plumisetosa*
   Body without pigment, plumate cirrate setae absent 3
3. Acicular setae present from setiger 1 .. .. *O. nuda*
   Acicular setae appearing from setiger 12–15 .... *O. annulata*
4. Dorsal or ventral cirri present 5
   Dorsal or ventral cirri absent 6
5. Both dorsal and ventral cirri present. Two preanal segments one acicular seta .... *O. drakei*
   Only dorsal cirri present, one preanal

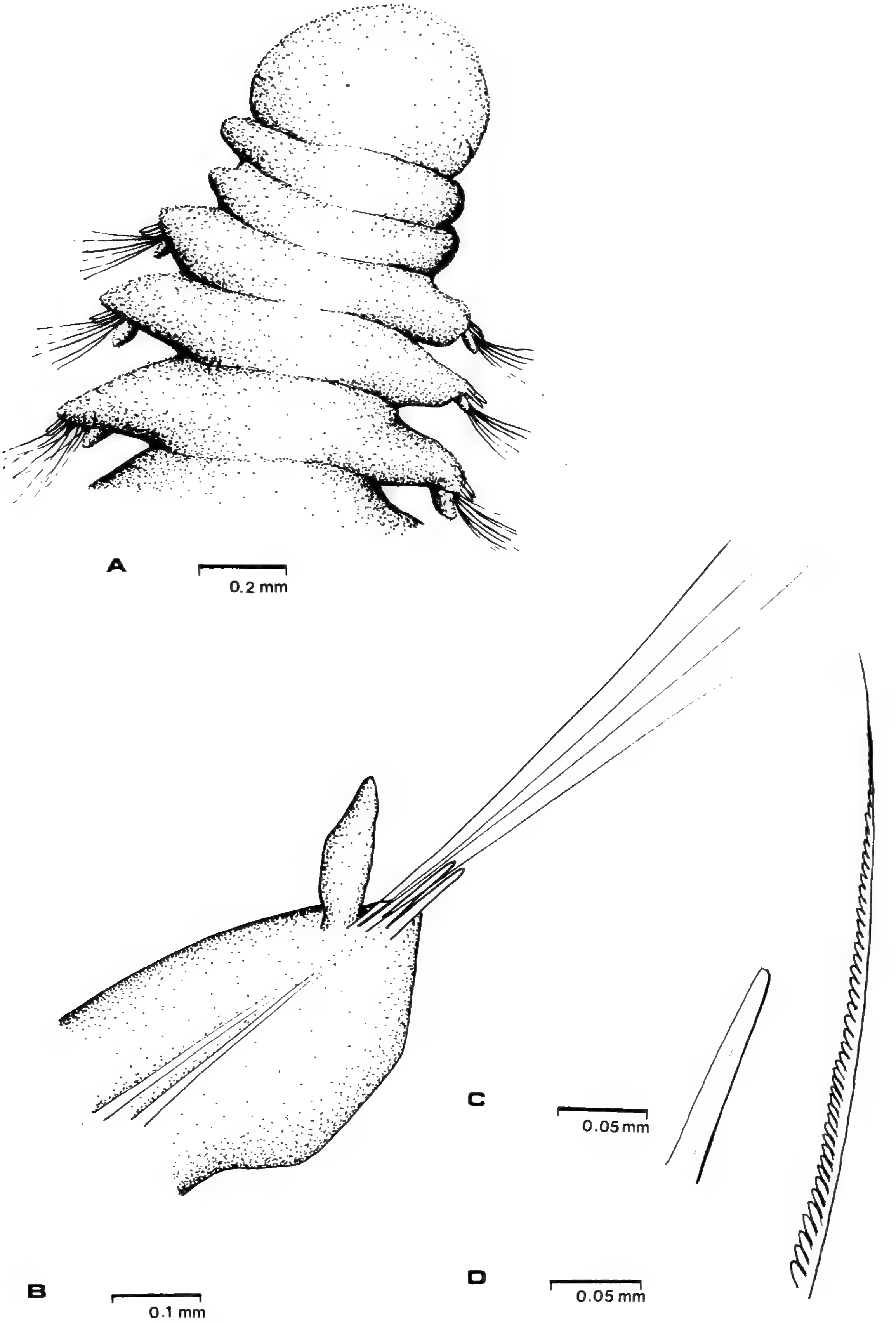

Fig. 1. *Orbiniella marionensis,* n. sp. (Holotype, I.R.F.A. ORB.015) A: Anterior region; B: Crenulate seta; C: Acicular seta; D: Parapodium.

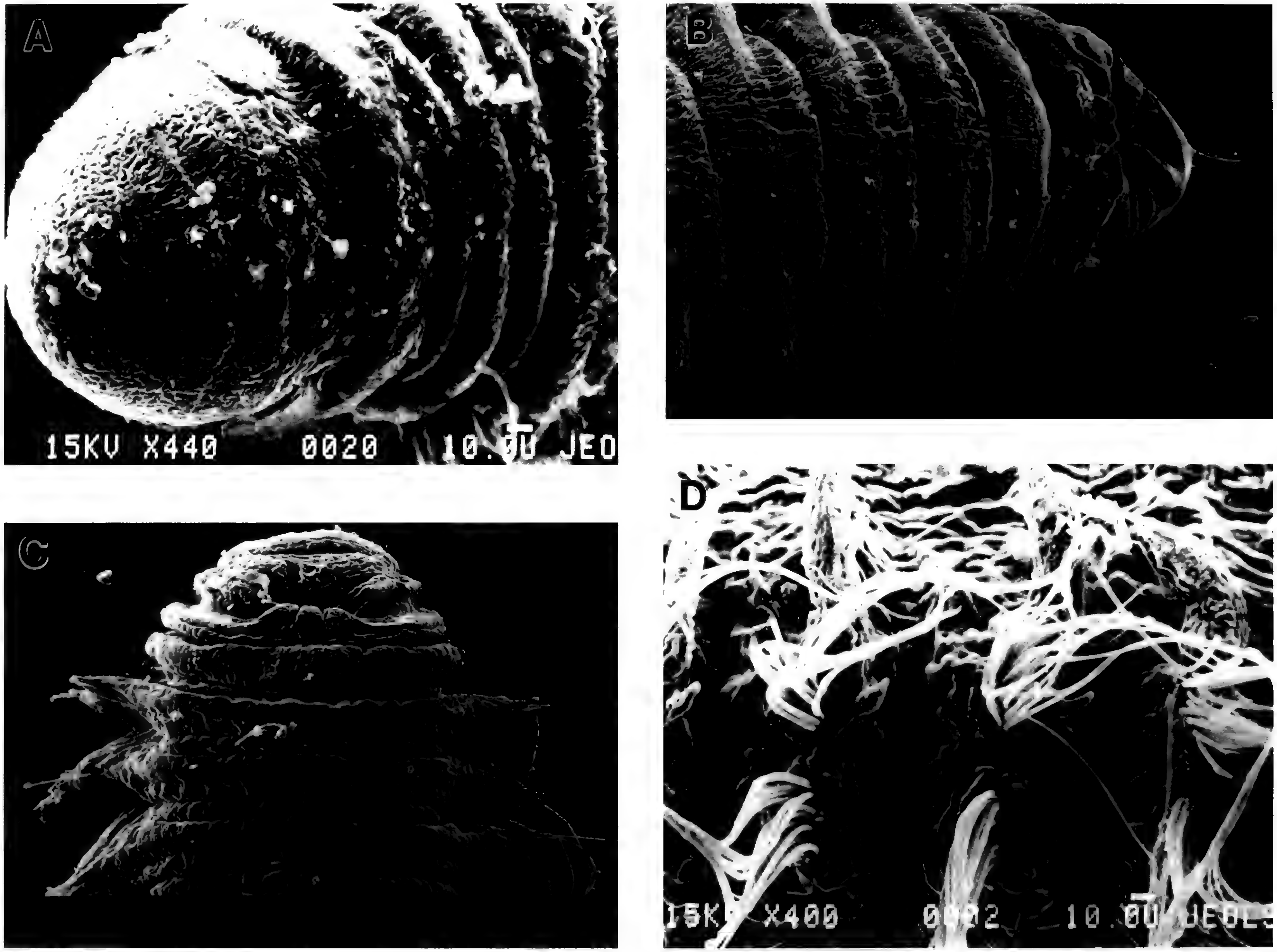

Fig. 2. Scanning Electron Microscopy photographs of *Orbiniella marionensis*, n. sp. A: Anterior region dorsal view; B: Anterior region ventral view; C: Posterior region; D: Parapodium.

Table 1.—A comparison of some important characteristics in existing species of the genus *Orbiniella* Day, 1954.

Species	Type locality depth	Number of preanal segments	Eyes	Cirri	Kinds of setae
O. aciculata Blake, 1985	Galapagos Rift 2727–2730 m	unsegmented	absent	absent	smooth acicular spines long capillaries
O. annulata Hartman, 1967	Falkland Islands 646–845 m	0	present	absent	2–3 acicular setae crenulated capillaries
O. dayi Branch, 1998	Marion Island 5–15 m	0	absent	absent	acicular simple crenulate capillaries
O. drakei Hartman, 1967	Antarctic 3312–3532 m	2	absent	ventral dorsal	1 acicular setae capillaries
O. hobsonae Blake and Hilbig, 1990	Juan de Fuca Ridge	0	absent	absent	1–2 barbed acicular 2–5 bristled capillaries
O. marionensis	Marion Island 95–204 m	1	absent	dorsal only	2–4 acicular capillaries
O. minuta Day, 1954	Tristan da Cunha Prince Edward Island 0–10 m	2	absent	absent	2 acicular setae crenulate capillaries
O. nuda Hobson, 1974	North American Pacific Ocean 0.6–2.4 m	–	present	absent	2–4 acicular setae 3–6 spinous capillaries
O. plumisetosa Buzhinskaja, 1992	Commander and Kurile Islands Littoral zone	0	present	absent	2–4 non plumose setae 1–7 plumose cirrate setae
O. uniformis Hartman, 1967	Antarctic 4 fms	2	absent	absent	1 acicular capillaries

segment, two-four acicular setae .... *O. marionensis*

6. Preanal segments present 7
   Preanal segments absent 9
7. Two preanal segments 8
   Preanal segment unsegmented .... *O. aciculata*
8. Crenulate setae present, two acicular setae .... *O. minuta*
   Crenulate setae absent, only one acicular seta .... *O. uniformis*
9. Acicular simple, crenulate capillaries .. .. *O. dayi*
   Acicular barbed, bristled capillaries .... *O. hobsonae*

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Redescriptions of *Grania americana, G. bermudensis* and descriptions of two new species of *Grania* (Annelida: Clitellata: Enchytraeidae) from Bermuda

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Abstract.—The diversity of the enchytraeid genus *Grania* is reexamined in Bermuda. Herein, four species, *G. bermudensis* Erséus & Lasserre, 1976, *G. americana* Kennedy, 1966, *G. laxartus,* new species, and *G. hylae,* new species, are described from intertidal and subtidal sand habitats of Bermuda. *Grania americana* and *G. laxartus* are also reported from the Caribbean area and *G. hylae* from Florida. *Grania bermudensis* is recognized as a separate species rather than as a subspecies of *G. macrochaeta* (Pierantoni, 1901). *Grania americana* and *G. laxartus* have distinctive spermathecal structures and the latter has a penial stylet. *Grania bermudensis* and *G. hylae* can be easily separated from their Bermudian congeners by the dorsal position of spermathecal pores. Both *G. americana* and *G. hylae* have statocyst-like sensory structures associated with their brains. These studies provide new information diversity, distribution and taxonomy of *Grania* species of the North Atlantic and on the structural diversity of male duct systems and of statocyst-like sensory structures.

The taxonomic diversity of the abundant and widespread marine oligochaete genus *Grania* Southern, 1913 (Annelida: Clitellata: Enchytraeidae) in Bermuda has been poorly investigated, as have most genera of the marine Enchytraeidae (Healy & Coates 1999). Only one species, *Grania bermudensis* Erséus & Lasserre, 1976, has been described from Bermuda and it was recognized as a subspecies of *G. macrochaeta* (Pierantoni, 1901) (Erséus & Lasserre 1976, Locke & Coates 1998). However, a great degree of anatomical variability among *Grania* specimens collected from Bermuda has been recognized for some time (Erséus, pers. comm.). Furthermore, there are only four publications referring primarily to the Enchytraeidae of Bermuda (Moore 1902, Lasserre & Erséus 1976, Giere 1979, Healy & Coates 1999) and the most recent of these shows the species diversity of this family is much higher than previous studies indicated.

The single species of *Grania* described from Bermuda was reported prior to the recognition of a variety of important taxonomic characters for this genus. Coates (1984) provided new criteria for categorizing forms of the male duct system found in the genus. These characteristics have played a significant role in the distinction of several new species (e.g., Coates & Erséus 1985, Erséus 1990a, Coates & Stacey 1993). Recently, another interesting structural character was revealed by Rota & Erséus (1996). In a few new species from the Antarctic and Subantarctic, a structure was observed which they called the head organ (Rota & Erséus 1996, 1997). It was described as a vesicular body with refractile inclusions, located within the peristomium just anterior to the brain. Such advances in recognition of morphological characters have resulted in increased knowledge of specific diversity and provide additional clues that can be applied to discovering evolutionary relationships among species of *Grania* (Locke 1999a).

Observations of type specimens of *G. bermudensis* revealed undescribed, diagnostic characteristics of the spermathecae of this species. These observations, combined with additional information about the form of the male ducts (Coates 1984), suggested that *G. bermudensis* was in need of redescription.

A major marine faunal element in Bermuda is species with Caribbean and coastal southern U.S. distributions (Fig. 1) (Sterrer 1986, 1998). *Grania americana* is the only described species of *Grania* with such a distribution. This species was first reported from the shores of Florida and Bimini (Kennedy 1966) and there have been no subsequent records. In the most recent taxonomic discussion of this species, Erséus & Lasserre (1976) stated that *G. americana* must be considered a nomen dubium due to the poor condition of the type material and lack of detail in the original description. They also suggested it probably was very similar to *G. bermudensis,* implying that *G. americana* might also be a subspecies of *G. macrochaeta.* In fact, Lasserre (1967) had designated *G. americana* as a subspecies of *G. macrochaeta* along with many other species of *Grania.* The basis for this designation, as discussed by Locke & Coates (1998, also see Locke 1999a), was probably largely historical and possibly eurocentric. Oligochaetes have long been considered a lineage that originated and diversified in non-marine habitats and, thus, a low species diversity in marine systems was expected. In contrast to the early opinion of Lasserre (1967), Erséus (1974) had noted *G. americana* and *G. macrochaeta* were probably separate species based on definite and consistent morphological differences, but that additional information about intraspecific variation of each taxon was needed.

New taxonomic characteristics and complete redescriptions are presented to substantiate the morphological differences among *G. americana, G. bermudensis* and *G. macrochaeta* sensu stricto. Redescriptions of the first two taxa and a survey of *Grania* species in Bermuda were undertaken in order to advance understanding of the diversity, zoogeography and evolution of marine oligochaetes.

Materials and Methods

Sediments were collected from three intertidal sites and nine subtidal sites within Bermuda. Intertidal sites were Ferry Point Bridge, Whalebone Bay and Rocky Hill Park, where samples were taken from an accumulation of sand inside dissolution tubes in limestone rock and from two rocky limestone beach areas, respectively. Subtidal sites were from Castle Harbour: Eastern Castle Roads, Rushy Island, and a patch reef 100 m from Rushy Island; St. George's Harbour: ENE and SE Paget Island; Ferry Reach; NW Pearl Island in Great Sound; NE entrance of Smith's Sound; and Bailey's Bay. Other specimens were provided by C. Erséus, from Hutchinson Island, Florida; Fowey Rocks, Miami, Florida; North of Angelfish Key, Florida Keys; and Carrie Bow Cay, Belize (Table 1).

Specimens collected by the authors in Bermuda were obtained by washing samples on a 300 μm sieve and then sorting the residue in seawater using a dissecting microscope. Specimens were fixed in Kahle's fluid, stained lightly with borax carmine, dehydrated and cleared, and mounted in Canada balsam for morphological observations. Only mature specimens were identified. Specimens of all *Grania* species found in Bermuda were also observed while alive.

Type specimens of *G. americana* (USNM 33005) and *G. bermudensis* (USNM 53202), Castle Island, were borrowed from the United States National Museum of Natural History (USNM) (Smithsonian Institution), Washington, D.C., and

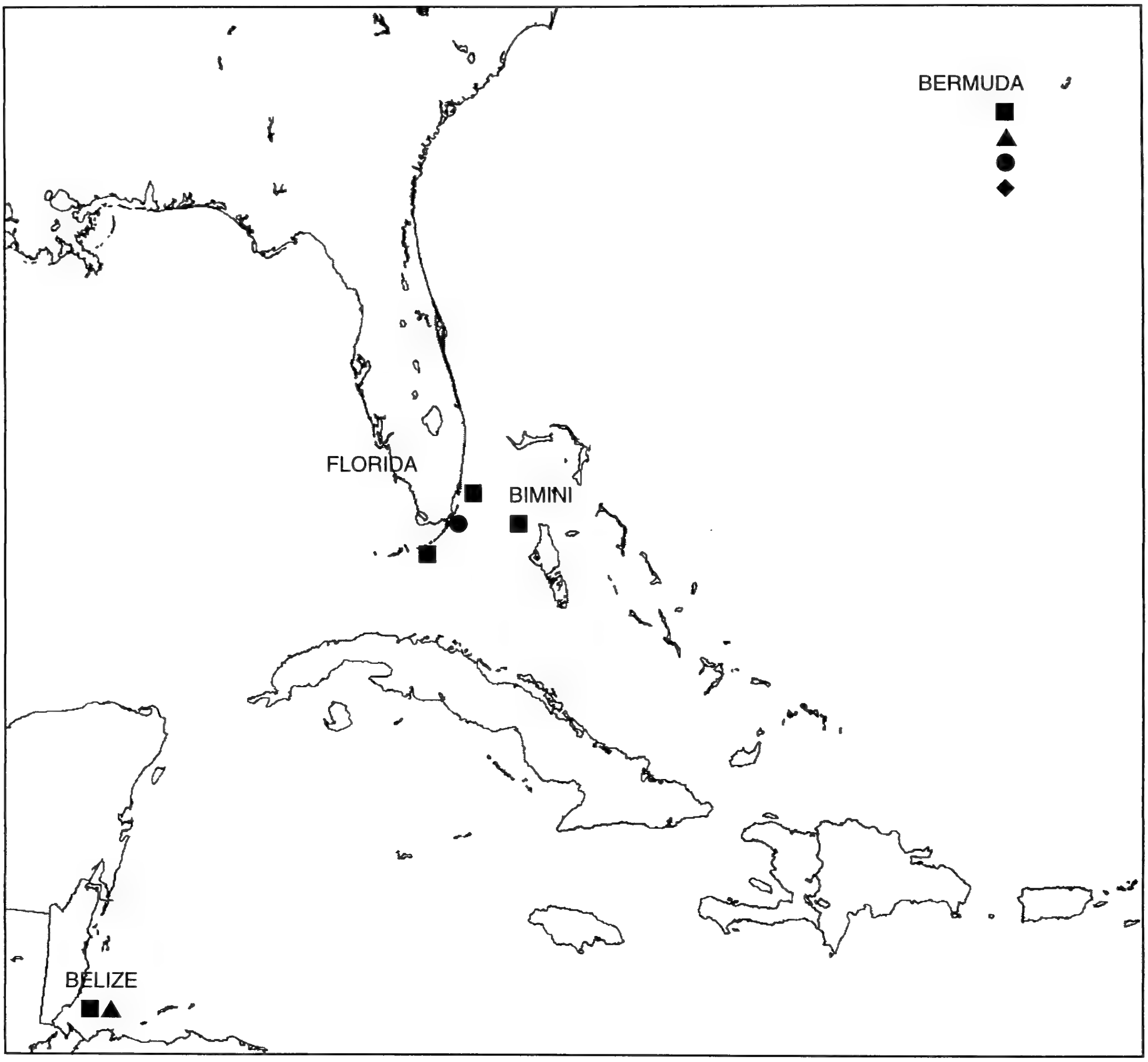

Fig. 1. Distribution of *Grania* species found in Bermuda in coastal North American, Bermudian and Caribbean waters. ■ *G. americana,* ▲ *G. laxartus,* ● *G. hylae,* ◆ *G. bermudensis.*

examined for identification of and comparison with the new specimens. Whole mounted specimens of *Grania monospermatheca* Erséus & Lasserre, 1976, *G. americana, G. bermudensis,* and *Grania atlantica* Coates & Erséus, 1985, and the new species described herein were also examined from the collections of the authors (KAC) and C. Erséus.

Observations of specimens were made using differential interference contrast light microscopy and videomicroscopy. Thirty-five mm photography was done with a Wild MPS46 photoautomat on Kodak Technical Pan film ASA 100. Drawings were made with the aid of a drawing tube. An Olympus AX70 Provis microscope and Toshiba 3CCD camera with Image-Pro Plus™ software were utilized for video microscope image capture analysis and morphological measurements. Measurements were also taken with the use of Jandel Video Analysis Software (JAVA) and with the aid of an ocular micrometer. The mean ($\bar{X}$) and standard deviation (*SD*) were calculated for morphometric data.

Measurements for *G. americana* and one new species were made from Bermuda and Carrie Bow Cay whole mounted specimens; for the other new species and *G. bermu-*

Table 1.—Site location and substrate description. For more complete Carrie Bow Cay data, refer to Erséus (1990b).

Site	Date	Position	Depth	Description	Species
Bermuda					
Whalebone Bay	Dec 1977	32°21′90″N 64°42′75″W	intertidal	fine to coarse	*G. laxartus, G. americana*
Ferry Point Bridge	1996–1998	32°21′70″N 64°42′80″W	intertidal	dissolution tubes	*G. laxartus, G. americana*
Rocky Hill Park	Oct 1998	32°22′60″N 64°41′40″W	intertidal	coarse with rocks	*G. hylae, G. americana*
Pearl Island	Aug 1977	32°17′50″N 64°50′19″W	2.5 m	fine	*G. laxartus, G. americana*
Ferry Reach 1	Nov 1977	32°22′05″N 64°41′44″W	0.2 m	medium to coarse	*G. laxartus, G. americana*
Ferry Reach 2	Dec 1977	32°22′05″N 64°41′44″W	0.5 m	medium to coarse	*G. laxartus*
NW Smith's Snd	Dec 1977	32°22′14″N 64°39′21″W	4 m	fine with seagrass	*G. laxartus*
Castle Island	Aug 1977	32°20′40″N 64°40′25″W	15 m	medium to coarse	*G. hylae, G. bermudensis*
Bailey's bay	Aug 1977	32°20′94″N 64°43′30″W	6.5 m	fine to medium	*G. hylae, G. americana*
ENE Paget Island	Dec 1977	32°22′38″N 64°38′57″W	17 m	medium to coarse	*G. hylae*
SE Paget Island	Dec 1977 & Mar 1998	32°22′35″N 64°39′30″W	8 m, 15 m	medium to coarse	*G. hylae, G. bermudensis*
E Castle Roads	Aug 1977	32°20′30″N 64°40′20″W	8 m	coarse	*G. bermudensis*
Rushy Island	Aug 1977	32°20′18″N 64°40′45″W	8–9 m	coarse	*G. bermudensis*
Patch Reef	Aug 1977	32°20′19″N 64″40′26″W	8–9 m	coarse	*G. bermudensis*
Florida					
Fowey Rocks	Nov 1977	25°35.5′N 80°05.8′W	3 m	coarse	*G. hylae*
N. Angelfish Key	Nov 1977	25°10′N 80°13′02″W	6 m	*Thalassia,* fine	*G. americana*
Hutchinson Island	Nov 1972/May 1973	27°20′24″N 80°13′04″W	10 m	shell rubble	*G. americana*
Carrie Bow Cay, Belize		all stations all stations			
cbc-85-2	Nov 1985	16°48′N 88°05′W	1.5 m	medium to coarse	*G. laxartus, G. americana*
cbc-85-2-14	Nov 1985		0.5 m	medium to coarse	*G. americana*
cbc-85-15	Nov 1985		0.2 m	*Thalassia,* rubble	*G. americana*
cbc-85-26	Nov 1985		1 m	muddy	*G. laxartus*
cbc-85-36	Nov 1985		0.2 m	grey, coarse	*G. americana*
cbc-85-41	Nov 1985		1 m	medium to coarse	*G. laxartus*
cbc-85-57	Nov 1985		1 m	medium to coarse	*G. americana*
cbc-85-65	Nov 1985		0.1 m	*Thalassia,* coarse	*G. laxartus*
cbc-85-68	Nov 1985		0.3 m	coarse, rubble	*G. americana*

densis, measurements were taken from whole mounts of Bermuda specimens. Terminology for the head organ was adapted from Rota and Erséus (1996, 1997) and for penial bulb types from Coates (1984). Observations of the "head organ" indicate that a more appropriate name for this structure would be the anterior brain vesicle.

Grania Southern, 1913

For a recent synonymy of the genus refer to Locke & Coates 1998.

Grania laxartus new species
Figs. 2–6; Table 1

Holotype.—USNM 185951, stained, whole mounted specimen, collected Feb. 1996 by KAC.

Type locality.—Ferry Point Bridge, Bermuda. 32°21′70″N, 64°42′80″W. Intertidal coarse biogenic sands within dissolution tubes.

Paratypes.—Three whole mounted specimens, USNM 185952 Ferry Reach, Bermuda, BBS-77-38, C. Erséus 1977; USNM 185953 Carrie Bow Cay, Belize, CBC 85-41, C. Erséus 1985; and Bermuda Aquarium, Museum and Zoo, BAMZ 1999 180 006 Ferry Reach, Bermuda, BBS-77-41, C. Erséus 1977.

Other material examined.—About 45 live specimens from the type locality collected by the authors over the period 1996–1998. Twenty-six whole mounts from type locality, collected (KAC) February and March, 1996. Fourteen whole mounts collected by C. Erséus from Bermuda. Five whole mounts collected from Carrie Bow Cay, Belize, by C. Erséus (Table 1).

Description.—External characteristics: Live specimens translucent white with a pink tinge due to colored blood within their vessels. Preserved length 4.7–8.3 mm (n = 18, $\bar{X}$ = 6.7, SD = 1.1). Number of segments 33–64 (n = 20, $\bar{X}$ = 50.0, SD = 9.3). Diameter at 4/5 90.0–160.0 µm (n = 29, $\bar{X}$ = 129.4, SD = 15.9), diameter at clitellum 100.0–198.2 µm (n = 26, $\bar{X}$ = 138.0, SD = 18.3) (Fig. 2). Head pore located in anterior region of peristomium. Setae (Figs. 2 & 3) present from IV ventrally and XVI–XVIII laterally; setae absent in XII of mature worms. Ventral setae anterior to the clitellum appear more robust and thicker than postclitellar setae. Setae are pointed distally and somewhat broad at base and with a curve and slight toe at the proximal end but no distinct heel (Fig. 3). Length of anterior ventral setae 38.0–56.0 µm (n = 16, $\bar{X}$ = 48.4, SD = 5.1); midbody ventral setae 34.0–50.0 µm long (n = 28, $\bar{X}$ = 42.0, SD = 4.35); postclitellar lateral setae 38.0–48.0 µm long (n = 18, $\bar{X}$ = 42.4, SD = 2.8). In ten posterior-most segments ventral setae ranged from 37.3–75.5 µm (n = 9, $\bar{X}$ = 45.7, SD = 11.7) and lateral setae from 36.0–45.2 µm in length (n = 11, $\bar{X}$ = 42.5, SD = 3.2). Spermathecal pores paired, lateral, immediately posterior to 4/5. Clitellum extends from mid XI to mid XIII. Male pores ventral, in line with ventral setae of preceding segments, located at about midpoint of XII. Female pores more lateral than male pores, just posterior to 12/13.

Internal somatic characteristics: Brain narrow anteriorly and indented posteriorly. No anterior brain vesicle. Ventrolateral pharyngeal gland lobes very small in IV. Small dorsolateral lobes at 4/5; two pair of small ventrolateral lobes in V and one dorsolateral pair at 5/6; in VI, two or three pairs of ventrolateral lobes and one lateral pair at 6/7 (Fig. 2). Coelomocytes numerous anteriorly, not found posterior to clitellum. Patterned chloragogen cells covering posterior regions of the intestine, which often contains pennate diatoms. Nephridia not seen. Dorsal blood vessel transition to blood sinus in XXVI. No glands on ventral nerve cord.

Internal reproductive characteristics: Spermathecae (Fig. 4) paired in anterior of V, ampulla with narrow, ventrolateral, ental connection to esophagus; connection more ventral than line of ectal spermathecal pores. Spermathecal ectal duct has large subspherical dilation midway between pore

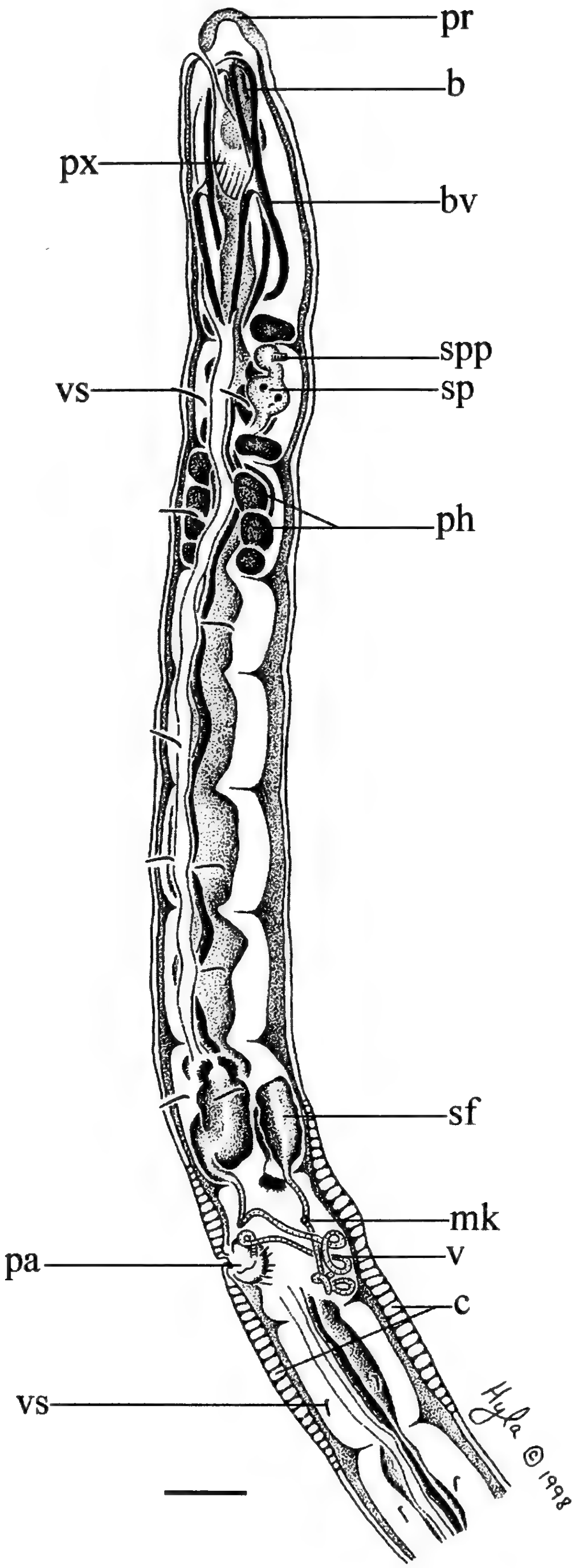

Fig. 2. *Grania laxartus,* new species, specimen from Bermuda. Semischematic ventrolateral view of whole mounted specimen showing only one of the penial apparatuses; prostomium to segment XIV, illustrating position and relative sizes of diagnostic structures. Scale equals 100 μm. b, brain; bv, blood vessel; c, clitellar gland cells; mk, muscle knot on vas deferens; pa, penial apparatus; ph, pharyngeal glands; pr, prostomium; px, pharynx; sf, sperm funnel; sp, spermatheca; spp, spermathecal ectal pore; v, vas deferens; vs, ventral seta.

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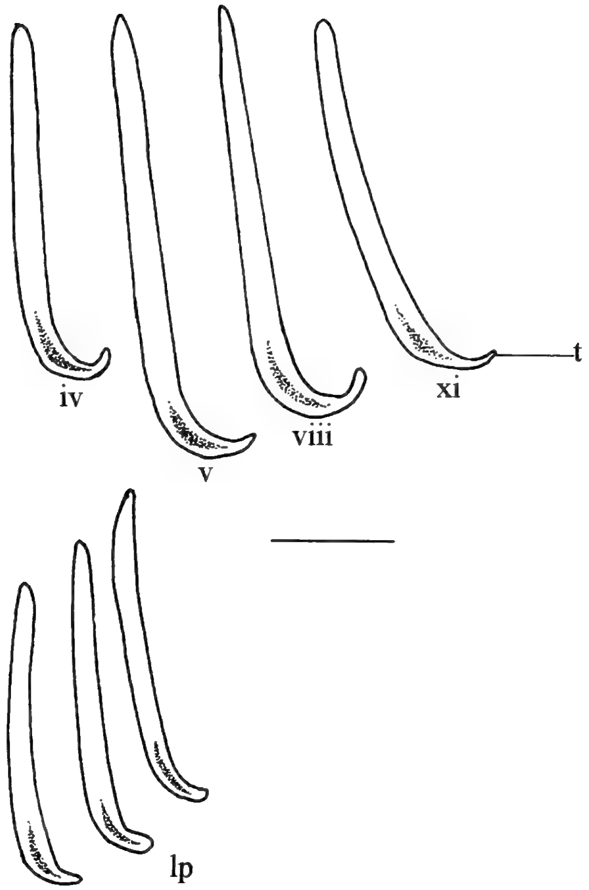


Fig. 3. *Grania laxartus,* new species, from Bermuda. Setae from various positions, showing broad base and slight toe. Scale equals 20 μm. lp, lateral posterior seta, t, setal toe.

and ampulla (Fig. 4). Ectal duct runs at about 90° from body wall to dilation, where it turns 90° to run parallel to body wall. The ectal duct then penetrates the ampulla as a cone-like protrusion (Fig. 4). Diameter of the ectal duct dilation 18.0–32.6 μm (n = 54, $\bar{X}$ = 25.0, *SD* = 3.0) (Fig. 4). Width of spermathecal ectal duct 10.0–21.9 μm (n = 46, $\bar{X}$ = 15.5, *SD* = 2.7) between dilation and ampulla and 10.0–14.0 μm (n = 31, $\bar{X}$ = 11.2, *SD* = 1.5) between dilation and ectal pore. Ampulla roughly spherical, greatest diameter 26.0–50.0 μm (n = 54, $\bar{X}$ = 42.5, *SD* = 4.7). Rings of sperm in wall of ampulla of reproductive specimens. No glands at ectal pore (Fig. 4). Sperm funnels 80.0–160.0 μm long ($n = 25$, $\bar{X} = 112$, $SD = 23.5$), 25–55 μm maximum width ($n = 25$, $\bar{X} = 41.4$, $SD = 9.2$) or, length about three times width; attached sperm with straight heads (acrosome & nucleus) (Fig. 5A). Laterally paired vasa deferentia possess a muscular "knot" at one quarter their total length, near sperm funnel (Fig. 5A); muscle bands run around vas and constrict it, but there are no obvious longitudinal extensions of the muscle bands. Vas confined to XI–XIII. Width of vas 6.3–8.8 μm ($n = 26$, $\bar{X} = 7.6$, $SD = 0.8$) both before and after "knot". Penial apparatus with small gland and lateral aglandular sac formed by extended invagination of male pore, muscles extend from body wall to outer wall of sac (Fig. 5A, B). Vas enters gland from a dorsolateral position, extends through glandular material to medial side. Penial stylet present, walls of vas deferens thin, with pronounced nuclei where stylet begins. Stylet extends from ectal end of vas deferens, tapering toward blind end of sac-like extended invagination of male pore. Length of stylet 30.0–47.7 μm ($n = 12$, $\bar{X} = 33.9$, $SD = 6.5$); maximum width of stylet 1.7 μm (measured for only two specimens) (Fig. 5B). Posterior extension of sperm sac XVIII through XXI. Egg sac extends to XXIII, with primary oocytes located only at posterior end of sac.

Etymology.—The species is named in allusion to the unique shape of the spermathecal ectal duct; laxartus from the Latin *laxus* meaning wide or broad, combined with *artus* meaning joints; a noun in apposition.

Taxonomic remarks.—Lateral setae are reported as commencing in XVI–XVIII, however, one specimen was an exception with lateral setae beginning in XXV and with ventral setae lacking from XVIII–XXIII. The ventral setal distribution for *G. laxartus* is similar to *G. bermudensis*, *G. americana* and *G. hylae* (Fig. 6) from the Northwest Atlantic. The last three species are easily distinguished from *G. laxartus* by dorsal spermathecal pores and a muscular sac-like penial apparatus in both *G. bermudensis* and *G. hylae,* and by the absence of both a penial stylet and muscular vas deferens (Coates 1984) in *G. americana.* Furthermore, *G. bermudensis, G. hylae* and *G. americana* each have very different spermathecal morphologies, lacking the distinct dilation of the spermathecal ectal duct that is present in *G. laxartus* (Fig. 6).

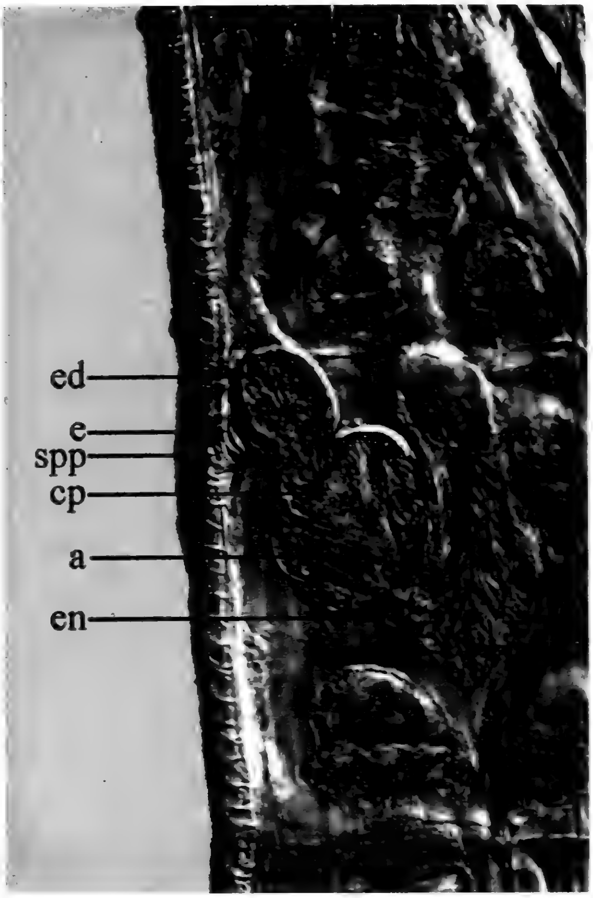


Fig. 4. *Grania laxartus,* new species, from Bermuda. Dorsal view of spermatheca in V. Scale equals 20 μm. a, ampulla; cp, conical protrusion of spermathecal duct; e, spermathecal ectal duct; ed, ectal dilation; en, spermathecal ental duct; see Fig. 2 for other symbols.

This form of dilation of the spermathecal ectal duct is reported in one other species of *Grania* from the Northwest Atlantic, *G. monospermatheca,* and is not known in any other species of *Grania* (Locke & Coates 1998; Rota & Erséus 1996, 1997; Coates & Stacey 1993, 1997; Coates 1990; Erséus 1990a; Coates & Erséus 1985; Coates & Erséus 1980; Erséus & Lasserre 1976). The ectal duct dilation of *G. monospermatheca*

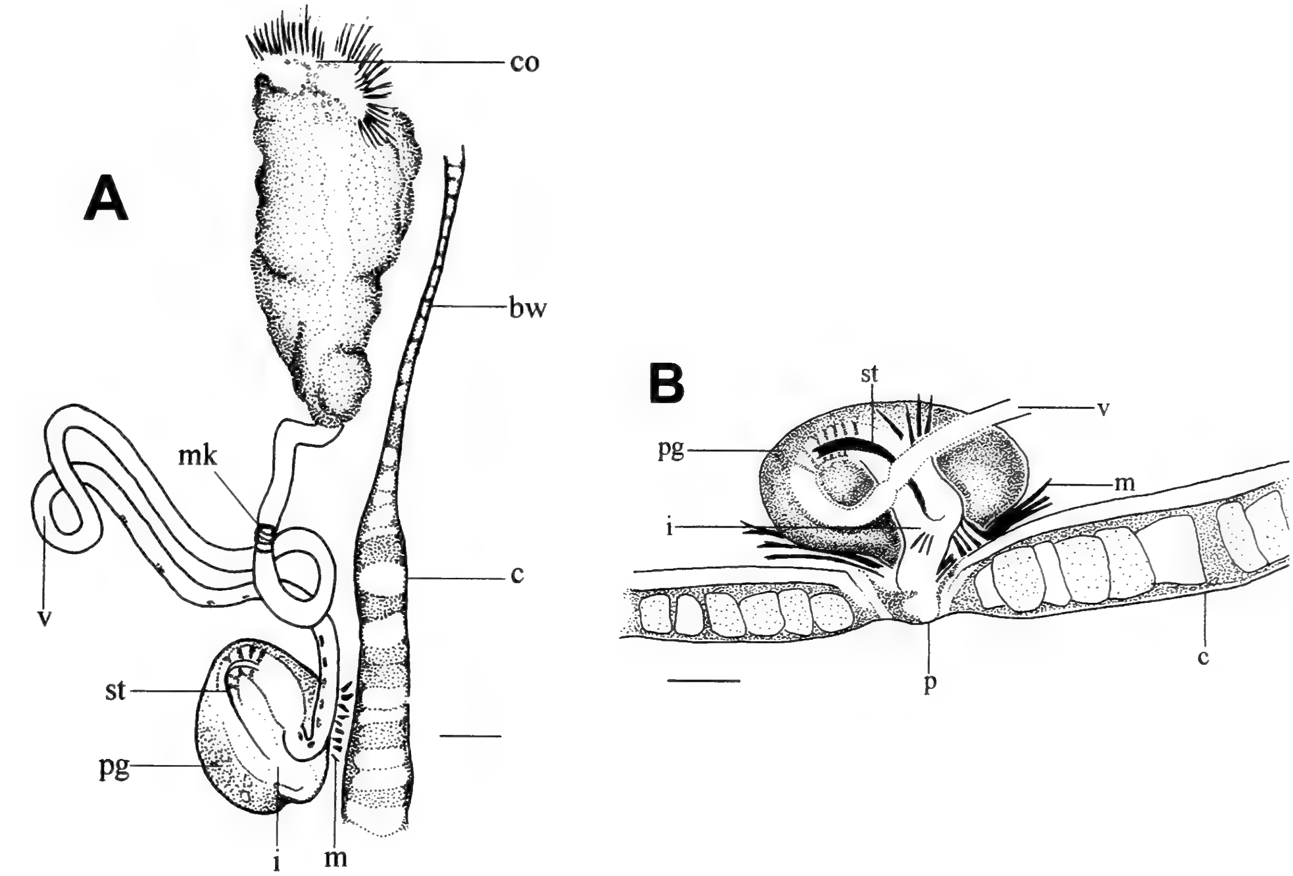


Fig. 5. *Grania laxartus,* new species, from Bermuda. A, ventral view of male duct system showing sperm funnel, vas deferens and penial apparatus. B, lateral view of penial apparatus. Scales equal 20 µm. bw, body wall; co, sperm funnel collar; i, invagination at male pore; m, muscle; p, male pore; pg, penial gland; st, stylet; see Fig. 2 for other symbols.

occurs immediately before the ampulla and is not as distinctly bulb-like as the medial dilation of the spermathecal ectal duct in *G. laxartus. Grania monospermatheca* is also readily distinguished from *G. laxartus* by the absence of lateral setae and the presence of a single spermatheca with a dorsal pore instead of a pair of spermathecae which open laterally.

Habitat and distribution.—Intertidal pools with accumulations of sand, in dissolution tubes formed by the erosion of limestone rock. Also occurs subtidally. Found in sand samples with debris along with *G. americana* and various Tubificidae, Nematoda and Sipunculida. Sand particle size for samples ranged from fine (occurring with *Thalassia testudinum* Koenig) to medium coarse calcareous coral sand. Known from Ferry Point Bridge, Whalebone Bay, Pearl Island, Ferry Reach and Smith's Sound, Bermuda; and Carrie Bow Cay, Belize (Table 1).

Grania hylae new species
Figs. 6, 7–11; Table 1

Holotype.—USNM 185954, stained, whole mounted specimen, BBS-77-42, collected by C. Erséus 1977.

Type locality.—ENE of Paget Island, Bermuda, 32°22′38″N, 64°38′57″W. Subtidal in 17 m, medium to coarse coral sand.

Paratypes.—Three stained, whole mounted specimens, USNM 185955 M77-6, North of lighthouse, Fowey Rocks USA, C. Erséus 1977; USNM 185956 BBS-77-15 Castle Island, Bermuda, C. Erséus 1977; and BAMZ 1999 180 007 BBS-77-15 Castle Island, Bermuda, C. Erséus 1977.

Other material examined.—Live material from Rocky Hill Park, Bermuda. Fourteen

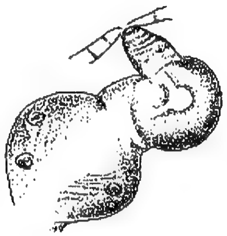
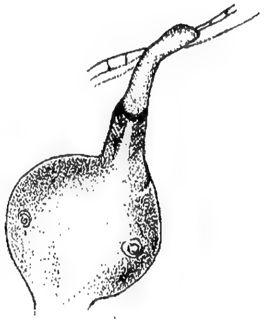
	Grania laxartus	**Grania hylae**	**Grania bermudensis**	**Grania americana**
Length (mm)	6.7	8	7.8	10.8
Number of segments	50	52	51	64
Diameter 4/5 (µm)	129.4	155.9	180.7	168.7
Setal origins ventral lateral	IV XVI-XVIII	IV XV-XVII	IV XVI-XX	IV XVI-XX
Spermathecal pores	lateral	dorsal	dorsal	lateral
Spermathecal shape				
Glands at spermathecal pore	no	no	no	yes
Glands on nerve cord	no	yes	yes	yes
Head organ	no	yes	no	yes
Sperm funnel	L3XW	L2.5XW	L4XW	L8XW
Vas deferens muscular	yes knot	yes thin with constrictions	yes spiral and thick	no
Penial apparatus type (Coates 1984)	5	6	6	3

Fig. 6. Comparison of *Grania* species. Measurements are shown as averages. Spermathecae of *G. bermudensis* and *G. americana* are shown at one-half the magnification used for *G. hylae* and *G. laxartus.*

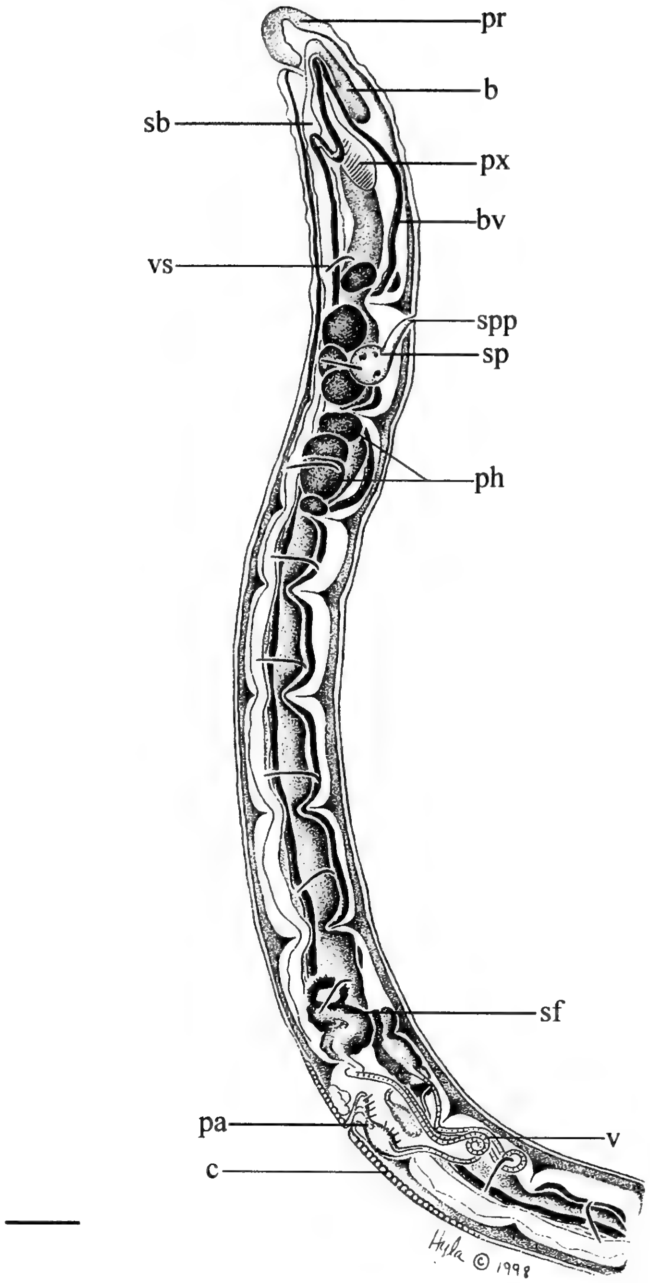


Fig. 7. *Grania hylae,* new species, specimen from Bermuda. Semischematic lateral view of whole mounted specimen; prostomium to segment XIV. Scale equals 100 μm. sb, subesophageal ganglion; see Fig. 2 for other symbols.

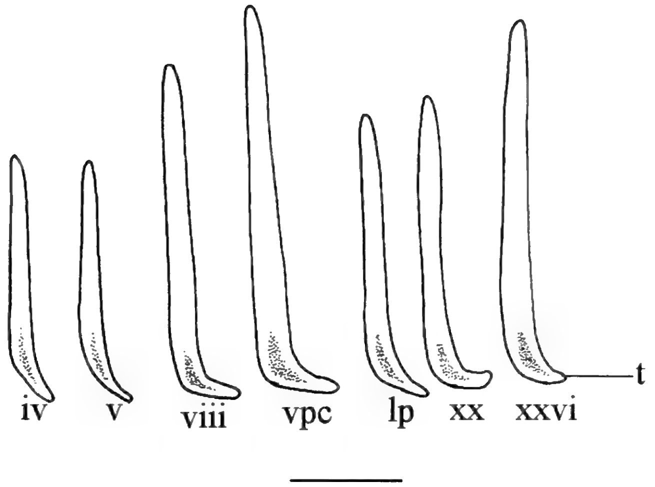


Fig. 8. *Grania hylae,* new species, from Bermuda. Setae from different segments. Scale equals 20 μm. vpc, ventral postclitellar seta; see Fig. 3 for other symbols.

whole mounted specimens from the collection of C. Erséus, from three different localities in Bermuda, and Fowey Rocks, Florida, U.S.A. (Table 1).

Description.—External characteristics: Fixed specimen length 5.3–11.5 mm (n = 7, $\bar{X}$ = 8.0, SD = 2.1). Number of segments 41–61 (n = 6, $\bar{X}$ = 52, SD = 8.1). Diameter at 4/5 139.5–192.0 μm (n = 7, $\bar{X}$ = 155.9, SD = 17.3), diameter at clitellum 154.0–196.0 μm (n = 7, $\bar{X}$ = 171.4, SD = 17.3) (Fig. 7). Head pore in anterior of peristomium. Ventral setae (Figs. 7 & 8) present from IV and laterally from XV–XVII. No setae in XII of mature specimens. Length of anterior ventral setae 37.0–66.4 μm (n = 10, $\bar{X}$ = 51.3, SD = 8.9); midbody ventral setae 49.8–91.0 μm (n = 35, $\bar{X}$ = 71.8, SD = 8.5); postclitellar lateral setae 59.8–80.0 μm long (n = 31, $\bar{X}$ = 69.6, SD = 5.8). In ten posterior-most segments ventral setae 53.7–71.0 μm (n = 17, $\bar{X}$ = 62.8, SD = 5.2) and lateral setae 49.0–74.0 μm (n = 14, $\bar{X}$ = 62.2, SD = 8.4). Setal shaft widening proximally, with sloping toe, distinct heel absent (Fig. 8). Spermathecal pores paired, dorsal, immediately posterior to 4/5 (Fig. 7), distance between pores 46.0–37.5 μm (n = 2, $\bar{X}$ = 41.8, SD = 6.0), no epidermal papilla at pore. Clitellum extending from post XI to mid XIII. Male pores ventral, in line of setae, at midpoint of XII. Female pores posterior to 12/13, opening just lateral to position of male pores.

Internal somatic characteristics: Brain indented posteriorly with narrow transition to small anterior brain vesicle. Membrane-bound, anterior, brain vesicle lies below head pore, with one refractile inclusion (Fig. 9). Pharyngeal glands present in segments IV through VI; one ventrolateral pair of lobes in IV and one dorsolateral pair at

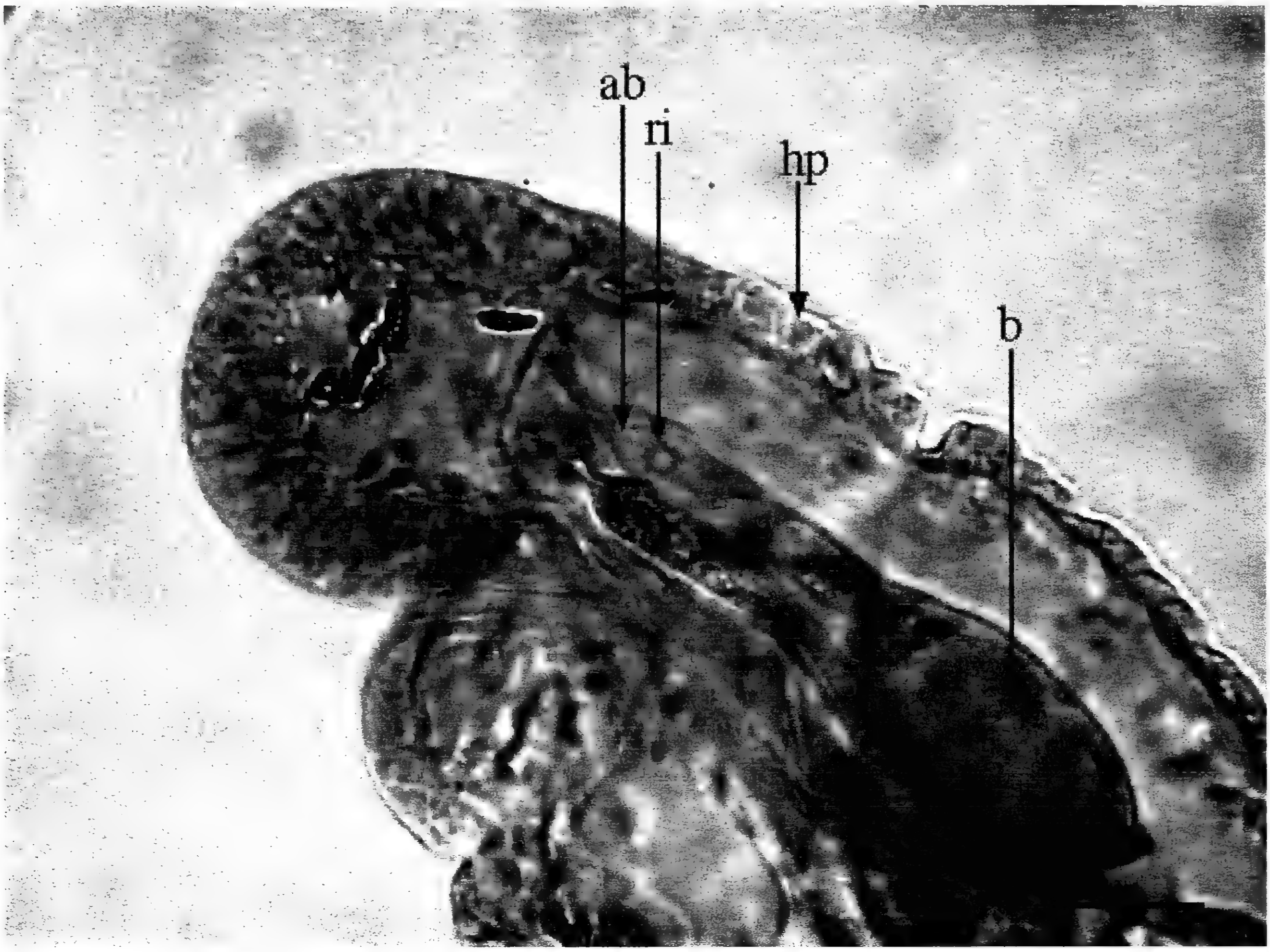


Fig. 9. *Grania hylae,* new species, from Bermuda. Lateral view of anterior brain vesicle with one inclusion. Scale equals 20 μm. ab, anterior brain vesicle; hp, head pore; ri, refractile inclusion; see Fig. 2 for other symbols.

4/5, two paired ventrolateral lobes in V and one dorsolateral pair at 5/6; three pairs of ventrolateral lobes in VI and one dorsal pair at 6/7. No nephridia observed. Dorsal blood vessel transition to blood sinus at XX or XXI. Gland on ventral nerve cord in XIV.

Internal reproductive characteristics: Spermathecae lie dorsal to pharyngeal glands in segment V (Figs. 7 & 10). Spermathecal ectal duct of uniform, narrow width with slight curvature toward pore, length of duct about 1.2 times maximum diameter of ampulla. Glands lacking at ectal pore. No protrusion of duct tissue into ampulla. Spermathecal ampulla small and round to ovoid, maximum diameter 32.0–52.0 μm ($n = 11$, $\bar{X} = 43.8$, $SD = 6.3$); ampullae lie close together, dorsal to gut, sometimes even touching; sperm rings present (Fig. 10). Narrow ental connection of spermathecal ampulla to esophagus. Sperm funnel length two and a half times the width, with non-granular section posterior to collar. Vasa deferentia confined to XII and XIII. Wall of vas deferens constricted at three almost equally spaced points immediately posterior to union with sperm funnel; with slight muscularization ectal to constrictions (Fig. 11A); vas possesses large, obvious nuclei along length, diameter of vas uniform along length 6.7–10.0 μm ($n = 13$, $\bar{X} = 8.4$, $SD = 0.9$). Penial apparatus bipartite, with horizontal and erect sections. Penial stylet present, originating within the vas deferens, extending just into the penial apparatus (Fig. 11A, B). Stylet long, 55.4–70.9 μm ($n = 6$, $\bar{X} = 61.8$, $SD = 7.1$). Vas terminates at ental end of the saccate part of the bipartite penial apparatus, which lies parallel to body wall and gut. This sac may appear longitudinally ridged or smooth, depending on whether it

Fig. 10. *Grania hylae,* new species, from Bermuda. Lateral view of spermatheca in V, with dorsal pore. Scale equals 20 µm. sr, sperm ring; see Fig. 4 for other symbols.

is contracted or relaxed. At anterior end of sac, there is an acute to right angle bend that unites the ridged, contracted sac to an erect extension of the male pore (standing more or less perpendicular to the body wall). Muscles run from the body wall to insert on both the longitudinal sac and onto the lateral wall of the perpendicular extension (Fig. 11A, B). Sperm sac extends to XVIII. Egg sac extends to XXII.

Etymology.—Named hylae in appreciation of Hyla Tibbitts' dedication and keen interest in the subject matter of her illustrations.

Taxonomic remarks.—*Grania hylae* has similarities to *G. bermudensis* in subtidal habitat, although it has also been found in the lower intertidal of rocky beaches, and in the structure of both spermathecae and the penial apparatus. Both species have dorsal spermathecal pores and round to ovoid ampullae. The average maximum diameter of the spermathecal ampulla for *G. hylae,* however, is only half that for *G. bermudensis.* An epidermal bump at the ectal pore is also seen only in *G. bermudensis* as well as a widening of the ectal duct near the ampulla.

Grania hylae possesses an anterior brain vesicle which is lacking in *G. bermudensis.* Differences between the two species are also seen in the details of the male duct systems. The walls of the vas deferens in *G. bermudensis* are highly muscularized whereas those of *G. hylae* have only a thin muscle layer. The maximum width of the muscular part of the vas deferens in *G. bermudensis* averages 22.9 µm and the non-muscular sections 12.3 µm; *G. hylae* has an average vas width of 8.4 µm. Both species do possess bipartite penial apparatuses with longitudinal sac-like parts but the junctions of vas deferens and penial sac are quite different.

There are a few other species of *Grania* which also have dorsally positioned spermathecal pores, including *Grania maricola* Southern, 1913 (see also Locke & Coates 1998) in which the pores are distinctly dorsal to the midlateral line although not fully dorsal. Both *Grania inermis* Erséus, 1990 and *Grania stilifera* Erséus, 1990 described from around Hong Kong (Erséus 1990a) have dorsal spermathecal pores but the first of these does not have a penial stylet and the second is reported to have a large gland associated with the penial apparatus. There are no separate glands on the penial apparatus of either of the species with dorsal spermathecal pores which are found in Bermuda, *G. hylae* and *G. bermudensis* (see below).

Habitat and distribution.—Subtidal, found in fine, medium and coarse coral sand, many Tubificidae also present. Intertidal, rocky limestone beach area, medium to course sand, with *G. americana,* Tubificidae and Nematoda. Known from Rocky Hill Park, Castle Island, Bailey's Bay, and ENE and SE Paget Island, Bermuda; and Fowey Rocks, Miami, Florida, U.S.A. (Table 1).

Grania bermudensis Erséus & Lasserre, 1976

Figs. 6, 12–15; Table 1

Grania macrochaeta bermudensis Erséus & Lasserre, 1976:122–124, fig. 3; Lasserre & Erséus 1976:453.

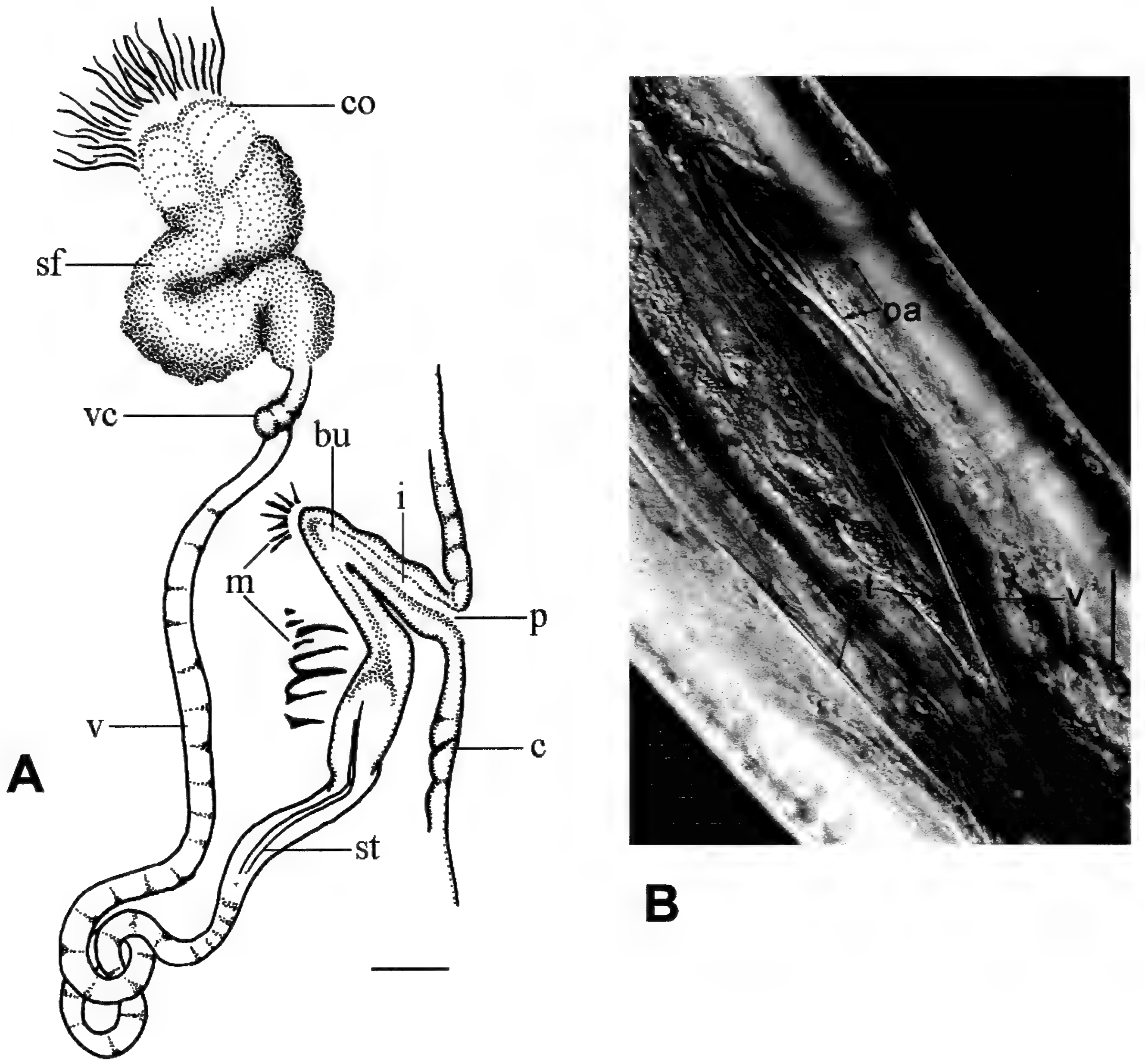


Fig. 11. *Grania hylae,* new species, from Bermuda. A, lateral view of male duct system showing sperm funnel, vas deferens and penial apparatus. B, photo of live specimen showing stylet orientation within vasa deferentia and bipartite penial apparatus. Scale equals 20 μm. bu, union of two sections of bipartite penial apparatus; vc, vas deferens constrictions; see Figs. 2 & 5 for other symbols.

Type material.—Holotype USNM 53202; paratypes USNM 53203; whole mounts. Collected by P. Lasserre, 12 Nov 1973.

Type locality.—Castle Island, Bermuda, 32°20′40″N, 64°40′25″W. Coarse coral sand with ripple marks, 8 m depth.

Other material examined.—Live specimens from the southeastern tip of Paget Island, Bermuda, collected March 1998 by JML. Eleven whole mounted specimens from the collections of C. Erséus collected from two sites in Bermuda, including the type locality (Table 1).

Description.—External characteristics: Length of preserved specimens 5.8–10.1 mm ($n = 7$, $\bar{X} = 7.8$, $SD = 1.4$). Number of segments 31–59 ($n = 7$, $\bar{X} = 51.4$, $SD = 9.4$). Diameter at 4/5 138.0–216.0 μm ($n = 6$, $\bar{X} = 180.7$, $SD = 27.5$), diameter at clitellum 159.0–258.9 μm ($n = 7$, $\bar{X} = 217.9$, $SD = 36.4$) (Fig. 12). Ventral setae from IV, lateral setae from XVI–XX ($n = 7$). No setae in XII of mature specimens.

Ventral setae at IV–V 48.0–72.0 μm (n = 14, $\bar{X}$ = 59.2, SD = 7.2); length of all other ventral setae 69.0–92.2 μm (n = 32, $\bar{X}$ = 80.6, SD = 5.9); postclitellar lateral setae 75.0–96.0 μm (n = 19, $\bar{X}$ = 83.4, SD = 6.3) (Fig. 13). In ten posterior-most segments ventral setae 68.9–74.4 μm (n = 6, $\bar{X}$ = 71.5, SD = 1.8) and lateral setae 64.7–75.6 μm (n = 6, $\bar{X}$ = 70.3, SD = 3.5). Setae thin with blunt proximal part possessing an upturned toe, no distinct heel present (Fig. 13). Head pore in anterior part of peristomium. Spermathecal pores paired, dorsal just posterior to 4/5, with thickened, glandular, epidermal papilla posterior to each pore (Fig. 12). Dorsal spermathecal pores about 60.0–64.4 μm apart (n = 2, $\bar{X}$ = 62.1, SD = 3.1). Clitellum extends from posterior XI to mid XIII. Male pores ventral, in line of setae, at mid XII. Female pores slightly more lateral than male pores, just posterior to 12/13.

Internal somatic characteristics: Brain indented posteriorly. Anterior brain vesicle lacking. Pharyngeal glands present in IV–VI: with one pair of dorsolateral lobes on anterior faces of each of 4/5 through 6/7; ventrolateral lobes, one small pair in IV, two pairs in V and three pairs in VI (Fig. 12). Nephridia not observed in live specimens, however, in fixed material five to seven pairs of complete nephridia were observed in segments posterior to egg sac, about four pairs in posterior-most segments and about two to three pairs near egg sac; small overall, with small funnels. Dorsal blood vessel transition to blood sinus as far back as XX. One specimen with small gland on ventral nerve cord in XIV.

Internal reproductive characteristics: Spermathecae paired in V with narrow ental connection of ampulla to esophagus (Figs. 12 & 14). Ampulla large and round, walls very grainy, maximum diameter 42.9–106.5 μm (n = 13, $\bar{X}$ = 80.7, SD = 23.5); sperm rings present (Fig. 14). Glands lacking at spermathecal ectal pore. Spermathecal ectal duct diameter wider closest to ampulla, diameter ranges from 10.5–19.5 μm (n = 12, $\bar{X}$ = 14.9, SD = 3.0). Ental duct runs ventrolateral to reach wall of gut, width about one half ampullar width. Sperm funnel length about four times width, non-staining, aglandular region posterior to collar (Fig. 15A). Vas deferens extending into XIII, thick and muscular along about one-third of length. Vas deferens relatively wide at sperm funnel, but lacking muscle on walls; then progressing to a short section with a spiral of muscle bands, first wound tightly around circumference of vas then unwinding so that the thick muscle bands run almost along length of the vas (Fig. 15B); muscular section followed by a thin-walled and narrow section, lacking muscle, which extends to a pad-like glandular junction with the penial apparatus (Fig. 15A, C). Maximum diameter of longitudinally muscled part is 18.0–25.5 μm (n = 8, $\bar{X}$ = 22.9, SD = 2.6) (Fig. 15A, B), non-muscular ectal and ental vas deferens diameter 7.5–18.0 μm (n = 9, $\bar{X}$ = 12.3, SD = 3.2). Penial stylet present, extends within ectal end of vas deferens causing that portion to be curved (Fig. 15A, C). Stylet length 91.8–130.1 μm (n = 6, $\bar{X}$ = 107.9, SD = 16.8); maximum width at origin (Fig. 15C) within vas deferens 7.3 μm (one specimen); stylet width along length 3.0–4.2 μm (n = 3, $\bar{X}$ = 3.4, SD = 0.7). Bipartite penial apparatus consists of an erect sac-like extension from the male pore running to a lateral, anterior-posterior oriented, longitudinally ridged sac lying parallel to the body wall; stylet terminates at pore on pad in posterior, ental end of ridged sac, and can be protruded through pore and into penial apparatus (Fig. 15C). Extensions of muscles from the body wall run to the erect extension and the lateral sac, and the whole of the penial apparatus can be everted through the male pore at the body wall. Sperm sac extends to XIX. Egg sac extends to XXI.

Taxonomic remarks.—The only species of *Grania* recorded in Bermuda prior to this study, *G. bermudensis,* was described as a subspecies of *G. macrochaeta* by Erséus &

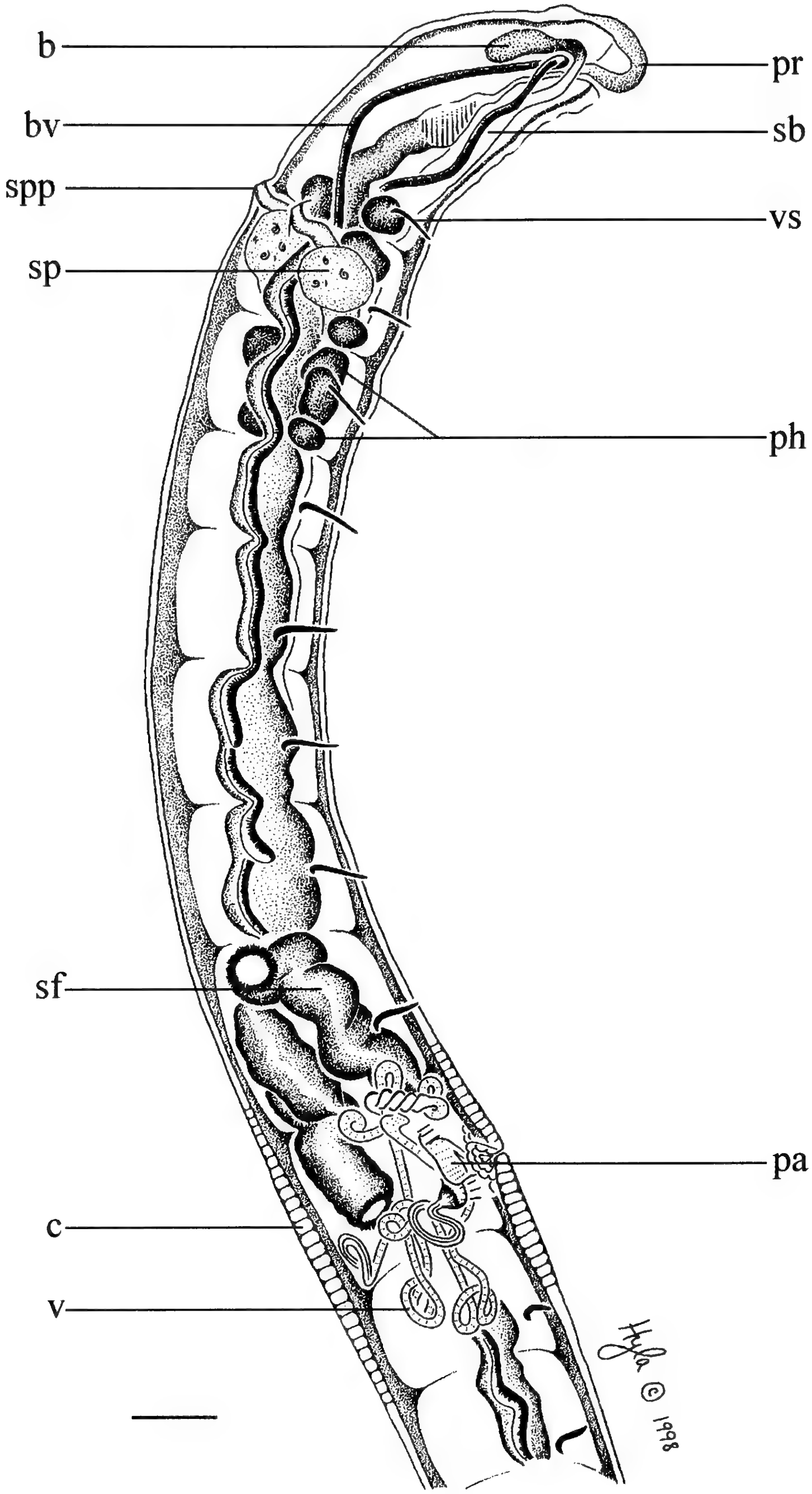


Fig. 12. *Grania bermudensis,* specimen from Bermuda. Semischematic dorsolateral view of whole mounted specimen, from prostomium to segment XIV. Scale equals 100 µm. See Figs. 2 & 7 for symbols.

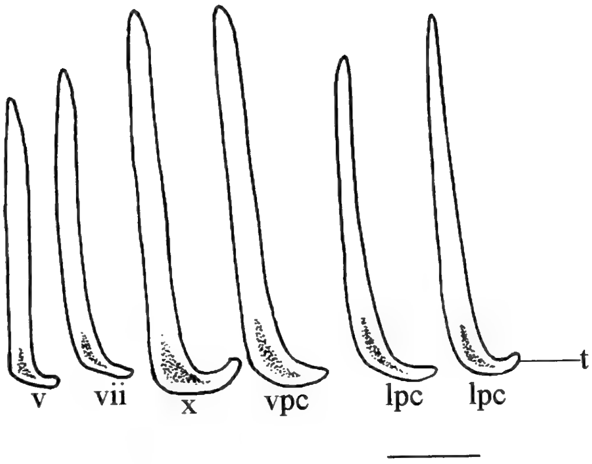


Fig. 13. *Grania bermudensis,* specimen from Bermuda. Various setae. Scale equals 20 μm. lpc, lateral postclitellar seta; see Figs. 3 & 8 for other symbols.

Lasserre (1976). The original description of the new subspecies was brief and indefinite about some characteristics, which in part explains the classification of *G. bermudensis* within *G. macrochaeta* s. l. The grouping of four subspecies, *G. m. macrochaeta, G. m. bermudensis, G. m. pusilla* and *G. m. trichaeta* was recently reevaluated as taxonomically invalid based on morphological characteristics (Locke & Coates 1998) and cladistically invalid as it is polyphyletic (Locke 1999a). *Grania pusilla* has been fully redescribed (Locke & Coates 1998). This redescription of *G. bermudensis* provides details of the dorsal spermathecal pore position and male duct structures which were omitted from the original description. The distribution of lateral setae is amended from previous records of their originating in XVIII–XIX to XVI–XX.

The dorsal spermathecal pore position, bipartite penial apparatus and highly muscularized vas deferens separate this species from *G. macrochaeta* s. s. (Locke & Coates 1998) and other Bermudian congeners (Fig. 6). *Grania hylae* does share comparable modifications of the first two characters with *G. bermudensis,* however, *G. hylae*

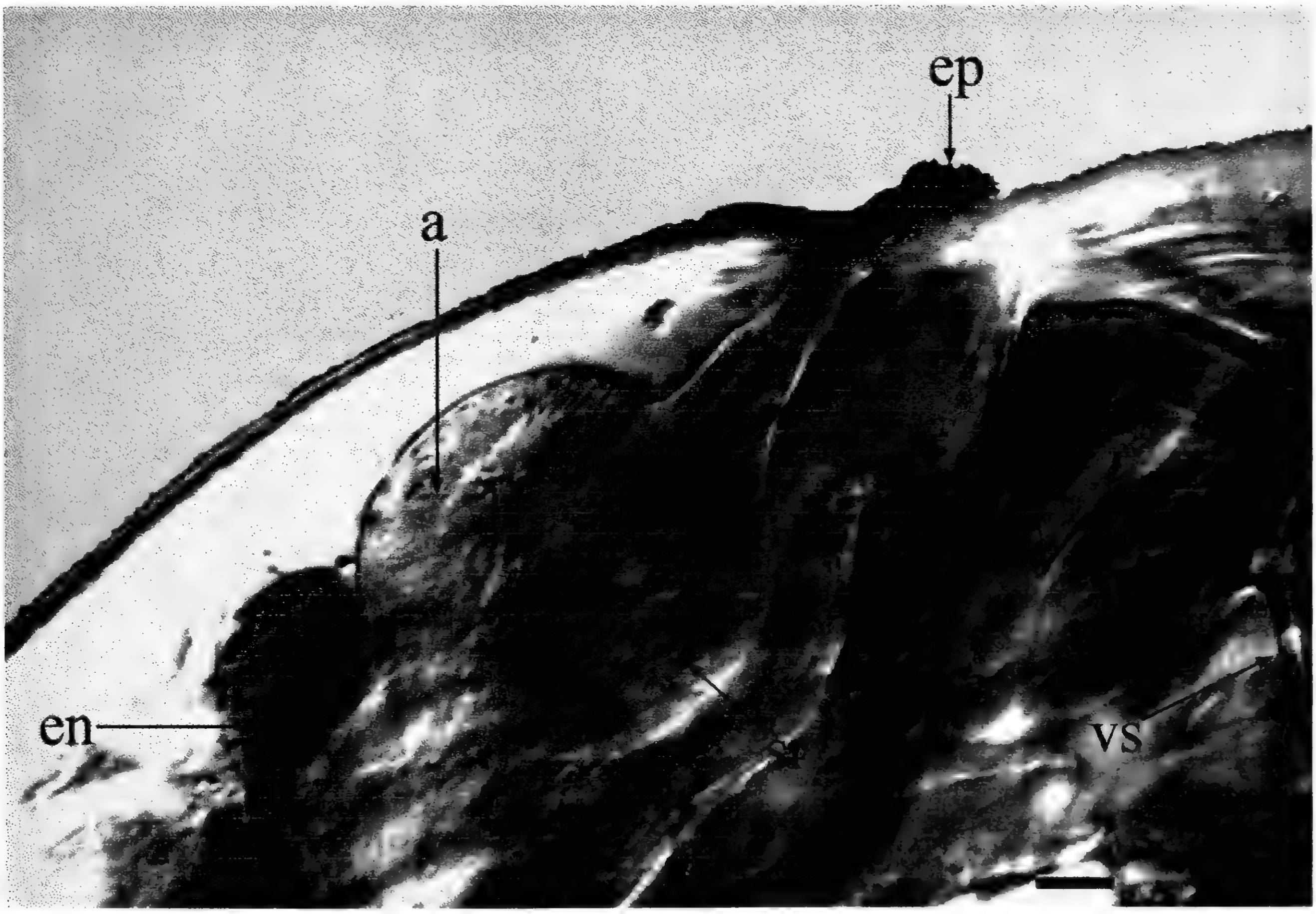


Fig. 14. *Grania bermudensis,* specimen from Bermuda. Lateral view of spermatheca with epidermal papillae. Scale equals 20 μm. ep, epidermal papillae; see Figs. 2, 4 & 10 for other symbols.

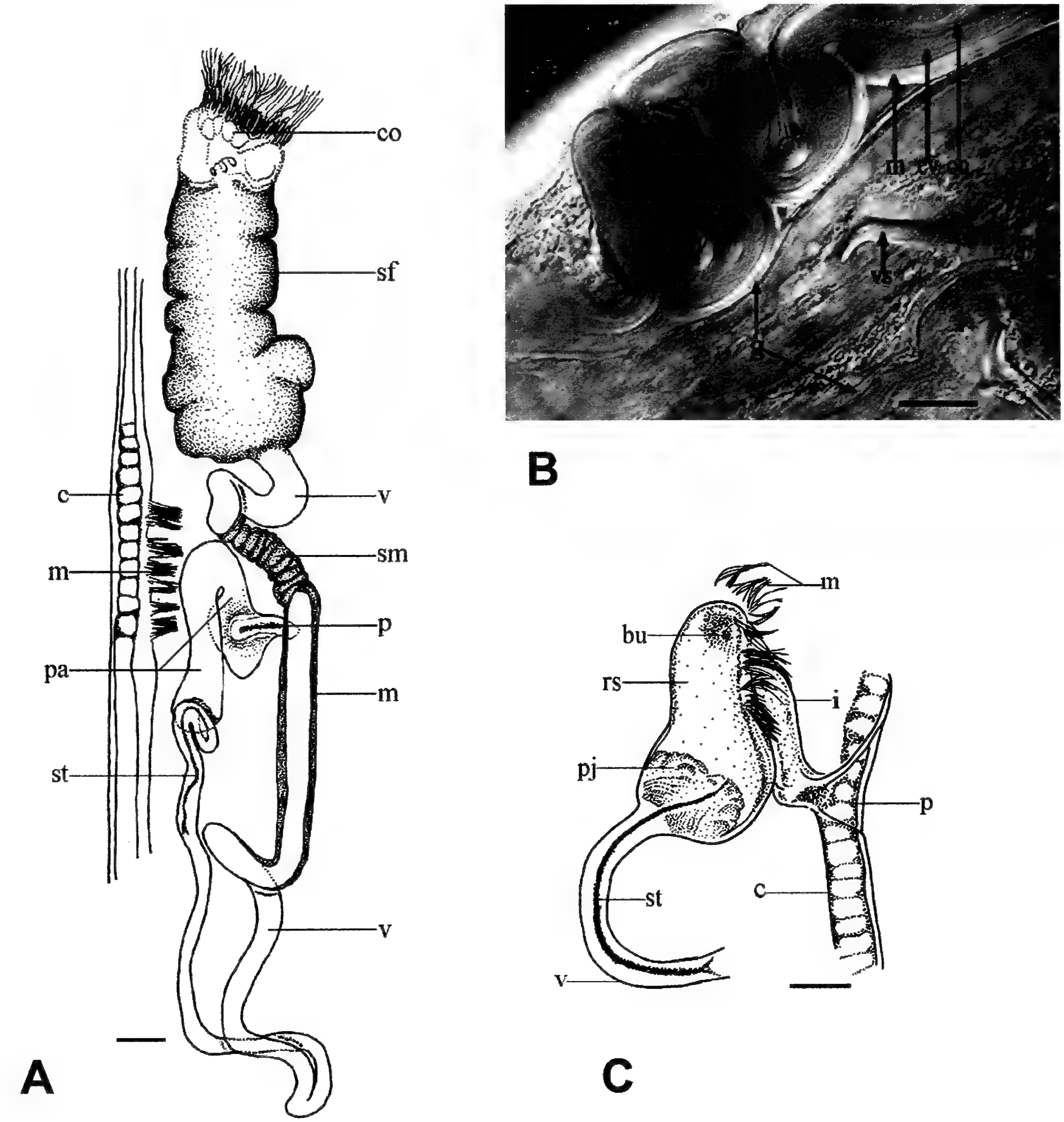


Fig. 15. *Grania bermudensis,* specimen from Bermuda. A, male duct system and penial apparatus. B, thick muscular area of vas deferens, in slightly compressed live specimen. C, lateral view of bipartite penial apparatus. Scale equals 20 μm. bu, union of two sections of bipartite penial apparatus; cc, ciliated canal; cv, cellular vas wall; g, gut; pj, pad-like glandular junction; rs, ridged sac; sm spiral of muscle; see Figs. 2 & 5 for other symbols.

lacks the extreme muscular modifications of the vas deferens. *Grania bermudensis* is named here as a distinct species.

Other species with dorsal spermathecal pores are considered in the taxonomic remarks following the description of *G. hylae* (above) and in the Discussion.

Habitat and distribution.—Subtidal, medium to coarse coral sand and gravel. Not found intertidally. Found in samples with Tubificidae. Known only from Castle Island, East Castle Roads, Rushy Island, a patch reef 100 m south of Rushy Island and SE Paget Island, Bermuda (Table 1).

Grania americana Kennedy, 1966
Figs. 6, 16–20; Table 1

Grania americana Kennedy, 1966:404–405, fig 3; Erséus 1974:90–93, table 1.

Grania macrochaeta americana: Lasserre 1967:278–280.

Grania americana nomen dubium: Erséus & Lasserre 1976:123.

Type material.—Holotype, USNM 33005, paratype USNM 33039. Whole mounts. Collected by M. L. Jones 27 Aug 1962.

Type locality.—0.5 km from North Entrance point, West side of North Bimini, 25°43.2′N, 79°19.0′W.

Other material examined.—Five stained, whole mounted specimens, BAMZ 1999 180 009, Pearl Island, Bermuda; USNM 185957, Ferry Reach, Bermuda; USNM 185958 Hutchinson Island, U.S.A.; and USNM 185959 and USNM 185960, Carrie Bow Cay, Belize. About 55 live specimens from Ferry Point Bridge, Bermuda, collected by the authors over the period 1996–1998. Twenty-four whole mounted specimens from the collections of C. Erséus, collected from Bermuda; Carrie Bow Cay, Belize; Angelfish Key, Florida Keys, and Hutchinson Island, Florida (Table 1).

Description.—External characteristics: Live specimens notably long, with pink blood in vessels, posterior segments yellowish to light brown due to colored granules within chloragogen cells. Prostomium pointed with anterior thin region; with many multi-ciliate epidermal papillae. Fixed length 8.7–12.6 mm ($n = 10$, $\bar{X} = 10.8$, $SD = 1.4$). Number of segments 60–74 ($n = 9$, $\bar{X} = 64$, $SD = 4.8$). Diameter at 4/5 140.0–196.5 μm ($n = 15$, $\bar{X} = 168.7$, $SD = 18.7$); clitellum diameter 150.0–208.9 μm ($n = 15$, $\bar{X} = 188.1$, $SD = 19.1$) (Fig. 16). Setae from IV ventrally and XVI–XX laterally ($n = 13$); no setae in XII of mature specimens. Setae broad at base, sometimes with slight toe and slight heel in posterior setae (Fig. 17). Anterior ventral setae 32.6–53.3 μm long ($n = 10$, $\bar{X} = 44.2$, $SD = 8.2$); midbody ventrals from 53.2–60.8 μm in length ($n = 8$, $\bar{X} = 56.3$, $SD = 2.4$). In ten posterior-most segments ventral setae 56.6–71.3 μm long ($n = 21$, $\bar{X} = 63.4$, $SD = 3.7$) and lateral setae 49.2–64.1 μm long ($n = 16$, $\bar{X} = 55.6$, $SD = 4.2$). Head pore at anterior of peristomium. Spermathecal pores paired, lateral, posterior to 4/5 (Fig. 16). Clitellum extending over XII–XIII. Male pores in line with ventral setae, at mid XII. Female pores at 12/13, slightly more lateral than male pores.

Internal somatic characteristics: Brain indented posteriorly. Anterio-medial brain vesicle present (Figs. 16 & 18). Divided into distinct lateral halves, each containing two inclusions (for a total of four) (Fig. 18). Inclusions in each compartment located at different levels, maximum diameter of inclusions 2.5–2.8 μm ($n = 6$, $\bar{X} = 2.7$, $SD = 0.1$) (Fig. 18). Total length across both compartments of head organ 20.5 μm (one specimen). Coelomocytes flattened and ovoid. Chloragogen cells, especially in posterior segments, very distinctive with peripherally clumped granules giving the cells the doughnut appearance of mammalian red blood cells, granules reddish-brown by transmitted light in both live and fixed specimens; outer surface of intestine, as a result, with leopard-spot pattern. Pharyngeal glands (Figs. 16 & 19) with one pair of small ventrolateral lobes in IV and a pair of dorsolateral lobes at 4/5; two pairs of ventrolateral lobes in V and a dorsolateral pair at 5/6; and with three pairs of ventrolateral lobes in VI and a dorsolateral pair at 6/7. Nephridia observed only in posterior segments, often unpaired, with small elongate funnel. Solitary, internalized, setae present in very few segments. Dorsal blood vessel transition around XXVI–XXVIII. Glands on nerve cord at XIV and/or XV.

Internal reproductive characteristics: Spermathecae (Figs. 16 & 19) paired in V with ental duct connecting ampulla to esophagus. Ampulla oviform with a maximum diameter of 42.0–90.0 μm ($n = 51$, $\bar{X}$

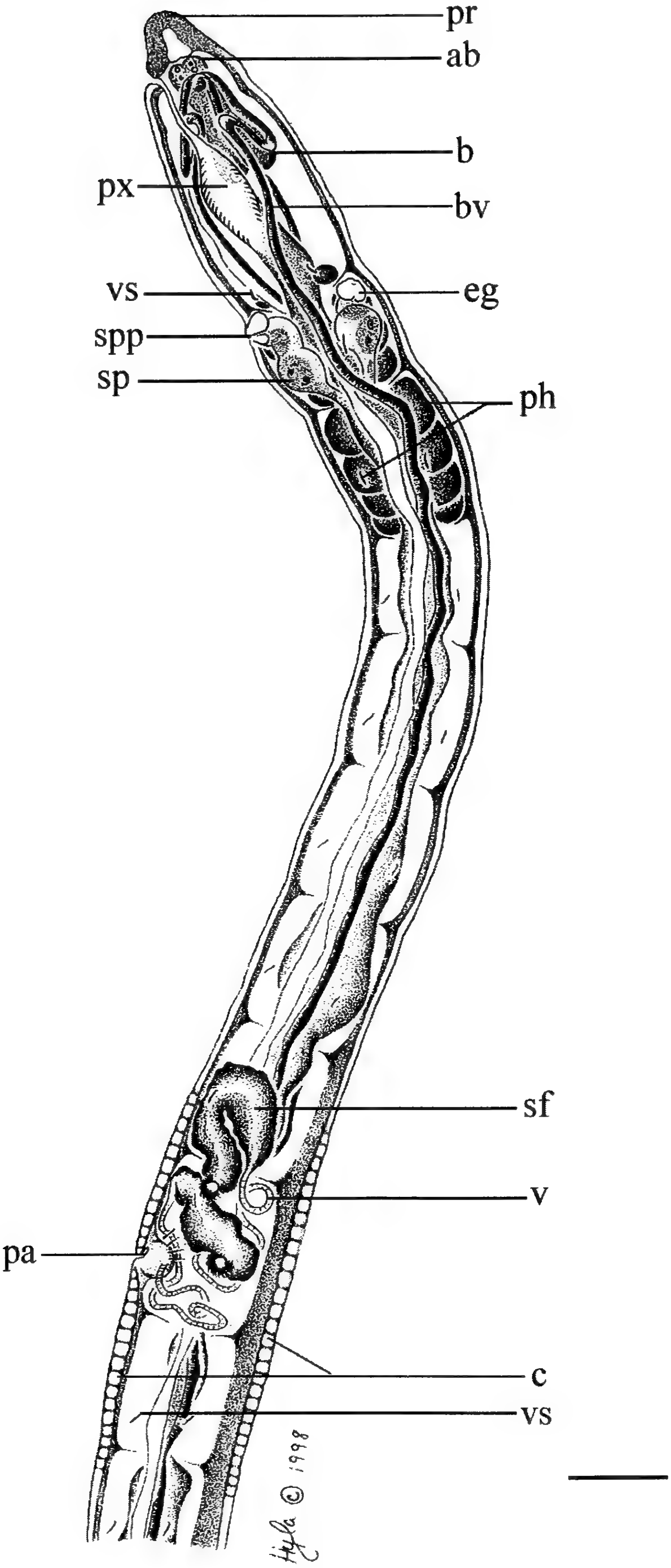


Fig. 16. *Grania americana,* specimen from Bermuda. Semischematic ventral twisted to lateral view of whole mounted specimen from prostomium to segment XIV. Scale equals 100 μm. eg; ectal gland of spermatheca; see Figs. 2 & 9 for other symbols.

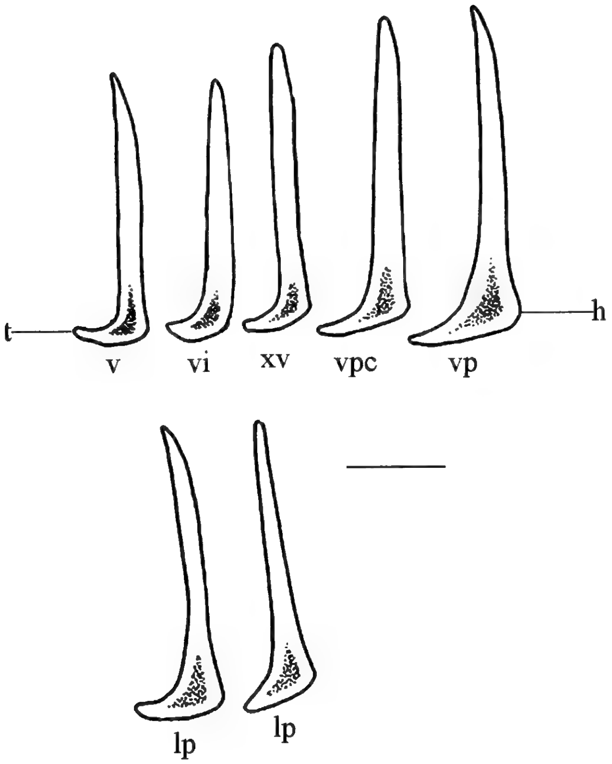


Fig. 17. *Grania americana,* specimen from Bermuda. Setae from various segments. Scale equals 20 μm. h, setal heel; vp, ventral posterior seta; see Figs. 3 & 8 for other symbols.

= 68.5, *SD* = 11.8). Spermathecal ectal duct with two glands at pore, one small and one large (Fig. 19). Ectal duct of spermatheca consists of two distinct parts: shorter part immediately adjacent to body wall with external glands and with wide canal; ental or proximal part with canal occluded by glandular cells (Fig. 19) that run as longitudinal segments around the narrow canal. Spermathecal ectal duct distal width 8.7–14.1 μm ($n = 6$, $\bar{X} = 10.8$, $SD = 2.1$), ectal duct medial width (max) 28.5–83.7 μm ($n = 8$, $\bar{X} = 42.7$, $SD = 17.4$), proximal portion of ectal duct 21.2–46.0 μm in width ($n = 21$, $\bar{X} = 34.0$, $SD = 6.7$). Spermathecal ectal duct length 54.0–94.7 μm ($n = 16$, $\bar{X} = 74.3$, $SD = 15.7$). Sperm rings present in walls of ampulla (Fig. 19). Sperm funnel length about eight times width, often displaced from XI to XII or XIII (Figs. 16 & 20A). Sperm funnel with a non-staining aglandular region immediately posterior to the collar; more posteriorly glandular tissue loose, giving funnel a very irregularly lobed surface (Fig. 20A). Sperm heads straight. Vas deferens long, extending through XIII, non-muscular, 6.8–11.4 μm wide ($n = 8$, $\bar{X}$

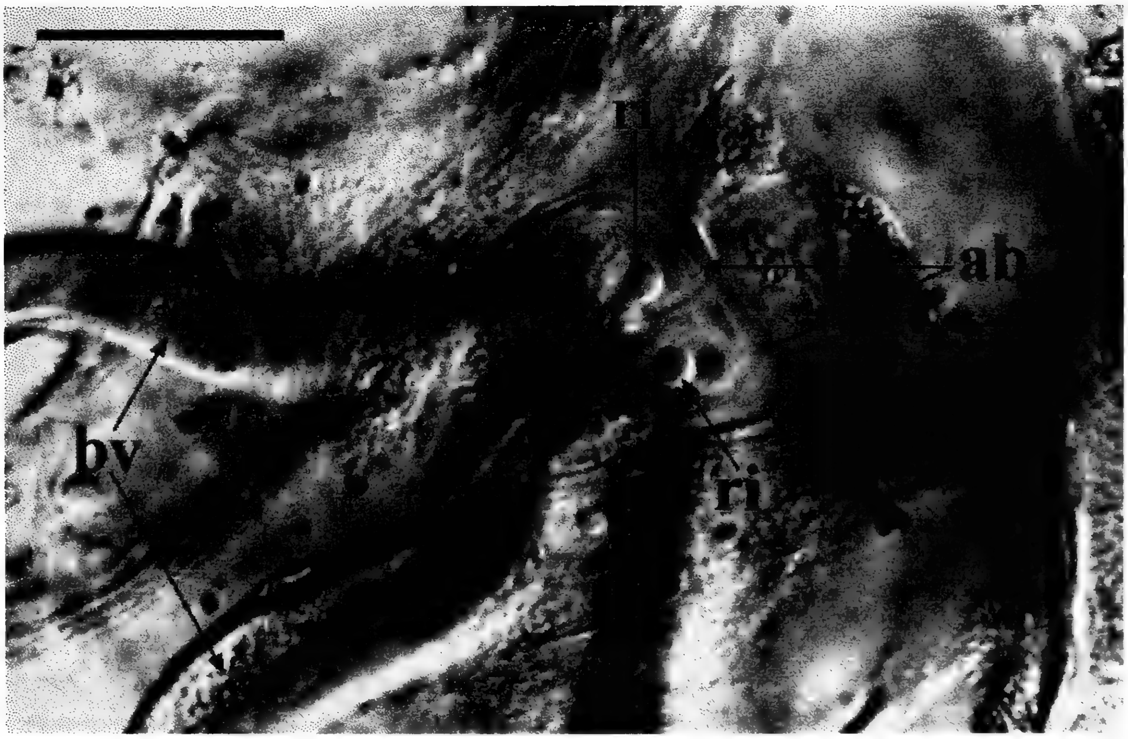


Fig. 18. *Grania americana,* specimen from Bermuda. Dorsal view of anterior brain vesicle showing inclusions. Scale equals 20 μm. See Figs. 2 & 9 for symbols.

Fig. 19. *Grania americana,* specimen from Bermuda. Dorsolateral view of spermatheca with glands at ectal pore. Scale equals 20 μm. See Figs. 4 & 10 for symbols.

= 9.6, *SD* = 1.7). No stylet. Penial apparatus relatively simple (Figs. 16, 20A, B), with a distinct bulbous gland and an elongate, saccate dorsal extension from the male pore which extends along the lateral side of the gland (Fig. 20A, B); vas enters gland from dorsomedial side and runs to the lateral side, extending to the elongate extension. Ventrally, near epidermal pore, the penial apparatus is narrower with little glandular mass and is surrounded by very strong elaborations of the muscle bands of the body wall (Fig. 20B). Sperm sac extends to XXI. Egg sac extends to XXVII.

Taxonomic remarks.—Kennedy's (1966) original description of *G. americana* differs in a number of respects from our description. This is probably due to his shortage of good specimens, which limited collection of both morphometric and structural data. Kennedy did provide approximate measurements for the overall length of the species (10 mm), the number of segments (50), and the ratio of length to width of the sperm funnels (several times longer than wide). However, the description was based on two specimens only. These were missing a few segments from their posterior ends and were eventually mounted in a macerating medium (pers. obs.).

The original description of *G. americana* states that the dorsal setae begin at XVI or XVIII (Kennedy 1966). In our redescription, the "dorsal" setae are described as lateral and the range of segments at which they begin is extended to XVI–XX. The presence of pharyngeal glands in VII (Kennedy 1966, Erséus 1974) was not seen in the type material when it was re-examined by us. The peptonephridia originally noted for *G. americana* have since been determined to be absent from the genus *Grania* (Erséus & Lasserre 1976) and what Kennedy observed, most likely, were the thick bundles of ducts running from the pharyngeal glands to the dorsal pharyngeal pad.

In more recent literature the taxonomic importance of the structure of the penial apparatus (Coates 1984) has become apparent, and therefore, *G. americana* which had a brief subspecies status, is not a subspecies of *G. macrochaeta* (sensu Lasserre, 1967). The penial apparatus of *G. americana* has a distinct bulbous gland, an elongate, saccate, epidermal invagination and is lacking a penial stylet. *Grania americana* also has ectal glands on the spermathecal ectal duct at the pore and these glands are visible in the type material of *G. americana.* Erséus & Lasserre (1976) had stated that these were absent in *Grania* even though they included *G. americana.* Similar glands have been noted in other recently described species (Coates & Erséus 1980, Erséus 1980, Rota & Erséus 1997) and the generic description amended accordingly.

Grania americana differs from other Bermudian congeners by the possession of glands at the spermathecal ectal pore, lack of penial stylet and muscular vas deferens

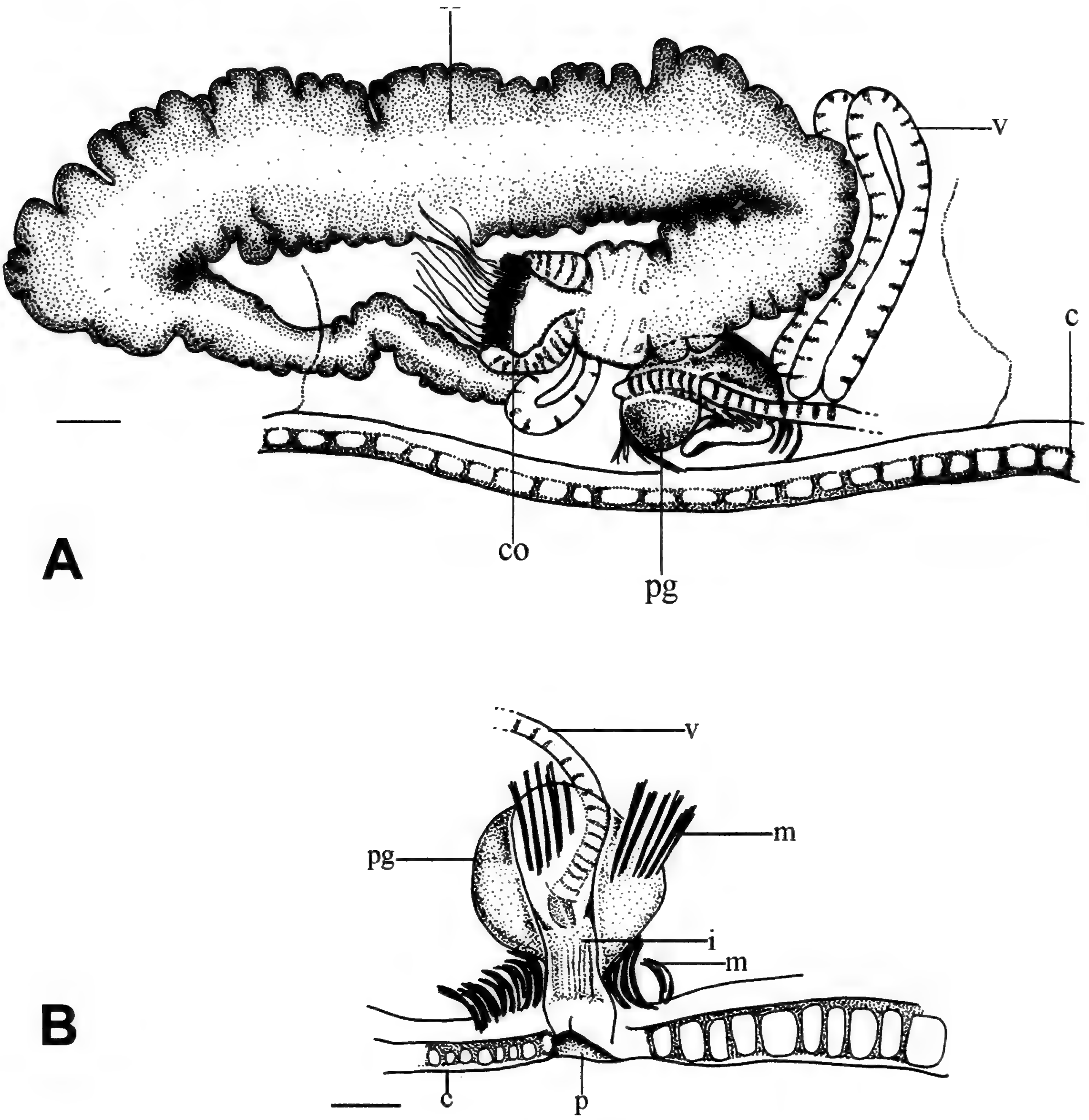


Fig. 20. *Grania americana,* specimen from Bermuda. A, dorsal view of male duct system and penial apparatus. B, lateral view of penial apparatus. Scale equals 20 μm. See Figs. 2 & 5 for symbols.

(Fig. 6). In addition, the length of *G. americana* is much greater than that of the other species described from Bermuda. *Grania americana* possesses an anterior brain vesicle with four inclusions, described as the "head organ" in other species of *Grania* by Rota & Erséus (1996, 1997). *Grania hylae* which is also found in Bermuda has a different form of anterior brain vesicle with only one visible inclusion. In *G. americana* this organ is located in the anterior of the peristomium, just below the boundary with the prostomium, as an anterior, medial bulbous extension of the brain. Previous accounts of this structure in recent species descriptions (Rota & Erséus 1996, 1997) have also noted the presence of four refractile bodies, but these authors (1996) also noted that some damaged specimens showed fewer inclusions or none. Quite possibly this organ has a geotactic function (Locke 1999b). A head organ has only been reported for eight subtidal species of *Grania*: five from the Ross Sea, Antarctica, two from South Georgia in the subantarctic, and one from the western Atlantic. It is possible that *G. americana* shares a unique apomorphy with this subgroup of *Grania,* but is an intertidal representative of the lineage.

Grania americana differs from all of the other species of *Grania* which are known to have head organs by its spermathecal form, in particular large glands at the ectal pore, and distinctive ectal duct structure, penial apparatus form, and setal distribution. Two species of *Grania* are known to have single, small glands at the spermathecal ectal pore, *G. monochaeta* (Michaelsen, 1888; amended Rota & Erséus 1997) an Atlantic species and *G. paucispina* (Eisen, 1904). The first does not have a head organ with refractile inclusions, although a vesicle is present, and for the second no head organ has been described.

Habitat and distribution.—Coarse intertidal sand within dissolution tubes at Ferry Point Bridge and rocky limestone beach areas at Whalebone Bay, Ferry Reach, and Rocky Hill Park, Bermuda. In Bermuda also recorded from Pearl Island and Bailey's Bay in fine to medium subtidal sands. Found in samples with *G. laxartus,* various Tubificidae and Nematoda. First reported from Bimini, Bahamas; Panama City and Miami, Florida, U.S.A. Habitat at type location in Bimini was probably subtidal as Kennedy (1966) recorded that the specimens were collected "off the coast". In Florida, collected from coarse sand in *Thalassia* beds, and in shell rubble (Table 1). At Carrie Bow Cay, Belize, also found in medium to coarse sands and *Thalassia* beds (Table 1).

Discussion

This is the first addition to our knowledge of the species diversity within *Grania* for the Northwestern Atlantic since the study by Coates & Erséus (1985). Many other species of the North Atlantic remain to be described (pers. obs.) and further studies are required to develop an understanding of the speciation patterns and evolution of this genus. An illustrated dichotomous key to the species of *Grania* of the Northwest Atlantic can be found on the world wide web at *http://www.bbsr.edu/users/kcoates/Grania/Grania.html* (Locke 1999a).

The distributions of *Grania* species found in Bermuda pose some interesting questions about speciation and dispersal patterns, particularly because of the relatively young geological age of Bermuda, 52-34 MY. *Grania americana, G. laxartus* and *G. hylae* are all known from the Caribbean and Bermuda. This distribution pattern is considered typical for Bermudian fauna (Sterrer 1986, 1998). The absence of a larval stage in the development of these worms makes it difficult to explain how regular genetic exchange between Bermudian and coastal populations might be maintained. Genetic studies of Bermudian and Caribbean coastal populations could reveal information about effective "population" sizes, frequency of colonization events, and whether any existing genetic flow is unidirectional, as would seem likely due to prevailing currents. Morphological measurements for conspecific specimens from different localities did not indicate any notable differences between populations.

The intertidal pools formed within dissolution tubes at Ferry Point Bridge create an intertidal refuge for *G. laxartus* and *G. americana* which is rich in detrital matter. Healy (1996) noted the importance of crevices within the rocky intertidal as moist micro-climates during low tide. The dissolution tubes fulfill the same role as Healy's rock crevices in that they protect from wave disturbance, displacement by water currents and retain organic matter, but have high oxygen levels (Healy 1996), conditions in which enchytraeids thrive (Healy & Coates 1999). These small pots or tubes may also effectively isolate adjacent populations as the rock surface between is very exposed and barren. This is in contrast to the subtidal habitat occupied by *G. bermudensis* and *G. hylae.* These species are protected from wave action by the greater depth of the water in which they are found and the habitat is relatively continuous. The subtidal sites in Bermuda were located to the side of major channels into bays and harbours. Tidal currents through these openings bring nutrients and detrital matter to the areas, and these get deposited in the slower water and back eddies that border the main channel.

The presence of *G. laxartus* and *G. americana* within the same samples throughout the year could conflict with commonly held ideas about ecological divergence between congeneric species. There is some evidence, other than morphological discontinuities, to suggest that co-occurring populations of the two species are biologically isolated by temporal separation of reproductive periods. High numbers of mature specimens of each species were found at different times of the year.

The muscular, bipartite penial apparatuses found in *G. bermudensis* and *G. hylae* are different from the many types of glandular, bulb-like apparatuses previously described for *Grania* species (Coates 1984). This form of penial apparatus appears to be associated with species which possess dorsal spermathecal pores. It also is found in *G. monospermatheca* which possesses a single dorsally displaced spermathecal pore. Coates (1984) had previously designated a penial bulb "Type 6" as glandular penial bulbs reduced or absent, aglandular sac often absent; with a long penial stylet plus considerable modifications to other parts of the vasa deferentia. Representative taxa were *G. bermudensis* and *G. monospermatheca.* This grouping included more structural diversity than the other "types" recognized. Additional information from the species described herein is considered and Coates (1984) "Type 6" is revised. Penial bulb "Type 6" is now described as: bipartite, saccate penial apparatus lacking a distinct glandular bulb; saccate part with horizontal and erect parts. Stylet long and contained within vasa deferentia. Muscular modifications of the vasa deferentia. Spermathecal pores dorsal. Representative taxa: *G. bermudensis, G. monospermatheca, G. hylae,* and two undescribed species from Australia (Coates 1984). Documentation of dorsal spermathecal pores and complex penial apparatuses in *G. stilifera* Erséus, 1990 and *G. inermis* Erséus, 1990 present the possibility of their being included within the Type 6 grouping. Whereas, Erséus (1990a) designated these as "Type 5" and "Type 3" (sensu Coates 1984), respectively, penial apparatuses. Other forms originally "lumped" in Type 6 await further clarification and typification.

The presence of an anterior brain vesicle in *G. americana* and *G. hylae* are the first records in readily collected species. This structure, first reported as the "head organ" by Rota & Erséus (1996), has only been found in one other species from the North Atlantic, *G. atlantica* (Rota & Erséus 1996; pers. obs). The function of the anterior brain vesicle is still unknown, but it appears to be statocyst-like in structure (Locke 1999a, 1999b). Phylogenetic studies of *Grania* species which possess this structure may provide ecological and functional hypotheses underlying the origin of such a structure in clitellates.

Although Erséus & Lasserre (1976) stated their understanding of the morphology of *Grania* had improved, they still believed that morphological differences between widely separated populations were small, sufficient only to justify their recognition as subspecies. Nonetheless, they (Erséus & Lasserre 1976:131) stated that with further studies the reinstatement of their subspecies to species could easily be made and Erséus (1977) noted that the structural variation within *G. macrochaeta* s. l. was very broad. Erséus & Lasserre (1976) also noted the importance of spermathecae in the taxonomy of enchytraeids. Locke & Coates (1998) resurrected *G. pusilla* from subspecies status. Herein, *G. bermudensis* is recognized as even more distinct and *G. americana* is redeemed from nomen dubium (Lasserre & Erséus 1976) to full species status. The differences in spermathecal structures and in the male duct systems (Coates 1984) among these species provides sufficient support for the recognition of all the subspecies of *G. macrochaeta* as morphologically distinct species. Even more damning for *G. macrochaeta* s. l. is that this grouping of subspecies is clearly polyphyletic. Only one taxon in this group, *Grania macrochaeta trichaeta* Jamieson, 1977, awaits a full redescription.

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Maractis rimicarivora, a new genus and species of sea anemone (Cnidaria: Anthozoa: Actiniaria: Actinostolidae) from an Atlantic hydrothermal vent

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Abstract.—*Maractis rimicarivora* is a new genus and new species of medium-sized sea anemone (Actiniaria) from the TAG (Trans-Atlantic Geotraverse) hydrothermal vent fields (26°08.3′N, 44°49.6′W; 3650 m). The genus, which belongs to family Actinostolidae, is distinguished by the following combination of features: six pairs of complete mesenteries, mesenteries not arrayed according to the *Actinostola* rule, all mesenteries gametogenic, tentacles not thickened at the base, and no tentacular mastigophores. The species is distinguished by long, longitudinally-furrowed tentacles, and a roughened column. Anemones of this species encircle black smokers at distances from 15 to 60 m. This is the second species to be reported from hydrothermal vents of the Atlantic. Four species have been reported from Pacific hydrothermal vents.

Five species of sea anemones have been documented from hydrothermal vents (Desbruyères & Segonzac 1997). *Cyananthea hydrothermala* Doumenc & Van-Praët, 1988, and *Marianactis bythios* Fautin & Hessler, 1989, were described from Pacific vents. Doumenc & Van-Praët (1988) also identified from Pacific vents *Actinostola callosa* (Verrill, 1882) and *Chondrophellia coronata* (Verrill, 1883), species described from trawled specimens before the existence of hydrothermal vents was known. The only sea anemone thus far reported from Atlantic vents is *Parasicyonis ingolfi* Carlgren, 1942 (Segonzac 1992), another species described from trawled specimens. Certainly three and probably four of these five species belong to family Actinostolidae, one of the two richest families of deep-sea anemones (the other is Hormathiidae, to which *C. coronata* belongs).

We describe another member of Actinostolidae as a new genus and new species from the TAG (Trans-Atlantic Geotraverse) vent fields, located at 26°08.3′N, 44°49.6′W, and 3650 m. Part of the Mid-Atlantic Ridge (MAR), TAG is one of the largest submarine hydrothermal fields known (German et al. 1995, Van Dover 1998). We infer this to be the species Van Dover et al. (1997) reported preying on a shrimp of the species *Rimicaris exoculata* at the TAG site, and that is depicted in Fig. 3b of Van Dover (1995). Shrimp (along with fish and crabs) dominate high-temperature regions of the TAG vent field near active black smokers, and anemones occupy peripheral regions where the water is cooler (Van Dover 1995), attached to the crumbly substratum of oxidized sulfide.

Materials and methods.—The five specimens we studied were collected on 21 September 1994 using the claw of the submersible Mir 1. Within an hour of being brought to the surface, they were fixed in 10% seawater formalin; later they were transferred to isopropanol. Morphological aspects of this description are based on these preserved specimens; biological information is from the published literature and from P. A. Tyler, who provided the specimens to us. One well-expanded specimen, which we designated the holotype, was missing a few tentacles, but was otherwise in excellent condition. The four paratypic specimens were missing many tentacles and patches of ectoderm. Three of them were in good condition otherwise and were moderately expanded; the other was moderately contracted and its partly-everted actinopharynx was damaged.

Preparation of histological sections and the gathering of cnidae data followed methods of Fautin & Hessler (1989). Histological sections 8 μm thick were stained with hematoxylin and eosin. Cnidae were measured in smash preparations at 1000×.

Maractis, new genus

Definition.—*Maractis* has the following combination of diagnostic characters: member of family Actinostolidae having six pairs of complete mesenteries; mesenteries not arrayed according to the *Actinostola* rule; all mesenteries gametogenic; tentacles not thickened at the base; and no tentacular mastigophores. Further defining features include a broad base, at least 48 tapered tentacles, and column ectoderm that lacks papillae or other such structures. Animals of this genus are supple, unlike many deep-sea anemones, because the mesoglea is relatively thin.

Differential diagnosis.—In the key to some genera of Actinostolidae of Fautin & Hessler (1989), *Maractis* falls under options B), ff), hh), jjj), and kk) by virtue of having "All or all stronger mesenteries fertile . . . ," "Longitudinal tentacle muscles ectodermal," "No microbasic *b*-mastigophores in tentacles," "No tentacular mastigophores," and "Six pairs of mesenteries perfect," respectively.

Three genera fall under that option in the key: *Bathydactylus, Cnidanthea,* and *Epiparactis. Bathydactylus,* like *Maractis,* has a broad base. However, *Bathydactylus* has a very strong marginal sphincter muscle that forms a projecting wall, stout tentacles that are few in number, mesenteries that are not hexamerously arrayed, and papillae in the distal part of the column (at least in some species). *Cnidanthea,* like *Maractis,* has hexamerously arrayed mesenteries, but, unlike *Maractis,* has papillose nematocyst batteries on its column. *Epiparactis,* like *Maractis,* has more than 48 tentacles that are closely packed at the rim, and has broad pedal and oral discs. However, it has a smooth column and "thick, cartilaginous mesogloea" (Carlgren 1921, page 198).

The other genera of actinostolid sea anemones that have been reported from hydrothermal vents are *Marianactis, Parasicyonis,* and *Actinostola; Cyananthea* probably also belongs to this family. *Maractis* is similar to *Marianactis* Fautin & Hessler, 1989, in lacking microbasic *b*-mastigophores in the tentacles, but differs in lacking microbasic amastigophores in the tentacles. *Parasicyonis* Carlgren, 1921, and *Actinostola* Verrill, 1883, differ from *Maractis* both externally (both have short tentacles) and internally (in the former, mesenteries of only the last cycle are fertile, whereas in the latter those of the first two cycles are sterile). *Cyananthea* is incompletely known, but has twice as many mesenteries at the margin as at mid-column, in contrast to *Maractis.*

Etymology and gender.—*Maractis* is a composite of MAR (Mid-Atlantic Ridge) and "actis," Greek for ray or beam, a term often applied to anemones. Its gender is feminine.

Type species.—*Maractis rimicarivora,* new species.

Maractis rimicarivora, new species
Figs. 1–4

Description.—Pedal disc flat, margin scalloped because pulled inward at mesenterial insertions (Fig. 1), which are visible through disc. Diameter in animals examined 25–55 mm. Color in preservation same as that of column, oral disc, and tentacles—uniformly dull pink.

Column diameter 20–30 mm, length 10–

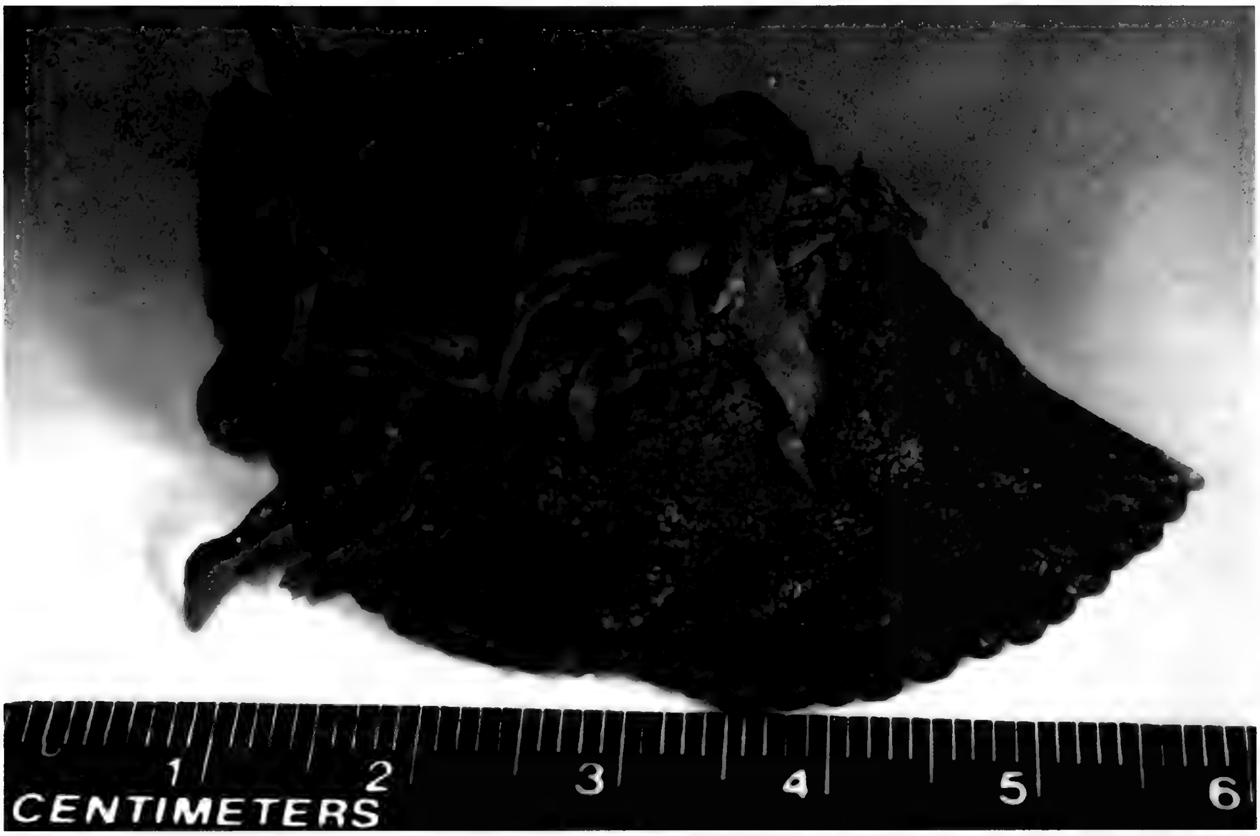

Fig. 1. *Maractis rimicarivora*: portion of holotype (KUNHM 01149). Note scalloped edge of pedal disc and long, longitudinally-furrowed tentacles. Raised circular spots are inferred to be artifacts—impressions of the perforations in a collecting device or storage container.

20 mm. P. A. Tyler (pers. comm.) remarked in life "the column looks very short" but was difficult to see because animals "always appear to have the [tentacle] crown [directed] to the camera."

Mesenterial insertions visible through body wall where ectoderm is missing. Ectoderm thin, eroded from many specimens. Surface texture rough: mesoglea and ectoderm thrown into short, relatively deep, complex folds (Figs. 2A, 3).

Oral disc torn or obscure in specimens examined. No fossa: outermost tentacles arise from margin (Fig. 2A). Tentacles 5–25 mm long (longest roughly equal to or slightly longer than column height). Flaccid, flattened in preserved specimens, longitudinally furrowed, tapering toward distal end (Fig. 1); number to nearly 100 in specimens examined. Cannot be withdrawn and covered when animal retracted. Longitudinal muscles ectodermal, continuous with radial muscles of oral disc (Fig. 2A).

Mesenteries regularly arrayed in 4 cycles, not according to the *Actinostola* rule; those of fourth cycle may not reach margin. Two pairs of directives, each attached to a siphonoglyph, lie diametrically opposite one another. Only mesenteries of first cycle complete. All fertile (including directives and those of highest order) (Fig. 3); sexes separate. No stomata. Retractor muscles well-developed, diffuse, arrayed in bolster-like strands (Fig. 3). Parietobasilar muscles developed only along stronger mesenteries; broad at base; each extends about half length of column, has very narrow free edge.

Marginal sphincter muscle mesogleal, moderately well developed. May fill entire width of mesoglea at margin but for most of length does not extend to ectodermal edge of mesoglea (Fig. 2B); at proximal end, occupies about half width of mesoglea, lying along endoderm (Fig. 2A, B). Small alveoli of equal size scattered along ectodermal side of sphincter; may be reticulate on endodermal side (Fig. 2A, B). Muscle cells relatively denser in larger individuals. Musculature weakly transversely stratified in parts of muscle of some individuals.

Actinopharynx about half length of column.

Animals, including tentacles, may remain fully extended upon preservation.

Cnidom.—spirocysts, basitrichs, microbasic *p*-mastigophores, holotrichs.

Size and distribution of cnidae.—Letters refer to illustrations in Fig. 4. Measurements in parentheses are of single capsules that fell outside the usual range. Number of capsules measured is indicated by "*n*"; ratio of the number of animals in which a particular type of cnida was found to the total number examined for that tissue is indicated by #.

Tentacles—distal end:		
Spirocysts (A, B) 30.0–78.5 × 2.8–7.3 (7.8) µm	*n* = 91	# = 5/5
Basitrichs (C) (15.6, 15.9) 17.2–25.5 × 1.6–2.9 µm	*n* = 54	# = 5/5
Basitrichs (D) 31.0–48.4 (54.6) × 2.5–3.8 µm	*n* = 50	# = 5/5
Holotrichs (E) 30.4–53.9 × 4.5–6.4 µm	*n* = 39	# = 5/5
Tentacles—proximal end:		
Spirocysts (A, B) 30.3–64.1 × 2.9–6.9 (7.7, 8.1) µm	*n* = 85	# = 5/5
Basitrichs (F) (16.8) 19.2–43.4 × 1.9–3.8 µm	*n* = 74	# = 5/5
Column:		
Basitrichs (F) 19.5–31.5 × 1.9–3.9 (4.9) µm	*n* = 71	# = 5/5
Microbasic *p*-mastigophores (G) 21.3–31.9 × 3.4–6.2 µm	*n* = 54	# = 4/5
Actinopharynx:		
Basitrichs (F) 23.4–34.9 × 2.3–3.2 µm	*n* = 9	# = 3/4
Microbasic *p*-mastigophores (G) 28.6–42.1 × 4.1–5.2 (5.7) µm	*n* = 31	# = 3/4
Mesenterial filaments:		
Basitrichs (C) 16.1–34.1 (39.3, 45.1) × 1.8–4.5 µm	*n* = 61	# = 5/5
Microbasic *p*-mastigophores (G) 26.9–38.9 (43.1) × 3.3–5.7 (6.0) µm	*n* = 61	# = 5/5

Most spirocysts could be assigned to one of two types (both shown in Fig. 4A), although rare ones shared characteristics of both. This distinction was not noticed until many measurements had been gathered, so our data are not divided by type. Spirocysts that were, on average, longer and wider had tubules wound in an untidy fashion and lacked space between the tubule and the capsule's posterior end (Fig. 4A, at left). Spirocysts that were, on average, shorter and narrower had neatly wound tubules and space between the tubule and the posterior end of the capsule (Fig. 4A, at right, and Fig. 4B). For example, in tentacles of paratype KUNHM 01150, 9 of the "neat" spirocysts measured 36.0–49.9 × 3.3–5.3 µm, and 10 of the "untidy" ones measured 37.3–59.2 × 5.1–7.7 µm.

Etymology.—The name *rimicarivora* refers to the ingestion (Latin vora: to eat) by this anemone of the shrimp *Rimicaris exoculata* Williams & Rona, 1986. [The taxonomy of vent shrimps is considered by Shank et al. (1998).]

Type locality.—TAG (Trans-Atlantic Geotraverse) hydrothermal vent fields: 26°08.3′N, 44°49.6′W; 3650 m.

Type specimens.—Holotype (Fig. 1) Division of Invertebrate Zoology, University of Kansas Natural History Museum (KUNHM) 01149: a dissected male specimen and 16 microscope slides made from it.

Paratypes: KUNHM 01150: a dissected specimen of indeterminate sex and 20 microscope slides made from it. The Natural History Museum, London 1999.80: a dissected male specimen and 9 microscope slides made from it. The Santa Barbara Museum of Natural History, Santa Barbara, California 145140: a dissected female specimen and 10 microscope slides made from it. The U.S. National Museum of Natural History 100132: a dissected specimen of in-

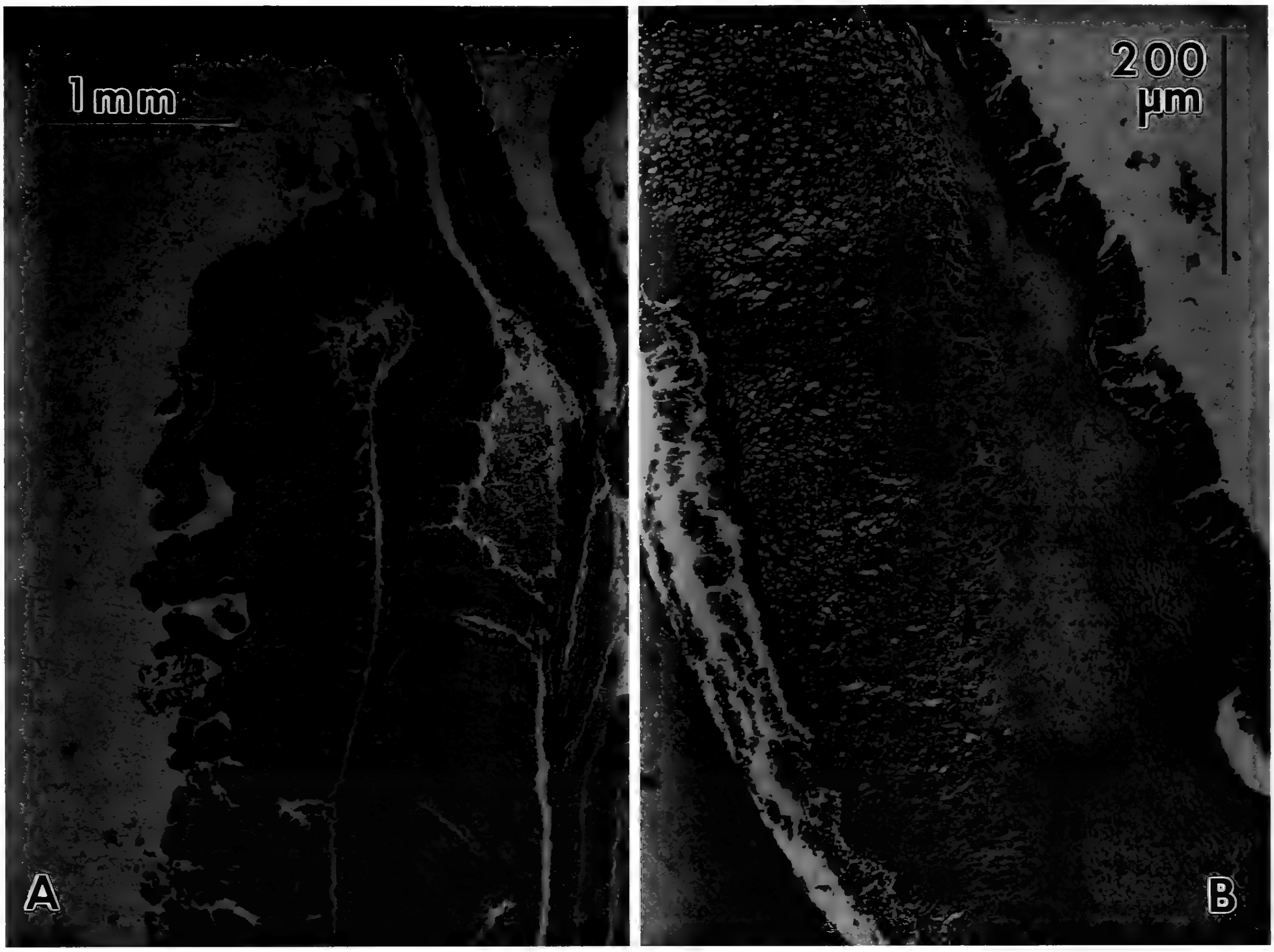

Fig. 2. Mesogleal sphincter muscle of *Maractis rimicarivora.* A: Longitudinal section at margin of paratype KUNHM 01150. Tentacles have ectodermal longitudinal musculature; outermost tentacle arises at margin. The surface of the animal is thrown into short, complex folds. B: Proximal end of sphincter muscle of holotype (KUNHM 01149).

determinate sex and 5 microscope slides made from it.

Discussion

The holotype (KUNHM 01149), a quarter of which is illustrated in Fig. 1, has conspicuous raised circular patches on part of its column, especially the lower portion. We initially thought these might be adhesive structures to which sulfide particles could adhere (see below). We concluded, however, that they are artifacts from a collecting device or storage container. Their position does not correspond to any anatomical feature of the animal, they are on only one side of the holotype, and they are not visible in the other specimens (although the ectoderm is eroded from several of them, patches persist).

We, like Van Dover et al. (1997), found no evidence of bacterial symbionts in *Maractis rimicarivora*: there were neither bodies that could be interpreted as bacteria nor structures of the animal that were likely to harbor bacteria. In addition, Van Dover et al. (1997) found no biochemical or physiological evidence of bacterial symbiosis. We infer, therefore, that *M. rimicarivora* is a typical cnidarian in depending on prey for energy and nutrients. Shrimp and anemones dominate the biota of TAG and most other Atlantic vent fields that have been studied, in contrast to Pacific vent fields, which are dominated by tubeworms, mussels, and clams (Van Dover 1995). At TAG, there appears to be little aside from shrimp on which the anemones could feed (P. A. Tyler, pers. comm.). The observation of predation

Fig. 3. Cross-section at mid-column level of the holotype (KUNHM 01149). Spermaries associated with mesenteries of the third and fourth (highest) orders are visible. Well-developed retractor muscles are diffuse. Scale bar = 1 mm.

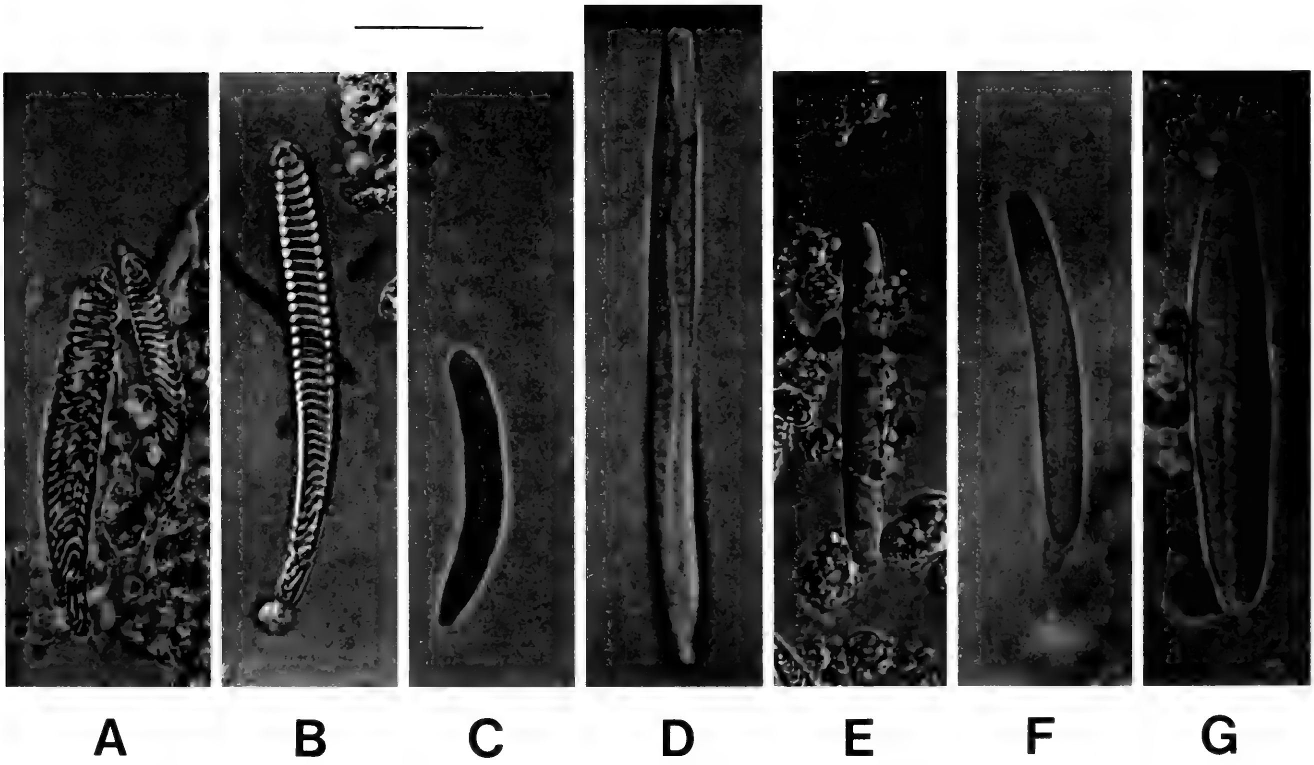

Fig. 4. Cnidae of *Maractis rimicarivora*. See text for explanation. Scale bar = 9 μm.

on a shrimp (Van Dover et al. 1997) is consistent with these data and inferences.

The size and color of the predatory anemone, and the length of its tentacles, were consistent with our specimens. However, our specimens lacked the black spots on the column that are conspicuous in the videotape on which the report of Van Dover et al. (1997) is based. Van Dover (pers. comm.) suggested they were sulfide particles. Although the specimens we studied lacked discrete adhesive structures, the large surface area of their wrinkled ectoderm (Figs. 2, 3) would seem likely to have adhesive properties. Indeed, some fine debris adhered to one specimen we studied. We therefore concluded the animal that is the subject of the report by Van Dover et al. (1997) is *M. rimicarivora.* Van Dover et al. (1997) found the anemone most abundantly 30–40 m from the center of a black smoker, where its density reached nearly 200 m^{-2}; its average density in the ring it formed around the black smoker at a distance of about 15–60 m was 3 m^{-2}, so the anemones probably do not experience water of elevated temperature.

Van Dover (1995) inferred there might be two species of anemones at TAG, one small and one large. One small anemone specimen we examined had a short, strongly reticulate mesogleal sphincter muscle, which was like that of neither *M. rimicarivora* nor *Paractinostola ingolfi,* the anemone collected at the Snake Pit hydrothermal vent field 3° south of TAG (Segonzac 1992). Therefore, there may be at least three species of anemones at TAG. Anemones also occur at the Broken Spur vent field 3° north of TAG (Van Dover 1995), but not at the Lucky Strike vent field 11° north of TAG (Van Dover et al. 1996).

Acknowledgments

We are grateful to Paul A. Tyler for specimens of anemones from TAG and for a copy of the videotape showing an individual of *Maractis rimicarivora* preying on a shrimp. We thank Tracy White for help with histology and Adorian Ardelean for technical assistance. Cindy L. Van Dover and Paul A. Tyler provided important information and helpful comments. Cadet Hand commented on an earlier version of this manuscript. Stanley F. Lombardo helped with the Latin. This research was supported by NSF grant DEB95-21819 (PEET) to Daphne Fautin. Collections were made under the auspices of NERC Grant BRIDGE 21 to Paul A. Tyler.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
112(3):632–633. 1999.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Applications published in the Bulletin of Zoological Nomenclature

The following Applications were published on 18 December 1998 in Vol. 55, Part 4 and on 30 June 1999 in Vol. 56, Part 2 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.

3036 *Haliotis clathrata* Reeve, 1846 (non Lichtenstein, 1794) and *H. elegans* Philippi, 1844 (Mollusca, Gastropoda): proposed conservation of the specific names.

3080 *Polydora websteri* Hartman in Loosanoff & Engle, 1943 (Annelida, Polychaeta): proposed conservation of the specific name by a ruling that it is not to be treated as a replacement for *P. caeca* Webster, 1879, and designation of a lectotype for *P. websteri.*

2911 *Spherillo* Dana, 1852 (Crustacea, Isopoda): proposed designation of *S. vitiensis* Dana, 1853 as the type species, with designation of a neotype.

3094 *Terebratula* Müller, 1776 (Brachiopoda): proposed designation of *Anomia terebratula* Linnaeus, 1758 as the type species.

3012 *Coluber infernalis* Blainville, 1835 and *Eutaenia sirtalis tetrataenia* Cope in Yarrow, 1875 (currently *Thamnophis sirtalis infernalis* and *T. s. tetrataenia*; Reptilia, Squamata): proposed conservation of the subspecific names by the designation of a neotype for *T. s. infernalis.*

3005 *Crotalus ruber* Cope, 1892 (Reptilia, Serpentes): proposed precedence of the specific name over that of *Crotalus exsul* Garman, 1884.

3058 *Arctocephalus* F. Cuvier, 1826 and *Callorhinus* Gray, 1859 (Mammalia, Pinnipedia): proposed conservaton by the designation of *Phoca pusilla* Schreber, [1775] as the type species of *Arctocephalus*; and *Otaria* Péron, 1816 and *Eumetopias* Gill, 1866: proposed conservation by the designation of *Phoca leonina* Molina, 1782 as the type species of *Otaria.*

3126 *Bulinus wrighti* Mandahl-Barth, 1965 (Mollusca, Gastropoda): Proposed conservation of the specific name.

3052 *Sphaerius* Waltl, 1838 and SPHAERIUSIDAE Erichson, 1845 (Insecta, Coleoptera): proposed conservation by the partial revocation of Opinion 1331.

3063 *Blennocampa* Hartig, 1837, *Cryptocampus* Hartig, 1837, *Taxonus* Hartig, 1837, *Ametastegia* A. Costa, 1882, *Endelomyia* Ashmead, 1898, *Monsoma* MacGillivray, 1908, *Gemmura* E.L. Smith, 1968, BLENNOCAMPINI Konow, 1890 and CALIROINI Benson, 1938 (Insecta, Hymenoptera): proposed conservation by setting aside the type species designations by Gimmerthal (1847) and recognition of those by Rohwer (1911).

3066 *Macrophya* Dahlbom, 1835 (Insecta, Hymenoptera): proposed designation of *Tenthredo montana* Scopoli, 1763 as the type species; and *Tenthredo rustica* Linnaeus, 1758: proposed conservation of the usage of the specific name by the replacement of the syntypes with a neotype.

3124 *Apis proava* Menge, 1856 (currently *Electrapis proava*; Insecta, Hymenoptera): proposed conservation by designation of a neotype.

Opinions published in the Bulletin of Zoological Nomenclature

The following Opinions were published on 18 December 1998 in Vol. 55, Part 4 and on 30 June 1999 in Vol. 56, Part 2 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.

1910. *Roeslerstammia* Zeller, 1839 and *Acrolepiopsis* Gaedike, 1970 (Insecta, Lepidoptera): conserved by the designation of *Alucita erxlebella* Fabricius, 1787 as the type species of *Roeslerstammia*; and *A. erxlebella* and *Tinea imella* Hübner, [1813] (currently *Roeslerstammia erxlebella* and *Monopis imella*): specific names conserved by the designation of a neotype for *A. erxlebella.*
1911. *Dasineura* Rondani, 1840 (Insecta, Diptera): *Tipula sisymbrii* Schrank, 1803 designated as the type species.
1912. *Pseudofoenus* Kieffer, 1902 (Insecta, Hymenoptera): *Foenus unguiculatus* Westwood, 1841 designated as the type species.
1923. *Trachelocerca* Ehrenberg (Ciliophora): authorship conserved as Ehrenberg (1840), and *Vibrio sagitta* Müller, 1786 fixed as the type species.
1924. *Helix draparnaudi* Beck, 1837 (currently *Oxychilus draparnaudi*; Mollusca, Gastropoda): specific name conserved.
1925. *Turrilites gravesianus* d'Orbigny, 1842 (currently *Hypoturrilites gravesianus*; Mollusca, Ammonoidea): specific name conserved and a replacement lectotype designated; *Turrilites tuberculatus* Bosc, [1802] (currently *Hypoturrilites tuberculatus*): placed on the Official List.
1926. DASYPODIDAE Börner, 1919 (Insecta, Hymenoptera): spelling emended to DASYPODAIDAE, so removing the homonymy with DASYPODIDAE Gray, 1821 (Mammalia, Xenarthra).
1927. *Lactura* Walker, 1854 (Insecta, Lepidoptera): conserved, and the specific name of *Eustixis pupula* Hübner, [1831] (currently *Lactura pupula*): conserved.
1928. *Waagenoconcha* Chao, 1927 and *Gruntoconcha* Angiolini, 1995 (Brachiopoda): conserved.
1929. *Cnemidophorus neomexicanus* Lowe & Zweifel, 1952 (Reptilia, Squamata): specific name conserved.

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112(3):634. 1999.

REVIEWERS

The following people reviewed manuscripts for the *Proceedings* in 1998. S. Ahyong, C. C. Baldwin, R. C. Banks, W. C. Banta, R. Bauer, R. W. Baumann, F. M. Bayer, J. A. Blake, J. P. Blanco-Rambla, G. A. Boxshall, A. Brandt, R. Brinkhurst, B. Brown, N. L. Bruce, G. Brusca, D. R. Calder, D. K. Camp, M. D. Carleton, M. Carvalho, F. A. Chase, Jr., A. H. Cheetham, C. M. Cleveland, K. A. Coates, C. O. Coleman, P. Cornelius, F. B. Crandall, N. Cumberlidge, F. D'Incao, M. Dillon, M. Elias-Gutierrez, D. Erwin, D. G. Fautin, D. L. Felder, F. D. Ferrari, J. F. Fitzpatrick, Jr., K. Fitzhugh, O. S. Flint, Jr., C. H. J. M. Fransen, S. L. Gardiner, A. L. Gardner, O. Gon, N. Gotelli, G. R. Graves, M. J. Grygier, D. Guinot, C. Hand, E. Hatfield, B. Healy, R. W. Heard, Jr., M. E. Hendrickx, W. R. Heyer, Jr., S. Hiruta, S.-S. Ho, H. H. Hobbs, III, V. N. Ivanenko, D. A. Jones, D. Kathman, B. Kensley, W. Kim, N. Knowlton, W. Kobusch, R. K. Kropp, J. H. Leal, D. B. Lellinger, R. Lemaitre, B. J. MacFadden, R. B. Manning, W. N. Mathis, J. Mauchline, J. McCosker, R. W. McDiarmid, J. McEachran, D. McKinnon, P. A. McLaughlin, J. McLelland, J. Moore, U. Muehlenhardt-Siegel, A. Myers, C. R. Nelson, D. R. Nelson, J. Nelson, P. K. L. Ng, W. Ngoc-Ho, J. Norenburg, S. Ohtsuka, G. Pohle, W. W. Price, J. Pruski, C. E. Ray, N. A. Rayner, Y. R. Reddy, J. W. Reid, J. V. Remsen, M. E. Retzer, R. P. Reynolds, K. Riemann-Zürneck, R. Ríos, C. B. Robbins, C. R. Robins, G. Rodríguez, R. Roman-Contreras, D. A. Rossman, M. C. Sanz, W. B. Saunders, J. M. Savage, S. Schaefer, R. B. Searles, E. K. Shea, D. Smarzly, J. P. S. Smith, III, H. Squires, K. C. Stuck, H. Suzuki, M. Tavares, C. A. Taylor, F. G. Thompson, C. Tudge, J. C. Tyler, S. Tyler, R. Vargas, V. S. Vassilenko, J.-W. Waegele, X. Wang, S. H. Weitzman, M. J. Wetzel, J. T. Williams, K. Wittman, M. Wolsan, K. Wouters, E. L. Yochelson, G. R. Zug.

The International Code of Zoological Nomenclature

The new and extensively revised 4th Edition of the *International Code of Zoological Nomenclature* will be published in September 1999. It will come into effect on 1 January 2000 and will entirely supersede the current (1985) edition. Some notes about the forthcoming edition, which contains many new provisions, will be found on the Commission's Website (www.iczn.org).

The price of the 4th Edition is £40 or $65; the following discounts are offered:

Individual members of a scientific society ordering one copy of the Code for personal use are offered a discount of 25% (price £30 or $48); the name and address of the society should be given.

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The Bulletin of Zoological Nomenclature (the Commission's quarterly journal)—discount valid for up to 5 years; for 1999 the discounted price would be £51 or $90.

Translations of the Code in a number of languages are planned and their availability will be announced on the Commission's Website.

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112(3):735–736. 1999.

BIOLOGICAL SOCIETY OF WASHINGTON

126th Annual Meeting, 20 May 1999

President Richard P. Vari called the meeting to order at 11:05 a.m. in the Waldo Schmitt Room, National Museum of Natural History. Society members present: T. Chad Walter (Treasurer), Carole C. Baldwin (Secretary), Michael D. Carleton, Susan L. Jewett, Rafael Lemaitre, Roy W. McDiarmid (Elected Council), C. Brian Robbins (Editor), Storrs L. Olson (Custodian of Publications), Austin B. Williams (Finance Committee), Frank D. Ferrari (Associate Editor, Invertebrates), and Janet Reid, Leslie Knapp, and Steven D. Cairnes (past BSW presidents). Elected Council not in attendance: W. Duane Hope and James N. Norris.

Following approval of the minutes of the 125th Annual Meeting of the Society, President Vari called on Chad Walter for the Treasurer's Report. For the period 1 January 1998 to 31 December 1998, income for the Society exceeded expenses by $23,337.65 (Table 1), but all expenses related to publication of Volume 111 of the Proceedings are not accounted for in this relative figure. The Society continues to make modest financial gains from the sale of back issues of the Proceedings and from interest on Society accounts.

Editor Brian Robbins then reported that Volume 111 of the Proceedings comprised 87 papers totaling 1008 pages, up from 70 and 692, respectively, in Volume 110. As of 1 May, there were 37 submissions for Volume 112. There is no backlog for accepted papers. The Guidelines for submissions that was printed in 1990 as a Supplement to issue no. 1 will be revised and reprinted; Robbins solicited input from the Society regarding modifications or additions that should be incorporated.

Custodian of Publications, Storrs Olson, then provided an update on his progress of sorting the Society's stock of unbound Proceedings separates from Volumes 6–89. Separates are being arranged by taxonomic category for future sale as sets. Olson asked that a committee be established to deal with issues relating to pricing, advertising, and marketing of the sets when complete. President Vari so agreed, and it was decided after much discussion that this same committee should look into the fate of the Society's stock of bound Proceedings issues and consider a proposal that the number of extra copies of each volume printed be reduced from about 100 to 50.

Before calling for the Report from the Finance Committee, President Vari announced that Richard Banks had recently resigned from the Finance Committee and has been replaced by Bruce Collette. Because of a work-related absence, however, Collette was not able to participate in the preparation of the 1998 Finance Committee report, and Don E. Wilson joined Finance Committee member Austin Williams in this endeavor. Williams reported that accounting of the Society's funds by the Treasurer is in good order and that continued attention will be given to establishing a meaningful annual budget for the Society, a task made difficult by the unpredictability of number of Proceedings pages published, amount of page charges recovered from authors, etc. Williams also noted that the Society's contract with Allen Press will expire soon and recommended that other publishers be considered along with Allen Press in efforts to achieve an expedient new contract for the Society.

During the President's call for New Business, Storrs Olson suggested that the Society consider revamping the cover of the

Table 1.—Summary financial statement for 1998.

	General fund	Endowment fund	Total assets
ASSETS: JANUARY 1, 1997	14,722.89	91,557.33	106,280.22
TOTAL RECEIPTS FOR 1997	98,904.60	12,554.27	111,458.87
TOTAL DISBURSEMENTS FOR 1997	88,121.22	—.—	88,121.22
ASSETS: DECEMBER 31, 1997	25,506.27	104,111.60*	129,617.87
NET CHANGES IN FUNDS	10,783.38	12,554.27	23,337.65

* The income from publication inventory ($3,797.50) and Merrill Lynch income ($8,756.77) are the income for the Endowment Fund.

Proceedings. Much discussion ensued regarding possible cover designs, and Vari asked Editor Robbins to investigate with Allen Press the cost of various options proposed.

Chad Walter and Brian Robbins were commended for their diligent efforts and longstanding dedication to Society affairs, and Storrs Olson and Austin Williams were recognized for recent contributions.

President Vari adjourned the meeting at 12:15 p.m.

Respectfully submitted,
Carole C. Baldwin
Secretary

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings of the Biological Society of Washington* contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers are published in English (except for Latin diagnoses/descriptions of plant taxa), with an Abstract in an alternate language when appropriate.

Submission of manuscripts.—**Submit three copies of each manuscript in the style of the Proceedings to the Editor, complete with tables, figure captions, and figures** (plus originals of the illustrations). Mail directly to: Editor, Proceedings of the Biological Society of Washington, National Museum of Natural History NHB-108, Smithsonian Institution, Washington, D.C. 20560. (Do not submit manuscripts to an associate editor).

Presentation.—Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is recommended for descriptions and diagnoses. The style for the Proceedings is described in ''GUIDELINES FOR MANUSCRIPTS for Publications of the BIOLOGICAL SOCIETY OF WASHINGTON,'' a supplement to Volume 103, number 1, March 1990. Authors are encouraged to consult this article before manuscript preparation. Copies of the article are available from the editor or any associate editor.

The establishment of new taxa must conform with the requirements of appropriate international codes of nomenclature. Decisions of the editor about style also are guided by the General Recommendations (Appendix E) of the International Code of Zoological Nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Review.—One of the Society's aims is to give its members an opportunity for prompt publication of their shorter contributions. Manuscripts are reviewed by a board of Associate Editors and appropriate referees.

Proofs.—Authors will receive first proofs and original manuscript for correction and approval. Both must be returned within 48 hours to the Editor. Reprint orders are taken with returned proofs.

Publication charges.—Authors are required to pay full costs of figures, tables, **changes in proofs ($3.00 per change or revision),** and reprints. Authors are also asked to assume costs of page-charges. The Society, on request, will subsidize a limited number of contributions per volume. Payment of full costs will facilitate speedy publication.

Costs.—Printed pages @ $65.00, figures @ $10.00, tabular material @ $3.00 per printed inch per column. One ms. page = approximately 0.4 printed page.

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Abyssal sea anemones (Cnidaria: Actiniaria) of the northeast Pacific symbiotic with molluscs: *Anthosactis nomados,* a new species, and *Monactis vestita* (Gravier, 1918)

Tracy R. White, April K. Wakefield Pagels, and Daphne G. Fautin

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Abstract.—We describe *Anthosactis nomados,* new species, which belongs to family Actinostolidae, and redescribe *Monactis, vestita* (Gravier, 1918), a species belonging to family Hormathiidae. Anemones of both species live attached to molluscs on the soft-sediment abyssal plain of the northeastern Pacific Ocean. *Anthosactis nomados* is known from 260 specimens, most of which were still attached to scaphopod shells when studied, and the others of which show evidence of having been attached to one. By altering the definition of genus *Anthosactis* to include all tentacles being of equal length, this species can be accommodated in it. The species also differs from the other six species previously ascribed to the genus in the size of its nematocysts. We examined about 600 specimens of *Monactis vestita,* more than 350 of which show evidence of having been attached to a gastropod shell but none of which was still associated with the host when studied. This is the first report of *Monactis vestita* in such a symbiosis and from the Pacific Ocean. We hypothesize that both anemone-mollusc symbioses are mutualistic. In that between *Anthosactis nomados* and the scaphopod, which is the third anemone-scaphopod symbiosis to be documented, the protection provided by the sea anemone may allow the scaphopod to avoid the corrosive environment of sub-surface sediments and to forage at the surface where it can obtain energy and calcium carbonate. For both symbioses, the mollusc may resuspend sediments and carry the actinian to food-rich areas, and the anemone may protect its host from predators.

Specimens of the two species of sea anemones we studied were collected as part of long-term research on the biota of the abyssal northeastern Pacific. Specimens of both *Monactis vestita* (Gravier, 1918) and a new species we describe below were collected by A. G. Carey, Jr. from stations centered around 45°N, 135°W, approximately 1200 km off the coast of Oregon, at 3700–3900 m (Table 1). Many more specimens of the new species were collected by K. L. Smith, Jr. at a site referred to as Station M by us and Smith (Smith et al. 1994, Lauerman et al. 1996) and as Station N by Reimers et al. (1992), 220 km off the coast of California, at 34°50′N, 123°00′W, and 4100 m (fig. 1 in Lauerman et al. 1996). We examined 161 specimens of the new species

Table 1.—Data for specimens of *Monactis vestita* (*M. v.*) and *Anthosactis nomados,* new species (*A. n.*) collected off the Oregon coast. Shape of *Monactis vestita* specimens are coded as follows: d = dome-shaped, f = flat, co = wrapped around cylindrical object. Shapes are illustrated in Fig. 2. Museum abbreviations are provided in the text.

Catalog number	Station number	Coordinates	Depth	Number of specimens
SBMNH 144459	BMT 233	44°40′48″N, 133°26′18″W	3717 m	8d, 10f, 1co *M. v.*
SBMNH 144422	BMT 303	45°05′06″N, 133°10′54″W	3700 m	9d, 1f, 1co *M. v.*
SBMNH 345404	″	″	″	43 *A. n.*
SBMNH 144424	BMT 305	45°05′12″N, 134°43′24″W	3900 m	20d, 4f, 15co *M. v.*
SBMNH 144423	BMT 306	45°02′00″N, 134°42′12″W	3900 m	67d, 83f, 3co *M. v.*
RBCM 999-262-1	″	″	″	2d, 1f *M. v.*
SBMNH 345405	″	″	″	45 *A. n.*
SBMNH 144461	BMT 307	45°03′30″N, 134°45′00″W	3900 m	52d, 18f, 1co *M. v.*
USNM 100314	″	″	″	2d, 2f, 1co *M. v.*
SBMNH 345406	″	″	″	5 *A. n.*
SBMNH 144419	BMT 308	45°01′06″N, 135°13′36″W	3932 m	173d, 65f, 10co *M. v.*
CAS 119154	″	″	″	3d, 2f, 1co *M. v.*
KUNHM 01210	″	″	″	8d, 1f, 2co *M. v.*
SBMNH 345407	″	″	″	5 *A. n.*
SBMNH 144460	BMT 309	45°02′00″N, 135°23′12″W	3990 m	63d, 5f, 6co *M. v.*
LACM 1972-386.001	″	″	″	2d, 2f, 3co *M. v.*
SBMNH 345408	″	″	″	1 *A. n.*

from 36 collections made at Station M from 1989 to 1995. No specimens of *M. vestita* were collected at Station M. At least four specimens from Station M superficially looked like *M. vestita,* but differed significantly in characteristics of their nematocysts.

Each specimen of the new species examined from Station M was attached to the concave surface of a shell of the scaphopod *Fissidentalium actiniophorum* Shimek, 1997. Sixty-two percent of scaphopods we examined carried a sea anemone and another 30% of the shells showed evidence of recent anemone attachment—a brown material secreted by the anemone's pedal disk. This is the third documented sea anemone-scaphopod symbiosis. As part of the redescription of *Hormathia pectinata,* Riemann-Zürneck (1973) mentioned that some specimens collected in 1970–1971 from Stations 251 (53°51′S, 59°54′W, 535 m) and 271 (52°40′S, 60°39′W, 405 m) of the *Walther Herwig* Expedition were attached to a *Dentalium* shell. Shimek & Moreno (1996) reported the symbiosis between *Fissidentalium megathyris* and the species we describe below. In addition, Zibrowius (1998) reported a symbiosis in the northwestern Pacific between the solitary scleractinian coral *Heterocyathus japonicus* (Verrill, 1866) and the scaphopod *Fissidentalium vernedei* (Sowerby, 1860), and Carlgren (1928b) found the anemone *Paracalliactis stephensoni* Carlgren, 1928b, on a large *Dentalium* shell inhabited by the hermit crab *Parapagurus pilosimanus* Smith, 1879, off the Irish coast.

Specimens of both species we studied from the Oregon sites had been removed from their substrata. However, we were given a photograph (Fig. 1) of a specimen of *M. vestita* attached to the shell of *Buccinum* sp. (probably *B. strigillatum* Dall, 1891; Henry Chaney, Santa Barbara Natural History Museum, pers. comm.). We do not know whether *M. vestita* associates with more than one species of snail, but we infer from variation in concavity of the pedal disk that *M. vestita* attaches to substrata other than snail shells (Fig. 2). For instance, the pedal disk of some specimens had been wrapped around a cylindrical object and a

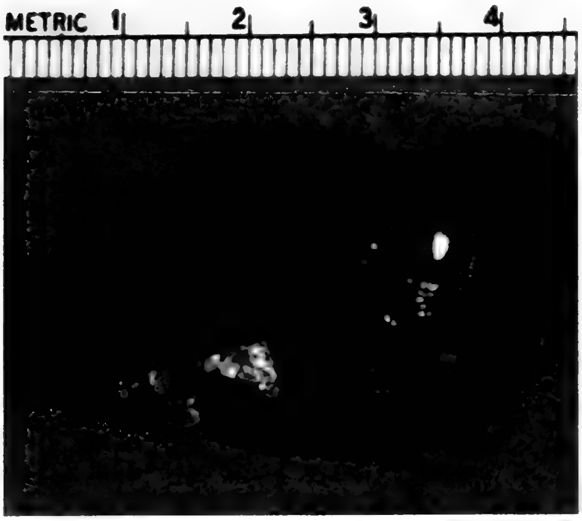

Fig. 1. Rounded specimen of *Monactis vestita* on *Buccinum*, probably *B. strigillatum*.

flat specimen (Fig. 3) was likely attached to a rock.

Paractis vestita Gravier, 1918 was described from 14 specimens collected during the voyages of the *Hirondelle* and the *Princess-Alice* from 1888 to 1913. Twelve specimens were collected in 1895 at Station 749 (38°54′00″N, 21°06′45″W, 5005 m) and two specimens were collected in 1905 at Station 2044 (32°28′00″N, 16°37′30″W, 2286 m). Eleven of the 12 syntypes from Station 749 bear catalog number 13 0022 and the two syntypes from Station 2044 bear catalog number 13 0080 in the Institut Océanographique of Monaco. Gravier's (1918) description was accurate except that he found no acontia. He therefore placed the species in family Paractidae, which is no longer valid. Recognizing acontia in 208 specimens she studied from six stations in the Venezuela deep-sea basin (3476–5060 m) and three stations off the Atlantic coast of Spain (4706–5320 m), Riemann-Zürneck (1986) created the genus *Monactis* for this species, which she placed in family Hormathiidae. The specimens Riemann-Zürneck (1986) studied were poorly preserved, so she could not provide information on internal anatomy or sources of cnidae. In 1992, Zamponi & Acuña described the reproductive structures of three specimens of *M. vestita* collected from 200-250 m near Mar del Plata, Argentina. Thus, *M. vestita* has been collected from only the Atlantic Ocean; we extend the range of *M. vestita* to the Pacific Ocean.

We infer these symbioses are mutualistic. Both species of sea anemones have increased access to food as they are carried across the sea floor by the mollusc. The scaphopod or snail, when covered by an expanded sea anemone, receives protection from predators. Scaphopods typically live buried within the sediment, but the symbiosis allows the scaphopod to live at the surface, where the sediment contains more calcium carbonate and energy (Smith et al. 1994). We initially hypothesized that the anemone also protects the aragonitic scaphopod shell from dissolution in this high-pressure, low-temperature environment where the water is undersaturated with respect to calcium carbonate (Edmond & Gieskes 1970, Berger 1976, Grotsch et al. 1991), but this hypothesis was not borne out.

Materials and Methods

Immediately after being trawled, some specimens of the new species from California and their host scaphopods were fixed in 10% buffered formalin and were later transferred to 70% EtOH; others were preserved immediately in 70% EtOH. Specimens of *M. vestita* were fixed at sea in buffered 10% formalin and later transferred to 70% EtOH.

Histological study was done of 41 specimens of the new species from California and 13 from Oregon. Five were embedded whole; the others were cut in half longitudinally through the center of the body, and the half on the larger-diameter (anterior) end of the scaphopod shell was removed for histology. Histological study was done of 16 specimens of *M. vestita.* Tissue was embedded in Paraplast® (melting point 56°C); 8 μm longitudinal sections or 10–20 μm cross sections were stained with hematoxylin and eosin (Humason 1979). Egg dimensions are reported as the average of the

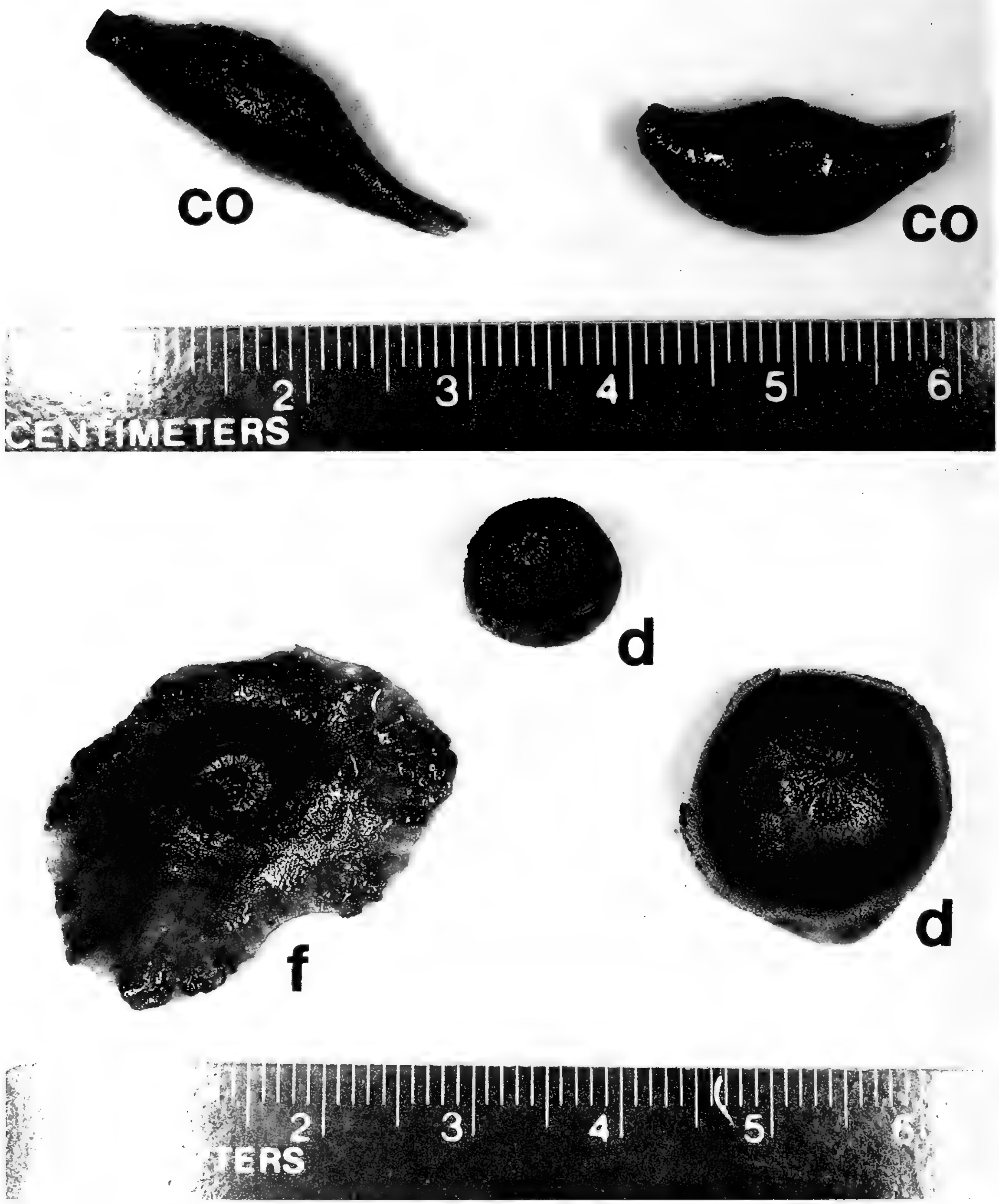

Fig. 2. Specimens of *Monactis vestita* (voucher: KUNHM 01210) demonstrating variety of shapes. (d) Dome-shaped specimens. (f) Flat specimen. (co) Specimens wrapped around cylindrical objects. Note cuticle on smaller specimen labeled d.

maximum diameter and the largest perpendicular diameter in one section of each egg with a visible nucleolus.

Tissue for cnidae squashes was taken from mesenterial filaments, acontia (in *M. vestita*), actinopharynx, tentacle tips, and oral and aboral sides of tentacle bases. Cnidae were studied with differential interference contrast optics; measurements are of undischarged capsules in squash preparations.

Anthosactis nomados, new species

Figs. 4–8

Column.—Freshly collected and preserved specimens white. All specimens contracted. Column smooth; ectoderm

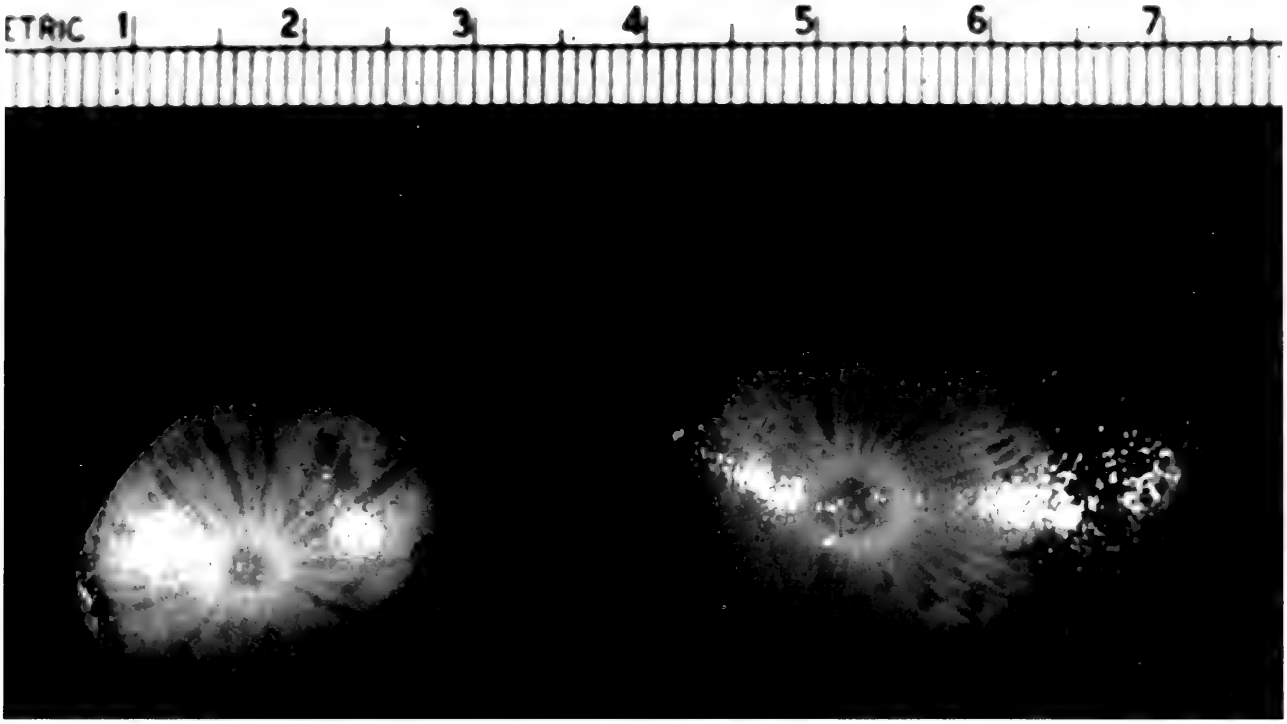

Fig. 3. Contracted specimens of *Monactis vestita* attached to rocks.

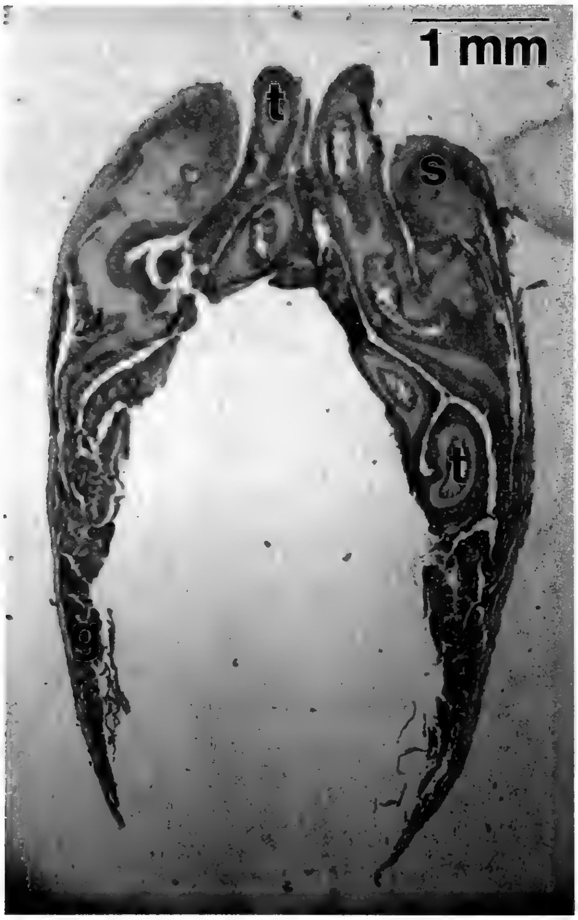

Fig. 4. Longitudinal section of *Anthosactis nomados*, new species. s = sphincter muscle, t = tentacle, g = gametes. Note that column ectoderm and pedal disk are absent (holotype: KUNHM 01019).

sloughed off in collected specimens (Fig. 4), a common condition in sea anemones collected from the deep sea (Carlgren 1928a, 1956; Fautin & Hessler 1989; Riemann-Zürneck 1993, 1994).

Sphincter.—Mesogleal. Thick at margin, without external evidence of projecting wall. Typically long: tapered at proximal end (Fig. 5A) but truncated in some (Fig. 5B). Commonly centered in mesoglea but typically closer to the endodermal side at proximal end; closer to ectodermal side in rare specimens. Muscle bundles dense and arranged transversely in most, scattered in others; reticulate in nature along endodermal side of some. Variability in appearance may be related to state of contraction or angle of section.

Pedal disk.—Broad; well-developed; so tightly adherent to shell of scaphopod *Fissidentalium actiniophorum* (Fig. 6) that it typically remains attached to shell when sea anemone is removed (Fig. 4). Maximum diameter never greater than length of scaphopod shell, ranging from 5 to 65 mm; median 44 mm. Midway along scaphopod shell, pedal disk typically covers 75% circumference of shell; coverage increases at

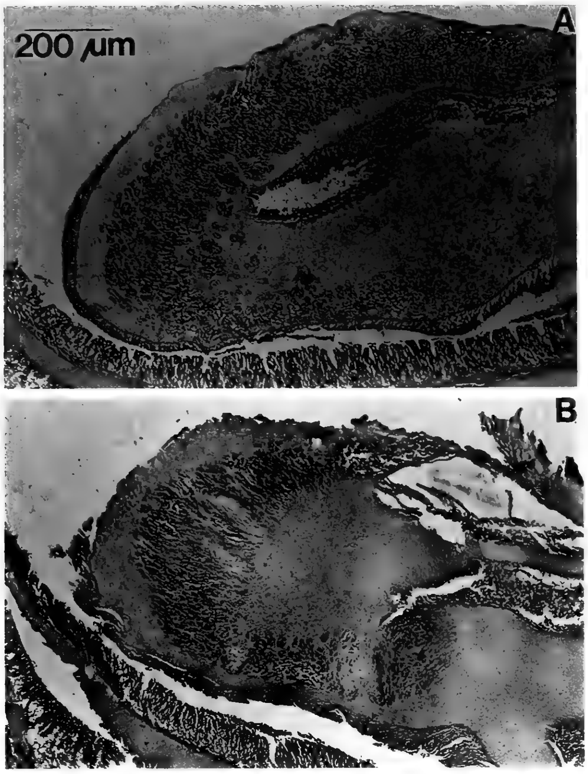

Fig. 5. Cross sections through mesogleal sphincter muscle of *Anthosactis nomados,* new species. Both figures are oriented so external side of sphincter is upward. (A) voucher: KUNHM 01020; (B) holotype: KUNHM 01019.

posterior end of shell, decreases at anterior end. Secretes brown cuticle onto scaphopod shell.

Oral disk and tentacles.—Oral disk not visible in specimens examined due to contracted state. Radial musculature of oral disk and longitudinal musculature of tentacles ectodermal (Fig. 7). Tentacles taper to a point; not thickened at base. Tentacle length uniform within an individual; range from 2 to 5 mm. Ratio of number of tentacles to number of mesenteries variable, ranging from 0.5:1 to 1:1, mean 0.7:1. Tentacles of preserved animals brittle and easily damaged or detached, which may explain variation in tentacle : mesentery ratio. Due to contracted state and morphology, number of siphonoglyphs and arrangement of tentacles could not be determined.

Mesenteries and internal anatomy.—Mesenteries hexamerously arrayed, in 3 cycles; first 2 cycles, including directives, complete, fertile, and filament-bearing; mesenteries in third cycle weak, sterile. Directive mesenteries aligned with long axis of scaphopod. Gametogenic tissue easily damaged or detached so pattern of fertile mesenteries difficult to determine. More mesenteries proximally than distally. Tertiary mesenteries develop asynchronously; either not all pairs of tertiary mesenteries present or not all reach distal portion of animal. Retractor muscles diffuse; due to morphology, structure of parietobasilar muscles could not be determined.

Sexes separate; 6 males, 1 female observed among sectioned specimens. Range of minimum and maximum diameter of sperm packets (n = 45) 34 × 36 µm–132 × 175 µm. In large packets, cells in various stages of spermatogenesis layered, with spermatozoa central. Diameter of three eggs 51–73 µm.

Cnidom.—Spirocysts, basitrichs, microbasic *p*-mastigophores, and microbasic *b*-mastigophores. Sizes and distribution of cnidae given in Table 2; cnidae illustrated in Fig. 8. No difference in cnidae on oral and aboral sides of tentacle base. All individuals have basitrichs of two size classes in tentacle tips; most have two size classes in tentacle bases. Robust spirocysts differentiated from typical ones by their thick and spiny tubules.

Etymology.—The specific epithet *nomados* is a Greek word for roving (Brown 1956), and was inspired by the nickname "crawling white anemone" bestowed on this sea anemone by Lynn M. L. Lauerman, then a graduate student at Scripps Institution of Oceanography. Its gender is feminine.

Specimens

Holotype.—University of Kansas Natural History Museum (KUNHM), Division of Invertebrate Zoology 01019, half a male intact on scaphopod shell and longitudinal histological sections of the other half (5 slides); collected 7 Nov 1993. Type locality 34°42′N, 123°08′W, 4100 m.

Paratypes.—United States National Mu-

Fig. 6. Contracted specimen of *Anthosactis nomados,* new species, attached to scaphopod shell. The oral disk of the sea anemone is approximately centered on the concave surface of the scaphopod shell. In a minority of the collected specimens, the pedal disk of the anemone is not wrapped tightly around the scaphopod shell but is bunched as shown in Shimek (1997: fig. 1).

seum of Natural History (USNM), Department of Invertebrate Zoology 96574, half a male intact on scaphopod shell and longitudinal histological sections of the other half (5 slides); collected 10 Feb 1994 from 34°41′N, 123°11′W at 4100 m. California Academy of Sciences (CAS), Department of Invertebrate Zoology and Geology 106264, half a male on scaphopod shell and longitudinal histological sections of the other half (5 slides); collected 17 Oct 1992 from 34°46′N, 123°08′W at 4100 m. Royal British Columbia Museum (RBCM), Department of Invertebrate Zoology 996-24-1, half a female removed from its scaphopod host and longitudinal histological sections of the other half (5 slides); collected 19 Jul 1993 from 34°43′N, 123°06′W at 4100 m. RBCM 996-25-1, one specimen intact on scaphopod shell; collected 1 May 1995 from 34°40′N, 123°03′W at 4100 m. Santa Barbara Museum of Natural History (SBMNH), Department of Invertebrate Zoology 143214, half a specimen intact on scaphopod shell and longitudinal histological sections of the other half (5 slides); collected 24 Feb 1993 from 34°45′N, 123°02′W at 4100 m. Los Angeles County

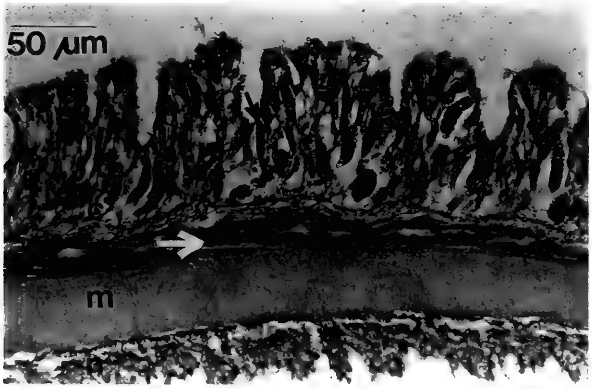

Fig. 7. Longitudinal section through tentacle of *Anthosactis nomados,* new species (voucher: KUNHM 01020). White arrow indicates ectodermal longitudinal muscle. A spirocyst is indicated by the black arrow. c = ectoderm, m = mesoglea, n = endoderm.

Table 2.—Size and distribution of cnidae of *Anthosactis nomados,* new species (letters refer to Fig. 8). "*n*" is the number of capsules measured and "#" is the proportion of animals examined in which that type of cnida was present. A single capsule that fell considerably outside the range of the others is distinguished by parentheses, following the convention of Dunn (1982).

Tissue/Cnida type	*n*	#	Capsule length (μm)	Capsule width (μm)
TENTACLE TIPS				
Spirocysts (A)	102	10/10	14.6–44.7 (51.5)	1.8–5.0
Robust spirocysts (B)	72	9/10	(16.7) 20.3–62.9 (66.6)	3.4–9.1 (9.6)
Basitrichs (C)	68	10/10	9.7–19.4	1.5–4.1
Basitrichs (D)	91	10/10	17.8–31.0 (32.8)	2.2–5.8
Microbasic *b*-mastigophores (F)	43	7/12	18.1–31.2	4.6–6.8
TENTACLE BASES				
Spirocysts (A)	101	10/10	14.8–37.8 (42.9)	2.3–5.7
Robust spirocysts (B)	114	10/10	(15.1) 18.2–45.6	3.0–10.9 (11.9)
Basitrichs (C)	60	7/10	10.6–17.9 (20.6)	2.3–4.1
Basitrichs (D)	135	9/10	18.5–30.9	2.6–5.1
ACTINOPHARYNX				
Microbasic *p*-mastigophores (E)	102	10/10	(30.2) 35.8–50.3	3.4–6.7
MESENTERIAL FILAMENTS				
Microbasic *p*-mastigophores (E)	100	10/10	28.9–44.7 (50.8)	(2.8) 3.3–6.6 (7.1)
Basitrichs (C)	102	10/10	(10.5) 11.3–15.9 (18.8)	2.2–5.4 (6.1)

Museum of Natural History (LACM), Department of Malacology and Invertebrate Paleontology 92-113.1, half a specimen removed from its scaphopod host and longitudinal histological sections of the other half (5 slides); collected 17 Oct 1992 from 34°46′N, 123°08′W at 4100 m.

Other material examined.—Sea anemones and scaphopods collected from August 1989 to October 1991 were borrowed from LACM. Scaphopods collected during 1992, from February 1993 to February 1994, during August 1994, and during February 1995 are housed at LACM; sea anemones from these collections are deposited in KUNHM. Scaphopods and sea anemones collected during July, September, and October of 1994, and May and June of 1995, are deposited in KUNHM.

Taxonomic Issues

Family Actinostolidae currently includes 22 genera (Fautin & Hessler 1989). The new species conformed in most respects to the definition of genus *Anthosactis.* To accommodate this species, we amend Carlgren's (1949) definition of *Anthosactis* slightly (change underlined):

> Actinostolidae with well developed pedal disc. Column smooth, rather low, often longitudinally sulcated in the contracted state. Sphincter strong, mesogloeal. Tentacles short, rather few, conical, robust, hexamerously or octamerously arranged, the outer only a little shorter than the inner ones or all tentacles of equal length. Outer tentacles on their aboral sides at the base provided with a stinging battery of microbasic *b*-mastigophors, which are sometimes distributed along the whole aboral side of the tentacle, though more numerous at the base. Longitudinal muscles of tentacles ectodermal, strongest on the oral side. Radial muscles of oral disc ectodermal to ecto-mesogloeal. Actinopharynx short with two well developed siphonoglyphs. Pairs of perfect mesenteries 6, 6+2 single, 8, or 12. 2 pairs of directives. Retractors rather weak, parietobasilar muscles fairly well developed. At least the younger mesenteries growing from the basal disc upwards. All stronger mesenteries fertile. Cnidom: spirocysts, basitrichs, microbasic *b*- and *p*-mastigophors.

See Table 3 for the differences between *A. nomados* and five of the six species listed by Carlgren (1949); a description of *A. georgiana* has never been published so is a nomen nudum.

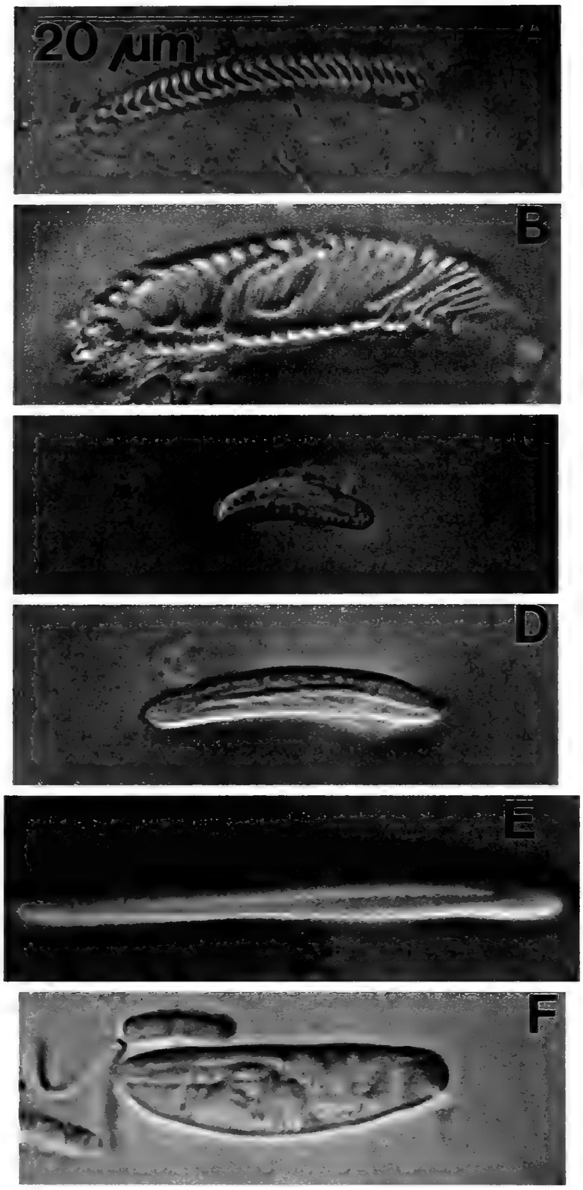

Fig. 8. Cnidae of *Anthosactis nomados,* new species. A and B are spirocysts; C and D are basitrichs; E is a microbasic *p*-mastigophore; F is a microbasic *b*-mastigophore. Size and distribution of cnidae are shown in Table 2.

Monactis vestita (Gravier, 1918)
Figs. 1–3, 9–11

Column.—Preserved specimens brown; most contracted. Scapus and scapulus distinct in extended specimens. Height of specimens 1.5 mm to 10 mm. Column covered in grainy cuticular material that flakes off (as reported also by Riemann-Zürneck 1986). Column of some specimens not entirely covered with cuticular material; may have been sloughed off during collection [as is common in sea anemones collected from the deep sea (Carlgren 1928a, 1956;

Table 3.—Major taxonomic attributes of *Anthosactis nomados* and the five congeners listed by Carlgren (1949).

Species	Describer (Redescriber)	Basitrichs of tentacles	Mesenteries	Tentacles
Anthosactis nomados	new species	11–18 × 2–4 µm 19–31 × 3–5 µm	hexamerous; 12 perfect; first 2 cycles fertile and with filaments	all equal length; not thickened at base
Anthosactis jan mayeni (type species)	Danielssen 1890 (Carlgren 1921)	74–93 × 12–13 µm	octamerous; 8 pairs perfect	inner thicker and longer than outer; outer thickened at base
Antholoba epizoica	Pax 1922 (Carlgren 1928a)	64–118 × 10–11 µm	hexamerous; 12? (6) pairs perfect	all same length
Anthosactis ingolfi	Carlgren 1921	53–75 × 11–13 µm	hexamerous; 6 pairs perfect; all fertile and with filaments	inner thicker and longer than outer
Paractis excavata	Hertwig 1882	no data	hexamerous; 12 pairs perfect; all fertile	inner shorter than outer; outer thickened at base
Anthosactis capensis	Carlgren 1938	19–24 × 3–3.5 µm	octamerous; 8 pairs perfect; first and second cycles fertile	no data

Fig. 9. Cross section through mesogleal sphincter of *Monactis vestita* oriented so external side of sphincter is upward (voucher: SBMNH 144423).

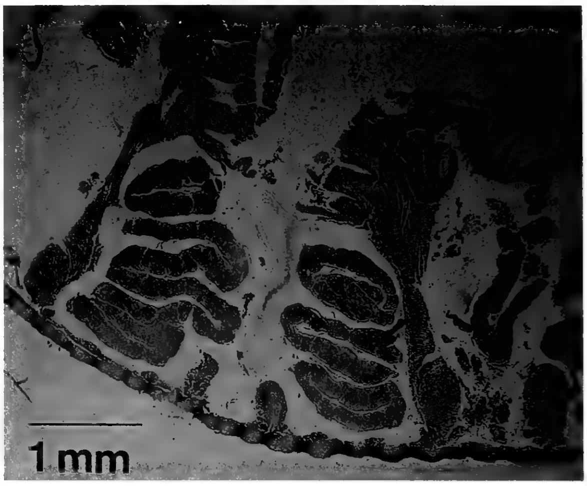

Fig. 10. Cross section of *Monactis vestita* (voucher: SBMNH 144460).

Fautin & Hessler 1989; Riemann-Zürneck 1993, 1994)]. Foraminiferans attached to pedal disk of few specimens; Gravier (1918) reported foraminiferans covering the column.

Sphincter.—Strong, mesogleal (Fig. 9). Centered in mesoglea; proximal end tapered and closer to endodermal side. Alveoli uniform in size.

Pedal disk.—Well-developed; so tightly adherent it usually remains attached to substratum when anemone is removed. Broad or narrow depending on substratum. Width (measured across surface of specimen) of flatter anemones 14.5 mm to 33 mm; 15 mm to 42 mm in anemones with concave pedal disks.

Oral disk and tentacles.—Oral disk not visible due to contracted state. Tentacles conical; base broad, tapering to pointed tip. One expanded specimen with 32 tentacles: 16 large inner tentacles and 16 small outer tentacles.

Mesenteries and internal anatomy.—Mesenteries hexamerously arranged in 4 cycles; only those of primary cycle complete. Two distinct siphonoglyphs moderately deep. More mesenteries proximally than distally. Retractor muscles diffuse, strong (Fig. 10). Acontia on primary mesenteries (as reported by Riemann-Zürneck 1986), inconspicuous; lighter in color than mesenterial filaments.

Sexes separate; 4 males, 8 females among those on which histology was done. Diameter of 25 eggs with visible nucleolus 53–107 μm.

Cnidom.—Spirocysts, basitrichs, and microbasic *p*-mastigophores. Sizes and distribution of cnidae given in Table 4; cnidae illustrated in Fig. 11.

Specimens

For repositories of voucher specimens, see Table 1.

Taxonomic Issues

Because Gravier (1918) did not find acontia in the specimens he studied, he identified them as *Paractis*; the new species differed from known species in number of complete mesenteries. In 1986, Riemann-Zürneck found acontia and established a new genus for the species now termed *Monactis vestita.* Carlgren (1949) listed 15 genera in family Hormathiidae; *Monactis* brings the number to sixteen.

Table 4.—Size and distribution of cnidae of *Monactis vestita* (letters refer to Fig. 11). "*n*" is the number of capsules measured and "#" is the proportion of animals examined in which that type of cnida was present.

Tissue/Cnida type	*n*	#	Capsule length (μm)	Capsule width (μm)
TENTACLE TIPS				
Spirocysts (A)	105	9/9	21.4–75.7	3.2–8.8
Robust spirocysts (B)	109	9/9	21.8–69.3	3.2–11.9
Basitrichs (C)	80	8/9	7.6–21.1	1.4–3.5
Basitrichs (D)	92	9/9	18.6–41.2	2.3–4.4
TENTACLE BASES				
Spirocysts (A)	71	7/7	23.8–62.3	3.4–8.8
Robust spirocysts (B)	81	7/7	24.1–53.1	4.1–12.6
Basitrichs (C)	62	7/7	9.8–17.7	1.4–3.3
Basitrichs (D)	71	7/7	19.3–32.7	2.5–4.4
Microbasic *p*-mastigophores (E)	67	7/7	16.7–23.4	3.0–5.4
ACTINOPHARYNX				
Basitrichs (D)	55	6/6	23.4–34.9	2.6–3.9
Microbasic *p*-mastigophores (E)	44	4/4	15.4–25.4	3.2–5.0
Microbasic *p*-mastigophores (F)	36	4/4	27.2–32.8	4.3–7.7
MESENTERIAL FILAMENTS				
Microbasic *p*-mastigophores (E)	66	7/7	19.8–25.6	3.4–5.1
Basitrichs (C)	68	7/7	10.6–19.3	2.0–3.1
ACONTIA				
Basitrichs (C)	40	4/4	10.9–20.9	1.8–3.2
Basitrichs (D)	40	4/4	27.6–37.7	3.1–4.6

The pedal disk was missing from most specimens we examined; presumably it was torn off when they were removed from their substrata. Acontia were found only in specimens with pedal disks that were intact or present at least at the margins. Gravier's (1918) not having found acontia may be explained if the specimens he studied had torn pedal disks.

Riemann-Zürneck (1986) could not determine the source tissue of cnidae except for acontia in the 208 poorly-preserved specimens of *M. vestita* she studied. Of more than 600 specimens we examined, many were in fine condition, so we could ascertain the cnidom of each tissue. Our data differ in two particulars from those of Riemann-Zürneck (1986): we found gracile spirocysts (in the tentacles) as well as the robust type found by Riemann-Zürneck, and the basitrichs we found fell into two size classes rather than three.

Discussion

Sea anemones of both species and their molluscan hosts from Oregon were separated by the time we obtained the specimens. We were therefore unable to ascertain which species of scaphopod hosted the specimens of *Anthosactis nomados* collected there. Likewise, we could not determine if *Buccinum strigillatum* is the only species of snail that hosts *Monactis vestita.* Gravier (1918) and Riemann-Zürneck (1986) studied specimens of *M. vestita* that were attached to objects such as stones. We are the first to document specimens of *M. vestita* attached to a snail as well as the first to record specimens from the Pacific Ocean. Perhaps only individuals from the northeast Pacific Ocean are symbiotic with molluscs. Despite the existence of other hard surfaces at Station M and off the Oregon coast, such as brachiopods, Mn nodules, snails, and sponge spicules, individuals of the sea

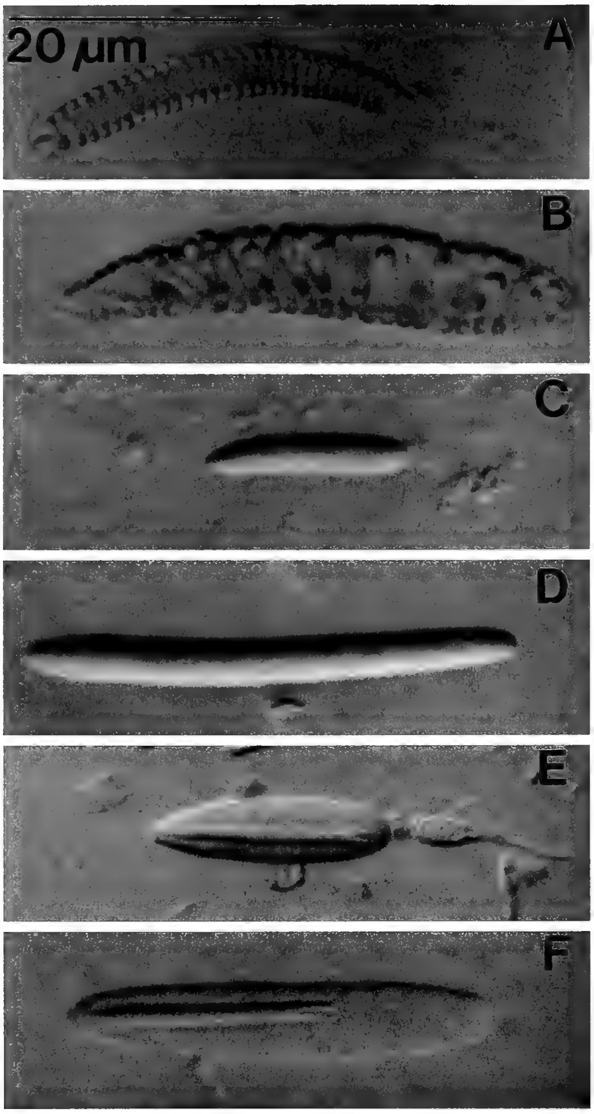

Fig. 11. Cnidae of *Monactis vestita.* A and B are spirocysts; C and D are basitrichs; E and F are microbasic *p*-mastigophores. Size and distribution of cnidae are shown in Table 4.

anemone *A. nomados* were found only on the shells of *Fissidentalium actiniophorum.*

We infer from the specificity of *A. nomados* that the scaphopod offers the anemone a benefit in addition to the hard substratum for attachment. By contrast, we infer that individuals of *M. vestita* attach to a variety of substrata. We hypothesize that *A. nomados* and *M. vestita* gain access to food by attaching to a mobile animal: food particles may be resuspended as the mollusc host moves through the sediment; if the sea anemone can pick prey off of the sea floor, it has access to a larger area than it would if it were stationary; and the mollusc host presumably can detect and move to food. Such benefits have been proposed for other sea anemones that are carried by hermit crabs or snails (Ross 1971, Dunn et al. 1980, Chintiroglou & Koukouras 1991, Riemann-Zürneck 1994).

We infer that the scaphopod and the snail are protected from predators by their actinian symbionts (e.g., Ross 1971, Brooks 1988) and thus that the symbioses are mutualistic. We further hypothesize that this protection provided by *A. nomados* enables its scaphopod host to forage in the upper layers of sediment that are rich in energy relative to sediments at depths in which such scaphopods typically live. The sediment at the surface has three times more ATP (an indicator of microbial activity) than that at a depth of 35 mm (Smith et al. 1994).

Living at the surface may also be favorable to formation and maintenance of the scaphopod's aragonitic shell. Scaphopods prey on foraminiferans (e.g., Shimek 1990, Langer et al. 1995). There are 1–18 × 10^3 m^{-2} calcareous foraminiferans in the surface sediments of Station M (Smith et al. 1994). Foraminiferans may be a source of calcium carbonate, as well as energy and nutrients, for the scaphopods (Shimek, pers. comm.). Very little carbonate carbon occurs in surface sediments of Station M (Reimers et al. 1992); absolute values of $CaCO_3$ in the upper 10 mm of sediment range from 5.14 to 16.36 mg (g dry weight)$^{-1}$ (Smith et al. 1994). The difficulty of producing and/or maintaining a calcareous shell at this site is reflected by a dearth of shelled organisms such as gastropods, bivalves, and brachiopods (Lauerman et al. 1996). The anoxic sediments below 2.5 to 3 cm (Reimers et al. 1992), the depth at which a scaphopod of this size might typically live, may be expected to be more corrosive to calcareous organisms than the surface sediments.

We had hypothesized the sea anemone might insulate the aragonitic shell of a surface-dwelling scaphopod from the surrounding sea water that is undersaturated with respect to $CaCO_3$. Geological thin-sections were made to compare shell thickness of host scaphopods in areas that had been covered by a specimen of *A. nomados* with areas that had not been covered. Fifteen scaphopod shells, 12 that had been partially covered by a sea anemone and three that showed no evidence of sea anemone attachment, were vacuum-embedded in clear epoxy resin. A 30 μm thin-section was made at one-third of the total shell length from the anterior end of each shell (one shell was sectioned at one-fourth of the total shell length) by Spectrum Petrographics, Inc. (Winston, Oregon). Two shells were thin-sectioned at two-thirds as well as one-third of the way along the shell. We compared cross-sectional area of the shell thin-section that had underlain the anemone with the portion that had been exposed. As a proxy for area, we used weight of the enlarged image of the thin-section traced onto matte board. Tracings of shells that had been bare or completely covered by a sea anemone were also divided into two parts, a portion that extended 270° around the shell, and a 90° portion. We normalized the weights to the length of the inner perimeter of the shell at that position. The ratios of normalized weights of the covered and exposed portions of each shell tracing were analyzed with the Sign Test (Samuels 1989).

Shell thickness in the areas covered and not covered by the anemone did not differ significantly (Sign Test, $p > 0.20$). The shells of *F. actiniophorum* are, however, unusually thin for a scaphopod, ranging in thickness from 189 μm to 479 μm (mean 309 μm; $n = 15$), which is a third to half as thick as the shells of *F. erosum* collected at 3000–3300 m (Shimek & Moreno 1996). [Shimek (1997:185) stated the thickness of the *F. actiniophorum* shell to be "about 150 μm"; he did not specify in which part of the shell his measurements were made. In one shell from which we had two sections, the anterior end was slightly thicker, and in the other shell there was no difference.]

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Urticina mcpeaki, a new species of sea anemone (Anthozoa: Actiniaria: Actiniidae) from the North American Pacific coast

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Abstract.—*Urticina mcpeaki,* a new species of sea anemone, is described based on specimens collected from the Coronados Islands, Baja California del Norte, Mexico; Santa Cruz and Anacapa Islands, Channel Islands, California; and Point Loma, California. Mesenteries and tentacles of the new species are arranged hexamerously, rather than decamerously as is typical for other species of *Urticina.* The new species is distinguished externally from other species in the genus by a radial banding pattern on the oral disc, longitudinal striping on the tentacles, and typically debris-covered adhesive verrucae on a bright-red column. We include the first detailed description of the two morphologically different types of microbasic p-mastigophores in the mesenterial filaments. Additionally, size ranges of holotrichs in the tentacle tips are given for the first time for a species in the genus *Urticina.*

Urticina Ehrenberg, 1834 is the most speciose genus of sea anemones on the Pacific coast of North America. Gotshall (1994) recognized five species: *Urticina columbiana* Verrill, 1922; *U. coriacea* (Cuvier, 1798); *U. crassicornis* (Müller, 1776); *U. lofotensis* (Danielssen, 1890); and *U. piscivora* (Sebens & Laakso, 1977). Sebens & Laakso (1977) recognized the same five species under the generic name *Tealia* Gosse, 1858, a junior synonym of *Urticina* (Williams *in* Manuel, 1981). In addition to these species, Zamponi & Acuña (1996) reported *Urticina asiatica* (Averincev, 1967) and *U. tuberculata* (Cocks, 1851) from Barkley Sound, British Columbia, Canada. On the west coast of North America, the genus *Urticina* ranges from Alaska to Baja California. Within this range, animals occur either in the subtidal or in both the intertidal and subtidal zones (Cutress 1949, Hand 1955, Sebens & Laakso 1977, Gotshall 1994, Zamponi & Acuña 1996). Sea anemones in the genus *Urticina* also occur in the Northwest Pacific and on both sides of the North Atlantic. Though originally applied to North Atlantic species, the names *U. coriacea, U. crassicornis,* and *U. lofotensis* are applied to Northeast Pacific species sensu Hand (1955).

External characters that have been used for distinguishing species in the genus *Urticina* are color pattern and the presence and nature of verrucae on the column (Cutress 1949, Hand 1955, Sebens & Laakso 1977, Gotshall 1994, Zamponi & Acuña 1996). Internal characters include size and distribution of cnidae, number and arrangement of mesenteries, and distribution of fertile mesenteries (Hand 1955, Sebens & Laakso 1977, Zamponi & Acuña 1996).

Materials and Methods

Divers collected nine animals in September 1995 at 25 m from 1.85 km southeast of the tip of South Coronado Island, the Coronados Islands, Baja California del Norte, Mexico. Ten animals were collected in May 1997 from Point Loma, San Diego, California at 15 m. Animals were held in tanks for observation before relaxation with magnesium sulfate and fixation with 10% formalin. Five museum specimens from the California Academy of Sciences Department of Invertebrate Zoology and Geology (CASIZ) were also examined: CASIZ 61487 (two specimens) and 61488 (one specimen) from Santa Cruz Island, Channel Islands, California, and CASIZ 61491 (two specimens) from Anacapa Island, Channel Islands, California.

Undischarged cnidae capsules from the column and structures at the margin, the actinopharynx, mesenterial filaments, and the tips and bases of the outer and inner tentacles were measured from squash preparations at 1000× magnification. Cnidae nomenclature follows Mariscal (1974). Display of cnidae data follows Dunn, Chia, & Levine (1980). Histological sections 8 μm thick were stained with hematoxylin and eosin (Humason 1979). Oocytes were measured following the method of Wedi & Dunn (1983).

Urticina mcpeaki, new species
Figs. 1A, B, 2–5

Pedal disc.—Circular, strongly adhesive. Color bright red; mesenterial insertions visible as darker red radiating lines. Well developed basilar muscles along each mesentery.

Column.—Bright red with many small, white, adhesive verrucae. Verrucae usually heavily encrusted with debris (Fig. 1A) and arranged in longitudinal rows corresponding to endocoels and exocoels. No verrucae on limbus. Well developed margin and fosse. Distinct round marginal structures; in life yellow, with dark-colored depression in center (Figs. 1A and 2A). Histology (Fig. 2B) and cnidae complement of marginal structures is not distinct from rest of column. When expanded, column generally wider than tall. Maximum size of animals smaller than other species in genus found in Northeast Pacific; not larger than 5–6 cm pedal disc diameter when expanded. Height generally not greater than 3–4 cm; oral disc diameter when expanded similar to pedal disc diameter. No cinclides present.

Tentacles.—Long and slender when expanded, short and blunt with longitudinal furrows when contracted. Arrangement hexamerous with up to 5 cycles; in most specimens fifth cycle incomplete. Number of tentacles 68–93. Base color of tentacles in most individuals red; in some pink, tan, or brown. Each tentacle encircled with light-colored band at base. Longitudinal stripe extends upward from band at base 1/2–2/3 length of tentacle on aboral side (Fig. 1A), then broadens, creating chevron shape on oral side (Fig. 1B). In most individuals stripe white; other colors such as orange may occur. Bases of tentacles outlined by dark red bands corresponding to mesenterial insertions (Fig. 1B). Longitudinal muscles strong, mesoectodermal; circular muscles weak, endodermal (Fig. 3).

Oral disc.—Color in most individuals red; in some orange or pink. Mesenterial insertions clearly visible. Broad, tentacle-free region around mouth, usually white or light olive green, gives way to distinctive radial banding pattern, such that 12 thick bands extend outward to spaces between first two cycles of tentacles (Fig. 1B). Actinopharynx red, ribbed, with 2 red siphonoglyphs. Radial muscles strong, mesoectodermal.

Mesenteries and internal anatomy.—Mesenteries arranged hexamerously in 4 cycles. Fourth cycle usually incomplete; fourth cycle mesenteries added in exocoels between first and third cycles first, then between second and third cycles. Typical arrangement from half of an animal, directive to directive: D 4 3 2 3 4 1 4 3 2 4 3 4 1 4 3 2 3 4 D. Number of mesentery pairs 29–44; one irregular individual with 52 pairs. Number of mesenteries same proximally and distally. Two pairs of directive mesenteries attached to siphonoglyphs. First and

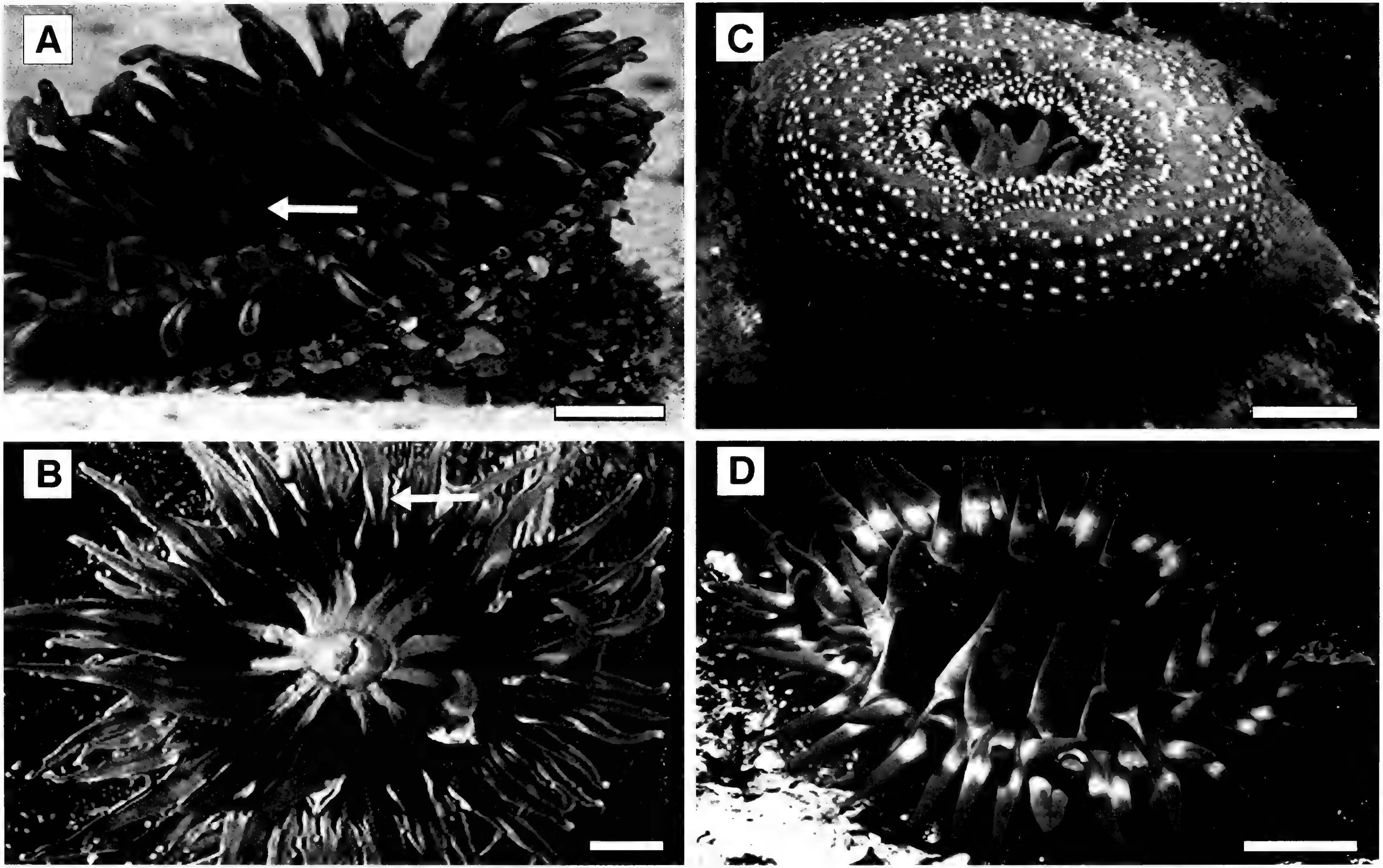

Fig. 1. A and B, *Urticina mcpeaki,* new species. A, lateral view showing longitudinal stripes on tentacles (arrow), structures on margin, and debris attached to column. Scale bar = 1 cm. B, oral disc view showing hexameral banding pattern on disc and chevron shape on tentacles (arrow). Scale bar = 1 cm. C and D, *U. lofotensis* (Danielssen, 1890). C, oral disc view showing white verrucae on column. Scale bar = 2 cm. D, oral disc view showing pattern of tentacles. Scale bar = 3 cm. Photo D by Neil McDaniel.

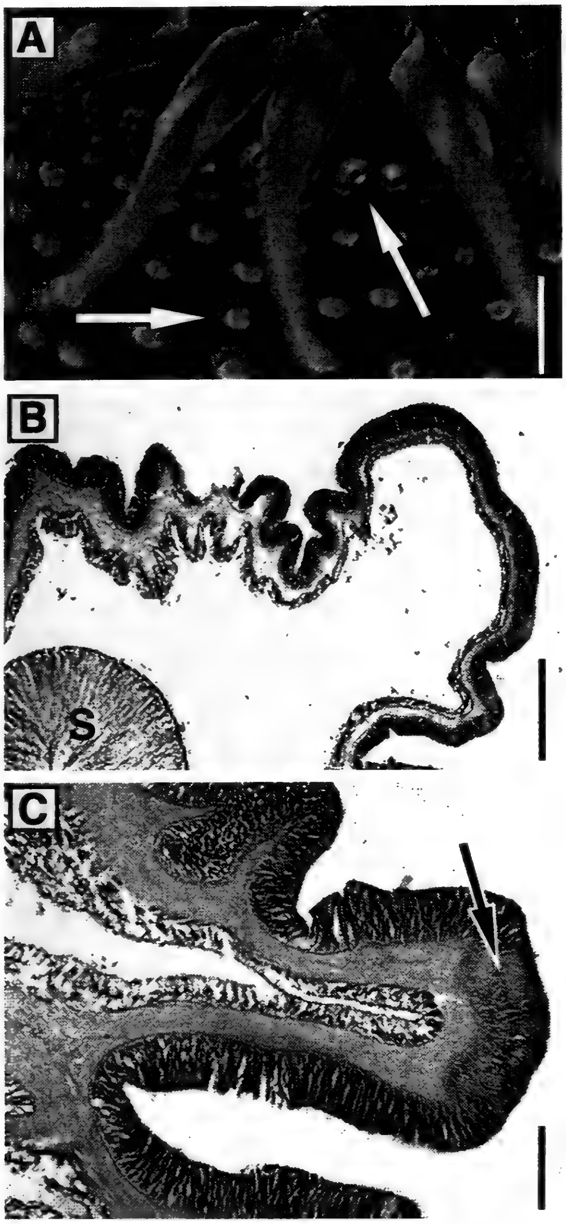

Fig. 2. *Urticina mcpeaki,* new species. A, View of column showing marginal structures (slanted arrow) and verrucae (horizontal arrow). Scale bar = 1.5 cm. B, Histological section showing marginal structure and sphincter (s). Scale bar = 0.2 mm. C, Histological section showing verrucae with modified glandular ectoderm (arrow). Scale bar = 0.2 mm.

second cycles perfect. First cycle sterile; all subsequent cycles may bear gametogenic tissue. Sexes separate. Maximum diameter of ripe oocytes in section approximately 450 μm. Retractor muscles strong, diffuse to restricted (Fig. 4). Parietobasilar muscles well developed and extending from half to entire distance from column to retractor muscle, terminating in free flap (Fig. 4). Marginal stomata present; oral stomata not seen.

Endodermal marginal sphincter muscle circumscribed, large, strong; circular to oval in shape (Fig. 3) and attached to column wall roughly halfway between fosse and parapet. Laminae arranged pinnately and of equal length on both sides of lamella.

Cnidom.—Spirocysts, basitrichs, holotrichs, and microbasic p-mastigophores (two types).

Distribution and size of nematocysts and spirocysts.—In the following table, *n* signifies the number of individual capsules measured, N signifies the ratio of the number of specimens in which a type of cnida was found to the number of specimens examined, and measurements in parentheses indicate individual capsules that fell outside the range.

Tentacles (tip and base of inner and outer):

Spirocysts (Fig. 5A) 12.5–39.9 × 1.4–4.4 μm; *n* = 528, N = 15/15
Basitrichs (Fig. 5B) 6.5–32.3 × 1.1–4.8 μm; *n* = 709, N = 15/15
Holotrichs (Fig. 5C) (found only in tips, particularly of outer tentacles) 13.8–23.3 × 2.9–4.9 μm; *n* = 111, N = 11/15

Column, including margin:

Basitrichs (Fig. 5B) 4.5–9.2 × 1.0–2.5 μm; *n* = 46, N = 10/11
Basitrichs (Fig. 5B) 13.4–23.1 (35.4) × 1.5–4.6 μm; *n* = 152, N = 11/11

Actinopharynx:

Basitrichs (Fig. 5D) 19.2–38.9 × 2.5–6.0 μm; *n* = 245, N = 14/14
Microbasic p-mastigophores type I (Fig. 5E) 16.5–29.2 × 4.0–7.6 μm; *n* = 64, N = 8/14

Mesenterial filaments:

Basitrichs (Fig. 5B) 11.5–29.8 (34.4, 36.2) × 1.9–4.1 μm; *n* = 207, N = 11/11
Microbasic p-mastigophores type I (Fig. 5E) 11.7–30.3 (33.1) × 3.5–6.8 μm; *n* = 122, N = 11/11

Fig. 3. *Urticina mcpeaki,* new species. Histological section showing sphincter muscle and cross section of tentacle. Scale bar = 0.25 mm.

Microbasic p-mastigophores type II (Fig. 5F) 19.8–42.9 × 3.6–8.6 μm; n = 113, N = 11/11

Distribution.—From Santa Barbara, California, south at least to Asuncion, Baja California, Mexico.

Habitat.—Subtidal, in shallow debris-filled depressions of rocks.

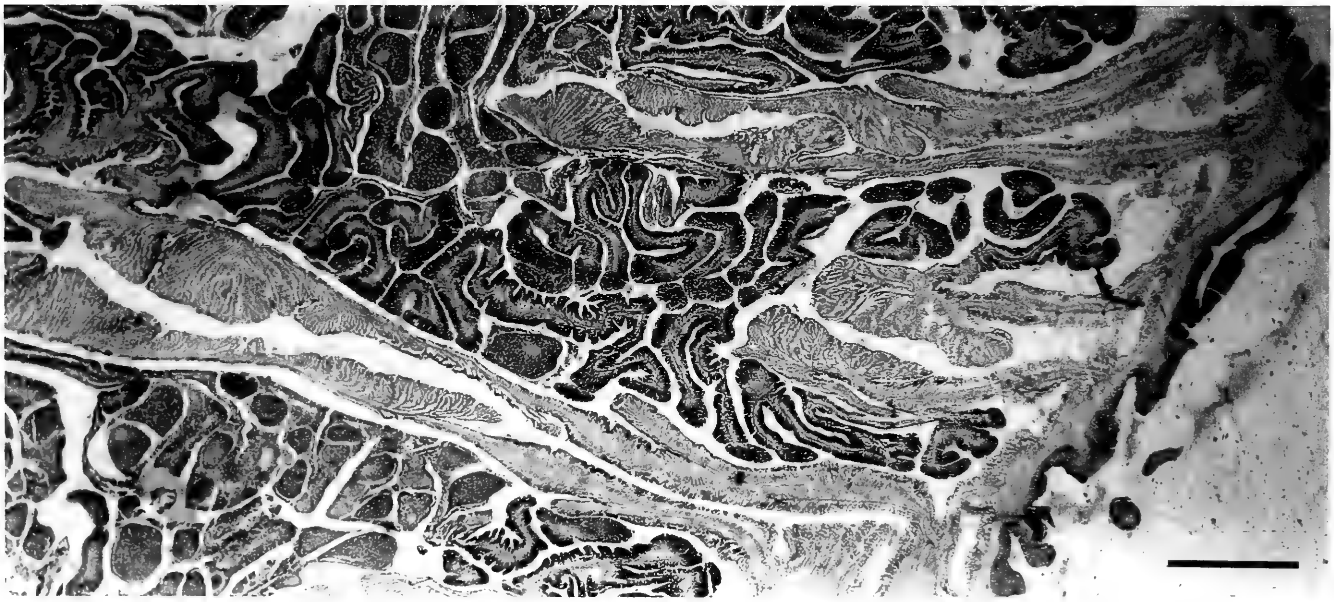

Fig. 4. *Urticina mcpeaki,* new species. Histological section showing oocytes and three pairs of mesenteries with retractor muscles and parietobasilar muscles. Scale bar = 1 mm.

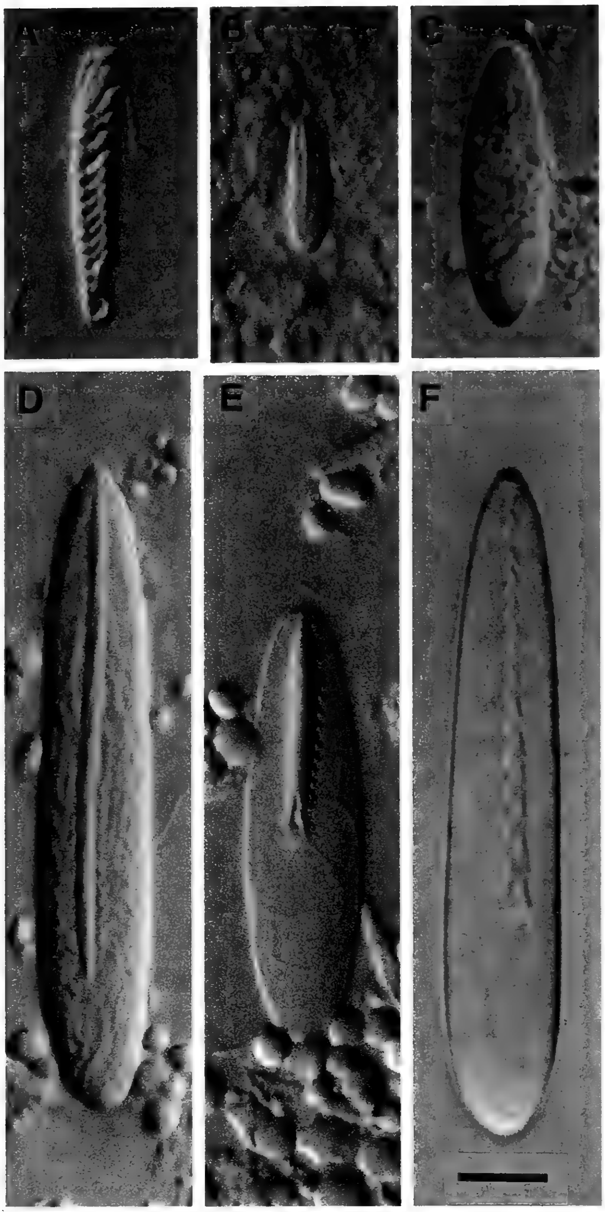

Fig. 5. *Urticina mcpeaki,* new species. Cnidae signature. See text for explanation. Scale bar = 5 μm.

Type material and locality.—Holotype collected May 1997 from Point Loma, San Diego, California at 15 m; deposited at the CASIZ 114595. Histological slides of specimen also deposited.

Paratypes from type locality CASIZ 114596 and 114597, Santa Barbara Museum of Natural History (SBMNH) 145138 and 145139, University of Kansas Natural History Museum (KUNHM) 001041, National Museum of Natural History (NMNH) 99971 and 99972, and Royal British Columbia Museum (RBCM) 998-221-1. Paratype from the Coronados Islands also deposited at RBCM 998-222-1. Additional specimens examined deposited at KUNHM 001038, 001162 through 001168.

Etymology.—The specific epithet *mcpeaki* honors Mr. Ron McPeak, who first noticed this species in 1958 and suspected it was a new species of *Urticina.* He provided many of the specimens examined.

Discussion and Differential Diagnosis

Urticina mcpeaki, new species, fits the generic description of *Tealia* (= *Urticina*) sensu Carlgren (1949). It is an actiniid with a well-developed pedal disc, adhesive verrucae on the column, and a well-developed fosse. It has a strong, circumscribed, endodermal sphincter, and the longitudinal musculature of the tentacles and radial musculature of the oral disc are mesoectodermal. The basitrichs of the actinopharynx are larger than those of the tentacles.

The major morphological difference between *U. mcpeaki* and other species in this genus is that mesenteries and tentacles of the first three cycles are always arranged hexamerously. Mesenteries in the fourth cycle are not added simultaneously, resulting in a break of the hexamerous pattern. In other species of *Urticina,* mesenteries and tentacles are usually arranged decamerously (Carlgren 1893, 1921, 1949; Hand 1955, Sebens & Laakso 1977, Manuel 1981). Hexametry in *U. mcpeaki* is unusual, but it is not unique within *Urticina.* Several authors (e.g., Carlgren 1902, 1949; Sebens & Laakso 1977, Zamponi & Acuña 1996) refer to specimens of *Urticina* in which the arrangement of either the mesenteries or the tentacles is not strictly decamerous, but rather hexamerous.

The new species can also be distinguished from other species in this genus by its geographic range. *Urticina mcpeaki* occurs as far north as Santa Barbara, California (Jack Engle, Ron McPeak, pers. comm.). The geographic ranges of all other species of *Urticina* on the west coast of North America extend at least as far north as Vancouver Island, British Columbia, Canada. Most species are found as far north as Alaska (Gotshall 1994). The range of *U. mcpeaki* overlaps with the ranges of *U. columbiana, U. coriacea, U. lofotensis,* and *U. piscivora* (Ron McPeak, pers. comm.).

Of all species of *Urticina* on the North American Pacific coast, *U. mcpeaki* most closely resembles *U. lofotensis* externally. Both species have a bright red column with distinct white verrucae arranged in longitudinal rows. However, *U. mcpeaki* can be distinguished externally from *U. lofotensis* by the color pattern of the tentacles and oral disc. *Urticina mcpeaki* has a distinct longitudinal stripe on the otherwise uniformly colored tentacles (Fig. 1A). *Urticina lofotensis* does not have stripes on the tentacles and the color changes from yellow at the base to red at the tip (Fig. 1D). In *U. mcpeaki,* the oral disc has a distinct radial banding pattern (Fig. 1B), while the oral disc of *U. lofotensis* lacks this pattern (Fig. 1D).

The structures at the margin of *U. mcpeaki* differ from those of *U. lofotensis.* In *U. mcpeaki* they are yellow and have a dark-colored depression in the center (Figs. 1A and 2A). The structures in *U. lofotensis* are white and do not differ in appearance from the verrucae on the column (Fig. 1C). Histologically the marginal structures in both species differ from verrucae. Verrucae, sensu Carlgren (1949), have modified ectoderm (e.g., Fig. 2C), which is lacking in the marginal structures. The distinct marginal structures of *U. mcpeaki* may be confused externally with other marginal specializations such as spherules or pseudospherules. However, they do not fit the definition of marginal spherules or pseudospherules, sensu Carlgren (1949), because they have no distinctive histology (Fig. 2B) or cnidae.

The verrucae of *U. mcpeaki* usually have debris attached to them (Fig. 1A). Although the verrucae of *U. lofotensis* are capable of attaching debris (pers. observation), specimens are usually found with no debris attached (Fig. 1C). In *U. mcpeaki,* verrucae are absent from the limbus. In *U. lofotensis,* verrucae extend to the limbus where they are smaller and closer together than the verrucae of the column.

Lastly, the two species differ in size. The pedal disc diameter in the largest specimens of *U. mcpeaki* is 6 cm, while in *U. lofotensis* it can reach to 18 cm (Sebens & Laakso 1977).

This is the first detailed description of the two types of microbasic p-mastigophores found in the mesenterial filaments. Microbasic p-mastigophore type I (Fig. 5E) is more oval than type II (Fig. 5F) and has pronounced serrations all along its robust shaft. Cnidae of type II are usually larger than those of type I; however, there is some overlap in size within individuals. Type II are more slender than type I, in proportion to their lengths, and the serrations of the shaft are not as distinct. In a few individuals, small numbers of microbasic p-mastigophores type I were also found in other tissues (column, actinopharynx, and tentacle base). These capsules were considered contaminations of those tissues. Microbasic p-mastigophore type II were found only in the mesenterial filaments. We have subsequently found both types of microbasic p-mastigophores in *U. columbiana, U. coriacea, U. crassicornis, U. lofotensis,* and *U. piscivora* from the Northeast Pacific. In his monograph on sea anemones of central California, Hand (1955) included line drawings of the two types of microbasic p-mastigophores he found in the mesenterial filaments of *Tealia crassicornis* (p. 74) and *T. lofotensis* (p. 85) and the one type he found in *T. coriacea* (p. 81). He did not describe the differences between the two types. Our type I corresponds to Hand's line drawing labeled "g" for *T. crassicornis* and *T. lofotensis,* and "k" for *T. coriacea.* Our type II corresponds to Hand's line drawing labeled "h" for *T. crassicornis* and *T. lofotensis.*

This is also the first description of a species of *Urticina* that includes a size range for tentacle holotrichs. In their report of several species of *Urticina* from British Columbia, Zamponi & Acuña (1996) did not give sizes and probably identified the type of cnidae we term holotrichs as atrichs. Holotrichs have armature along the entire tubule, as opposed to atrichs, which have no armature (Weill 1930). If the spines are very fine, holotrichs can be confused with atrichs (Cutress 1955). As Bigger (1976, 1982) pointed out, atrichs and holotrichs have been confused repeatedly throughout the literature. Sebens & Laakso (1977) mentioned a personal communication with C. Hand regarding the size of holotrichs found in the tentacle tips of several species of *Tealia.* The holotrichs were reportedly larger than other nematocysts in the tentacle tips. We found in *U. mcpeaki* that holotrichs overlap in size with the basitrichs and are never larger. Preliminary data suggest this is also true for *U. coriacea, U. crassicornis,* and *U. lofotensis* from the Northeast Pacific.

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Morphological observations on a hatchling and a paralarva of the vampire squid, *Vampyroteuthis infernalis* Chun (Mollusca: Cephalopoda)

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Abstract.—We present morphological observations on two very small vampire squids. One, a trawl-caught hatchling of 8 mm mantle length (ML), had embryonic features including internal yolk, broad arm-like filaments, and lack of mantle-head fusion. The other was a 9 mm ML paralarva collected by submersible and photographed alive aboard ship. Although only slightly larger than the hatchling, its morphology was much more like that of larger specimens than that of the hatchling, except for the oblique orientation of its fins.

The vampire squid, *Vampyroteuthis infernalis* Chun, 1903, is the only living member of the Vampyromorpha, the sister group to the Octopoda (Young & Vecchione 1996, Young et al. 1998). Through outgroup and ontogenetic comparisons, this species holds important clues to our understanding of cephalopod evolution and to the reconstruction of ancestral character states. Very little has been published, however, concerning its anatomy, behavior or embryology. As a result, any new information is valuable. We report here on two very small vampire squid. One, a hatchling captured by trawl, was dead but in excellent condition when retrieved. The other was a paralarva (= "stage 1 larva", Pickford 1949a) captured alive from a submersible and photographed in a shipboard aquarium. These are the first observations of a live vampire squid paralarva. Together, these observations support many morphological characters described by Pickford (1949a) from damaged specimens.

Materials and Methods

The hatchling *Vampyroteuthis* (8 mm ML, USNM 885891) was captured near the Hawaiian Islands on a cruise of the R/V *New Horizon* off leeward Oahu on 1 July 1996. The collecting gear was an opening–closing net that fished between 0130 and 0743 h at a depth of about 1050–1300 m (Sta. 62). The specimen was sorted from the catch soon after collection, and photographs were taken aboard ship shortly thereafter. The paralarva (9 mm ML, USNM 816886) was captured in the eastern Gulf of Mexico using a pelagic suction sampler from the manned submersible *Johnson Sea Link II* during dive 1453, 30 August 1987, 24°30′5″N, 83°45′12″W at 830 m depth. It was photographed while still alive immediately after the submersible returned to its support ship.

Observations

Hatchling.—The trawl-caught animal was clearly a hatchling (i.e., there was no chorion surrounding it), but morphologically it was an advanced embryo presumably incapable of feeding except from its internal yolk supply. A large mass of yolk globules, presumably within a large internal yolk sac, was seen through the transparent gladius ventral and lateral to the esophagus.

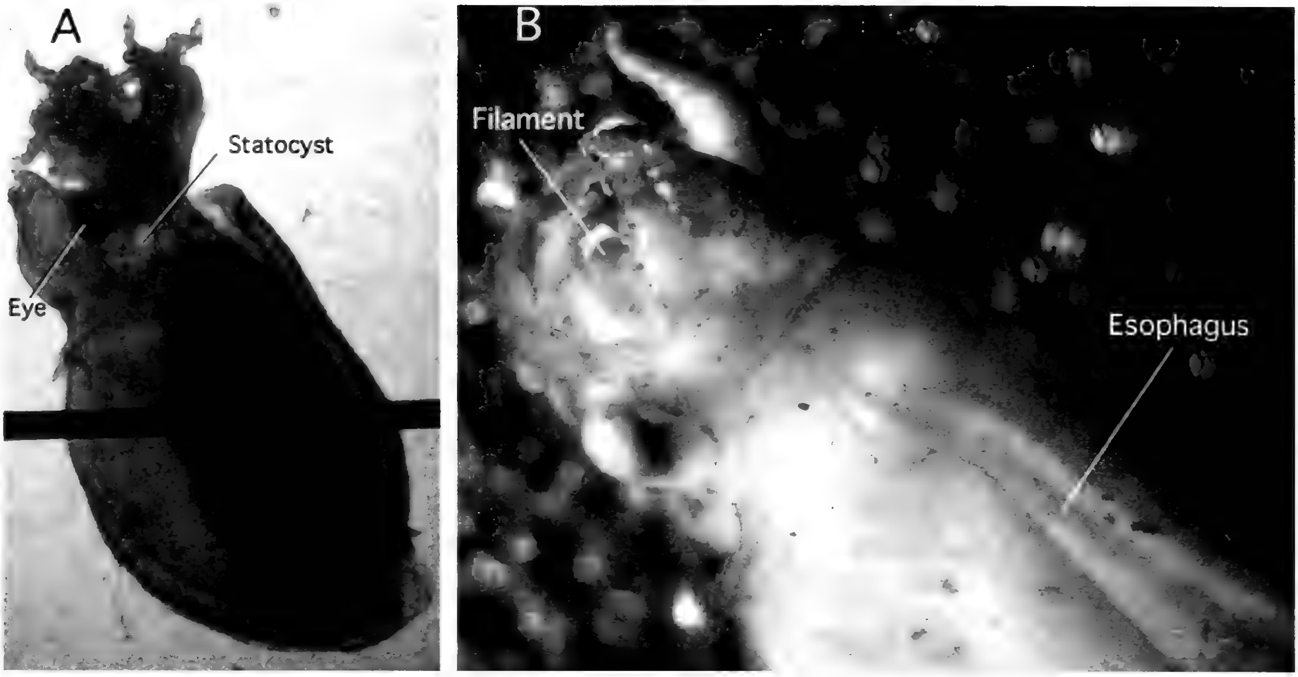

Fig. 1. Photographs of freshly collected *Vampyroteuthis infernalis* hatchling (8 mm ML). A, Lateral view with dissecting pin laying across mantle to prevent motion from the ship's rolling; B, Dorsolateral closeup of head and anterior mantle.

During attempts to photograph the embryo aboard ship, a pin was placed on top of the mantle to keep the animal from rolling (Fig. 1A). This resulted in a sausage-shaped extrusion of yolk from the buccal region.

The body of the hatchling was very large relative to the head and arms (compare Fig. 1A with Fig. 3), the eyes were very small and the mantle was not fused to the head in the nuchal region (Fig. 2). The eye fold formed a circular fold around the base of each eye, not yet enclosing the eye. Although squid eyes often are forced out through circular eyelids during capture, this

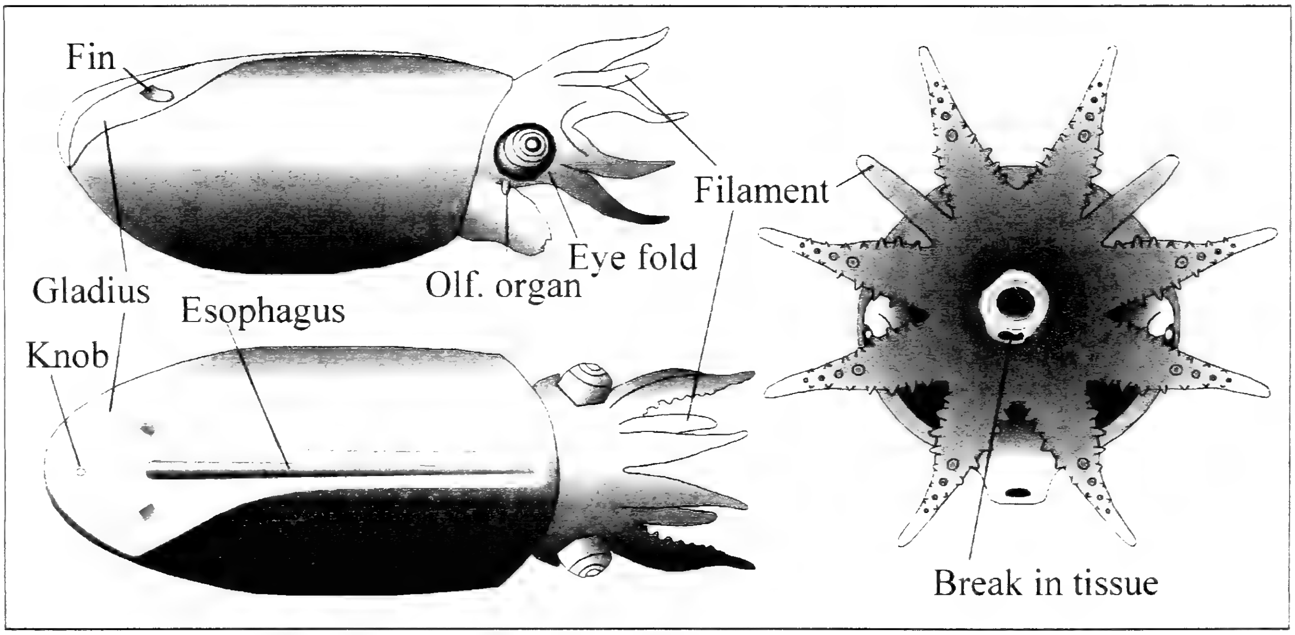

Fig. 2. Schematic drawings of *Vampyroteuthis infernalis* hatchling, lateral, dorsal, and oral views. From top to bottom on the oral view the arm pairs are dorsal (Arms I), filaments (Arms II), dorsolateral (Arms III), ventrolateral (Arms IV), and ventral (Arms V).

was not a case in this instance. The epithelial body could clearly be seen surrounding the lens of the eye even though the lens was partially covered by the iris.

Gelatinous tissue surrounded the arms and separated muscle layers in the mantle but did not cover the mantle muscle externally. At the posterior dorsal apex of the mantle a small knob (ca. 15 μm) was present in the epithelium and partially surrounded by a groove. This knob is in the position of the hatching organ of other cephalopods but we find it reminiscent of the peculiar circular feature in the photos of the paralarva (Fig. 3B–D) described below.

The filaments (= "velar filaments", Hochberg & Nixon 1992) were intact. Each was broad, short, of uniform thickness to the rounded tips (Figs. 1B, 2), and lacked both suckers and cirri. Their attachment to the brachial crown was as in the adult except that the filaments did not reside in a pocket, as a web was virtually absent. A slight ridge between arms III, IV and V (Fig. 2) appeared to be the web precursor. The arm tips were slightly damaged but all seemed to be subequal and armed with cirri and suckers. Four developing suckers were counted on one arm and we assume this to apply to all arms. Suckers had constricted bases but lacked obvious stalks. Four pairs of cirri preceded the first sucker and the suckers and cirri alternated as in the adult.

On the oral surface of the brachial crown, two circular lips and a more distal fold surrounded the beak. A break in the tissue ventral to the lips and medial to this fold was presumably the point where yolk came out. Unlike in adults, the large funnel was not embedded in the head, but no free adductor muscles were present. The exact orientation of the very small, but damaged, fins could not be determined. The pigmented esophagus, where it emerged from the brain, was clearly visible through the transparent gladius. The esophagus gradually increased in diameter posteriorly. The gladius was the same general shape as in adults but had a somewhat narrower median field.

The animal's coloration was faint pink-brown and fairly translucent. Black chromatophores were scattered at several points on the animal, especially on the oral surface of the arm bases and anterodorsally on the eye. A light reddish-brown epidermal pigment was present. The pigment was most obvious on the covering of the visceral mass, the ventral surface of the head and the oral surfaces of the arms. The animal seemed to be neutrally buoyant although small bubbles attached to the epidermis prevented actual determination.

Paralarva.—While nearly the same size (9 vs. 8 mm ML), the morphology of the paralarva was very different from that of the hatchling. Except as noted below, the overall appearance was similar to that of larger juveniles and adults (e.g., head/mantle fusion, pigmentation, etc.). The oblique angle of the fin noted by Pickford (1949a) is confirmed here in photographs (Fig. 3B, C) of the living paralarva. The fins were the first of two pairs to develop (= "juvenile fins" or "larval fins", Young & Vecchione 1996); the second pair ("adult fins" Ibid) were present only as minute precursors anterior to the fin-base photophore. Also apparent in these live photos (Fig. 3B–D) is a peculiar circular feature at the apex of the mantle. Examination of the preserved specimen, however, revealed no obvious structure at this location. Figure 3A shows the arms in a forward orientation, and Fig. 3B shows them in the lateral orientation. The filaments were very thin and emerged from pockets in the well-developed web, as in older specimens. The incompletely retracted but coiled filaments are seen most clearly in Fig. 3C. The eyes of this young vampire squid were relatively small (Fig. 3A, C), compared with those of an adult.

Discussion

Pickford (1949a) described a young vampire squid in the same stage of development as the hatchling described here. However, her specimen was badly damaged (mantle

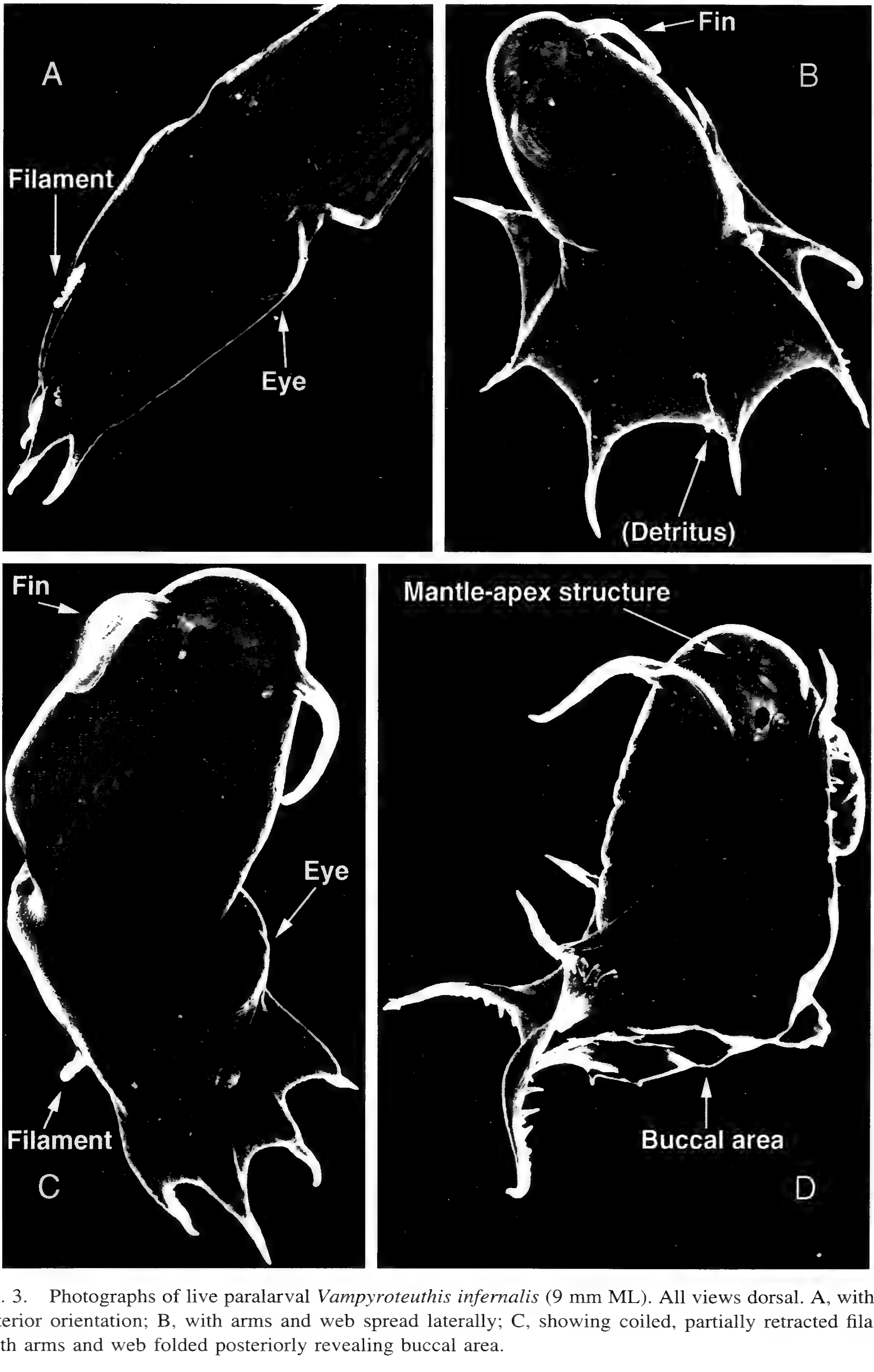

Fig. 3. Photographs of live paralarval *Vampyroteuthis infernalis* (9 mm ML). All views dorsal. A, with arms in anterior orientation; B, with arms and web spread laterally; C, showing coiled, partially retracted filament; D, with arms and web folded posteriorly revealing buccal area.

length was thought to be 5.7 mm) and, as a result, some of her conclusions have been in doubt. The description here confirms some of her more important findings (e.g., mantle free from head; thick filaments).

The vampire hatchling also confirms the fusion of the head and mantle in octopods and vampyromorphs to be independent, as predicted from morphology (Young & Vecchione 1996). The broad filaments are more arm-like than in older vampire squids and add support to the interpretation that the filaments are the second pair of arms. If they were ocular filaments, as suggested by Young (1967), one might expect that they would be especially small at this stage. The embryonic eye fold in cephalopods is continuous with the arm bases and the particular arms associated with the fold have been used to determine the homology of arm pairs in decapods and octopods (Boletzky 1993). Unfortunately, in the vampire hatchling the eye fold does not continue onto the arm crown, presumably because of its advanced stage of development. A fold surrounding the lips could be the remnant of a buccal crown that is otherwise absent in *Vampyroteuthis* (see Fig. 3D). More likely, however, this is the demarcation between the gelatinous tissue and the more muscular region where the arm muscles fuse with one another and has no phylogenetic significance.

Vampire hatchlings may drift freely in deep water until they change into the form of a typical paralarva. However, the specimen examined here could be an advanced embryo, hatched prematurely within the trawl. Pickford (1949b) stated that the egg size of spawned *Vampyroteuthis* eggs is up to 4.0 mm in diameter. Clearly the present hatchling with its embryonic features (e.g., yolk) was not derived from such a small egg. An egg size of ca. 8 mm (i.e., comparable to the mantle length) would be expected. The discrepancy cannot be explained at present.

Young et al. (1998) proposed that relaxed orientation of the arms in *Vampyroteuthis* might provide evidence to choose between alternative hypotheses about octopodiform evolution. However, the photographs of the paralarva with its arms both spread laterally and projecting anteriorly are equivocal on this question.

Vampyroteuthis infernalis currently is considered to comprise a single panmixic species. Therefore, although our specimens were collected in different oceans, we do not believe that the morphological differences between them reflect interspecific variability. The strong differences in morphology between our two specimens, which are nearly the same size, demonstrate the changes that occur in the early post-hatching ontogeny of *Vampyroteuthis.* Pickford (1949a) described the paralarval development of *V. infernalis.* One peculiarity of this species is that early paralarvae (Pickford's "stage 1 larvae" have one pair of fins; then a second pair develops ("stage 2") followed by absorption of the original pair ("stages 3 and 4"). She observed that the fins of the paralarva are set obliquely on the body, unlike the horizontal attachment of the adult fin, and suggested that the young vampire hangs head downward in the water. The present observations, which are the first live of a paralarval vampire squid, confirm Pickford's descriptions, such as fin orientation, which were based on preserved specimens.

The pucker-like circular structure seen near the posterior apex of the paralarva's mantle is similar to that recorded in a subadult *Vampyroteuthis* videotaped as part of a televison program about cephalopods ("Incredible Suckers"). No discrete structure is apparent on the preserved paralarva and we do not know the function of the structure.

Acknowledgments

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Nereidids (Polychaeta) from the Caribbean Sea and adjacent Coral Islands of the southern Gulf of Mexico

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Abstract.—In this study 23 species of nereidids from the Greater Caribbean region collected in different expeditions from 1930 to 1970 are recorded: six species of *Ceratonereis,* five species each of *Nereis* and *Perinereis,* four species of *Neanthes* and one species each of *Platynereis, Pseudonereis* and *Stenoninereis. Neanthes egregicirrata* is removed from the genus *Nereis,* because no homogomph falcigers are present in the atokous form, which is herein described for the first time.

In a recent study, Salazar-Vallejo & Jiménez-Cueto (1997) reported that for the Greater Caribbean region 48 species of nereidids are known. In the same study, 17 species of nereidids were recorded for the state of Quintana Roo's (Mexico) littoral waters, and a key was given for species of the Greater Caribbean Region.

In this study, 23 species of nereidids are recorded. The material comes from several oceanographic programs: collections made at Caribbean islands between 1930 and 1973 and deposited in the Instituut voor Taxonomische Zoölogie (Zoölogisch Museum) University of Amsterdam (ZMUA); collections made by the Smithsonian-Bredin Caribbean Expedition IV in 1960 in Quintana Roo, Mexico, and deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); and collections made by two of us (VS-W, VO-R) as part of the *Imca IV* (March 1989) and *Dinamo I* and *III* (March 90 and 91) oceanographic expeditions (see Ochoa-Rivera 1996) and deposited in the Laboratorio de Ecologia Costera, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de Mexico (ICML-UNAM), in the coral islands from the southwestern region of the Gulf of Mexico.

In addition, some type specimens from the Naturhistoriska Rijksmuseet Stockholm (NRS) and other specimens deposited at the Smithsonian Institution are included here.

Under Material Examined, the records are reported in the following order and as the case may be: the type material is listed first, then the material coming from the Instituut voor Taxonomische Zoölogie, followed by the Smithsonian-Bredin Caribbean Expedition IV material, and ending with the ICML-UNAM material. Dates are abbreviated in order of day, month and year. For each sampling station the number of specimens studied is in parentheses.

Ceratonereis (*Ceratonereis*) *excisa* (Grube, 1874)

Nereis excisa Grube, 1874:72.

Ceratonereis excisa.—Perkins, 1980:13, fig. 6.—Hartmann-Schröder, 1985:47.—Salazar-Vallejo & Jiménez-Cueto, 1997: 363.

Material examined.—ZMUA: Bonaire,

Lac entrance, 200 m West of Cai, 6 m depth, 11 Aug 1967 (3).

Distribution.—Western Atlantic, Cuba, Bonaire and Santa Catarina Island, Brazil.

Habitat.—Shallow waters, in sand trapped among *Thalassia* roots.

Ceratonereis (*Composetia*) *irritabilis* (Webster, 1879)

Ceratonereis irritabilis.—Taylor, 1984: 31.30, figs. 31.25, 31.26.—Salazar-Vallejo & Jiménez-Cueto, 1997:363.

Material examined.—ZMUA: Barbados, 0.5 mi off Holetown, 100 m depth, 19 Nov 1964 (14).

Distribution.—From Virginia, U.S.A., south to Panama.

Habitat.—Soft bottoms, intertidal to continental shelf.

Ceratonereis (*Ceratonereis*) *longicirrata* Perkins, 1980

Ceratonereis longicirrata Perkins, 1980:26, figs. 11–12.

Material examined.—ZMUA: Puerto Rico, Paraguera Mata de la Gata, 12 Sep 1963 (4); St. Martin, Etang aux Poissons, l'Embouchure, 3 Oct 1963 (1); Little Cayman, Owen Island, ca. 0.5 m depth, 7 Jun 1973 (5); Grand Cayman, south of Jackson's Point, 0–0.5 m, 9 Jun 1973 (1); Smithsonian-Bredin Caribbean Expedition IV, Est. 85-60, Ascención Bay, 200–300 yds. southwest of Suliman Point, 17 Apr 1960 (8); ICML-UNAM: *Dinamo I* and *III* expeditions, Alacran Reef, West bay 18 Mar 1990 (1); 18 Mar 1991 (1); Triangulos Oeste reef, West bay, 19 Mar 1991 (1).

Distribution.—Tropical Western Atlantic. Known from the Gulf of Mexico, and Caribbean Sea.

Habitat.—Soft bottoms in the continental shelf, in sediments accumulated among roots of algae attached to coral rocks.

Ceratonereis (*Ceratonereis*) *mirabilis* Kinberg, 1866

Ceratonereis mirabilis Kinberg, 1866: 170.—Perkins 1980:4, figs. 1–4.—Taylor, 1984:31.30, figs. 31.27–31.28.—Hartmann-Schröder, 1985:43, fig. 23.—Salazar-Vallejo & Jiménez-Cueto, 1997: 363, figs. 5, 20, 21, 42, 44.

Material examined.—Brazil, 09°S, 33 m, Werngren Coll., (Syntype, NRS 539). ZMUA: Bonaire, Kralendijk, near Pasanggrahan, Sep 1930 (1); St. Barts, S. Public near Gustaria, 4 Jun 1949 (1); North Bimini, Bahamas, 1 km offshore, 17 Aug 1949 (29); 18 Aug 1949 (13); Florida, east of Soldier Key, 2 m, 5 Sep 1963 (1); Barbados, 0.5 mi of Holetown, 100 m, 19 Nov 1964 (28) Little Cayman, South Hole Sound, The Bight; 0.5–1 m, 5 Jun 1973 (71); Jamaica, Drunkemans, Key, 0–0.5 m, 15 Jun 1973 (7). USNM: Smithsonian-Bredin Caribbean Expedition IV, Est. 11-60, Mujeres Island, 29 Mar 1960 (1); Est. 41-60, Espiritu Santo Bay, north shore, near Lawrence Point, 6 Apr 1960 (3); Est. 44-60, North end of Ascención Bay, small inlet behind Allen Point, 7 Apr 1960 (4); Est. 52-60, Ascención Bay, just behind center of Nicchehabin Reef, east of Allen Point, 10 Apr 1960 (6); Est. 53-60, Ascención Bay, 10 Apr 1960 (6); Est. 61-60, near Allen Point light, 12 Apr 1960 (129); Est. 67-60, Ascención Bay, 13 Apr 1960 (12); Est. 68-60, Ascención Bay, Allen Point, 13 Apr 1960 (2); Est. 72-60, Ascención Bay, central part of Nicchehabin Reef, 14 Apr 1960 (7); Est. 77-60, North end of Ascención Bay, beach just east of Halfway Point, 15 Apr 1960 (26); Est. 79-60, Ascención Bay, the electric light over ship's side at anchorage, 15 Apr 1960 (2); Est. 83-60, Ascención Bay, mangrove inlet behind Allen Point light, 16 Apr 1960 (2); Est. 85-60, Ascención Bay, along shore near Suliman Point, 17 Apr 1960 (2); Est. 91-60, Inner side, Nicchehabin Reef, 1/3 distance from north end Ascención Bay, 18 Apr 1960 (20); Est. 93-60, north end Ascención Bay, shore near Halfway Point, 18 Apr 1960 (2); Est. 95-60, Ascención Bay, Suliman Point, 19 Apr 1960 (5); Est. 100-60, north of Santa María Point, south end of Cozumel Island, 21 Apr 1960 (3); Est. 109-60, south end of Cozumel Island, 1¼ miles north of Santa Maria Point, 22 Apr 1960 (2).

Distribution.—Western Atlantic. Greater Caribbean region, Bermuda, Florida, Bahama Islands, south to Barbados and the Netherlands Antilles. Santa Catarina, Brazil.

Habitat.—Mixed bottoms, coral reefs, macroalgae, seagrass beds, shallow waters down to 60 m.

Ceratonereis (*Ceratonereis*) *singularis* (Treadwell, 1929)

Ceratonereis singularis Treadwell, 1929:1, figs. 1–8.—Perkins, 1980:17, figs. 7–10.—Hartmann-Schröder, 1985:45, figs. 36–39.—Salazar-Vallejo et al., 1990: 213.—Bastida-Zavala, 1993:29.

Material examined.—ZMUA: Antigua, Dickinson Bay, 26 Jul 1967 (5); 28 Jul 1967 (19).

Distribution.—Amphi-American. Gulf of California south to Panama, North Carolina south to Colombia.

Habitat.—Rocky substrates of the intertidal zone, sandy bottoms in the continental shelf.

Ceratonereis (*Composetia*) *versipedata* (Ehlers, 1887)

Nereis (*Ceratonereis*) *versipedata* Ehlers, 1887:116, pl. 36, figs. 5–10.

Ceratonereis versipedata.—Day, 1973: 39.—Gardiner, 1976:148, fig. 140.—Taylor, 1984:31.30, figs. 31.23; 31.24a–f.

Material examined.—ZMUA: Curaçao, Piscadera Baai, north part, 2nd buoy, 31 Oct 1963 (2); central part, 3rd buoy, 31 Oct 1963 (2); Piscadera Baai, northeast point, 11 Dec 1963 (3). USNM: Smithsonian-Bredin Caribbean Expedition IV, Est. 41-60, Espiritu Santo Bay, westward side of reef to east of anchorage, 6 Apr 1960 (3); Est. 52-60, Ascención Bay, just behind center of Nicchehabin Reef, east of Allen Point, 10 Apr 1960 (1); Est. 53-60, Ascención Bay, 10 Apr 1960 (1); Est. 77-60, north end of Ascención Bay, shore just east of halfway point, 15 Apr 1960 (1).). ICML-UNAM: *Dinamo III* expedition, Cayo Nuevo, 24 Mar 1991 (2); Cayo Arcas, 17 Mar 1991 (6).

Distribution.—Western Atlantic. Georgia, U.S.A., Gulf of Mexico and Caribbean Sea.

Habitat.—Soft bottoms and among interstices of coralline rocks, intertidal to 40 m.

Neanthes acuminata (Ehlers 1868)

Nereis acuminata Ehlers 1868:552.

Nereis (*Neanthes*) *arenaceodonta:* Pettibone, 1963:162, figs. 44i, 45e.

Nereis (*Neanthes*) *acuminata:* Day, 1973: 41.—Gardiner, 1976:149, fig. 15e–f.

Neanthes acuminata: Taylor, 1984:31.15, figs. 31.11; 31.12a–e.

Material examined.—ZMUA: Florida, Key Biscayne, northwest swamp (mangrove ditch), 31 Aug 1963 (2); Puerto Rico, Parguera, Mata de the Gata, 12 Sep 1963 (2); Curaçao, Piscadera Baai, northeast point, 25 Nov 1963 (1); 11 Dec 1963 (3); 18 Dec 1963 (6); central part, southeast point, 13 Dec 1963 (7); Jamaica, Kingston Harbour, Inlet W. of airport, 0–1 m, 7 May 1973 (1). USNM: Smithsonian-Bredin Caribbean Expedition IV, Stn. 17-60, Mujeres Harbor, 30 Mar 1960 (1); Stn. 83-60, Ascención Bay, mangrove inlet behind Allen Point light, 16 Apr 1960 (1); Stn. 100-60, north of Santa Maria Point, south end of Cozumel Island, 21 Apr 1960 (5).

Distribution.—Western Atlantic. From North Carolina down to the Gulf of Mexico.

Habitat.—Soft bottoms of the continental shelf.

Neanthes egregicirrata (Treadwell, 1924)
(Fig. 1a–h, 2a–f)

Nereis (*Leptonereis*) *egregicirrata* Treadwell, 1924:13, fig. 24.

Material examined.—Antigua Island, English Harbor, Coll. University of Iowa, 07/1918 (1, Lectotype USNM 071733), (4 Paratypes USNM 020224); ZMUA: Barbados Island, Conset Bay (St. John), 7 Jul 1967 (1); Little Cayman, South Hole Sound, The Bight, 0.5–1 m, 5 Jun 1973 (2). USNM: Smithsonian-Bredin Caribbean Expedition IV, Stn. 67-60, Ascención Bay, behind central part of Nicchehabin Reef, 13 Apr 1960 (2); Stn. 72-60, Ascención Bay, central part of Nicchehabin Reef, 14 Apr 1960 (2); Stn. 79-60, Ascención Bay, the elelectric light over ship's side at anchorage, 15 Apr 1960 (2); Stn. 85-60, Ascención Bay, along shore near Suliman Point, 17 Apr 1960 (1); ICML-UNAM: Ascención Bay, Pájaros Point, 6 Oct 1983 (1); Puerto Morelos, La Bocana, Francisco Solís-Marín coll., 17 Feb 1995 (9).

Diagnosis.—Atokous specimen collected in Little Cayman complete, light yellow, 14 mm long, 0.5 mm wide, with 83 setigers, prostomium and palps pigmented. Anterior median region of each segment with transverse diffusely pigmented stripe. Prostomium slightly longer than wide, with one pair of frontal small cirriform antennae. Two pairs of large eyes with a lens, in trapezial arrangement. Palps biarticulate, globose, with conical palpostyle. Peristomium with 4 pairs of tentacular cirri, largest pair extending to setiger 5 (Fig. 1a).

Paragnaths arranged on pharyngeal areas as follows: I: 0; II: 15 cones in 2 rows; III: 3 in one row; IV: 14 in two rows; V: 0; VI: 4 cones in a row; VII–VIII: 6 in one row. Jaws yellowish with 7 teeth.

First two parapodia uniramous, third biramous, notopodia with two ligules, dorsal one digitiform, short; median ligule larger, basally wide. Neuropodia with presetal lobe distally conical, postsetal lobe rounded, ventral ligule subulate. Dorsal cirrus wide, inserted proximally on ligule, larger than ventral cirrus (Fig. 1b). Sixth parapodium with dorsal cirrus elongate, with constriction in median part of cirrus, which results in distal cirristyle. Notopodial median ligule and neuropodial ventral ligule rounded distally; neuropodial postsetal lobe conical. Ventral cirri inserted proximally on body (Fig. 1c). Notopodial ligules of anterior parapodia posterior to setiger 6 rounded, shorter than in parapodia anterior to setiger 6. Neuropodial ventral ligule subulate (Fig. 1d). Notopodial ligules of posterior parapodia triangular, median ligule larger, slenderer than dorsal ones. Neuropodial postsetal lobes conical distally, presetal one rounded, ventral ligule slender (Fig. 1e).

All notopodial setae homogomph spinigers with long and slender appendix, finely spinulate on margin. Supraacicular neurosetae from first biramous parapodium, and from modified setiger 6, homogomph spinigers similar to notopodial ones, and heterogomph spinigers with short appendix, with long spines on margin (Fig. 1f); supraacicular neurosetae posterior to sixth parapodia, homogomph spinigers and heterogomph falcigers, with long and slender appendix, with spinulations along margin, distally ending in blunt tooth (Fig. 1g). Neuropodial infraacicular setae from first biramous parapodium to setiger 5, heterogomph spinigers with short appendix; neuropodial infraacicular seta from modified setiger 6 throughout body including heterogomph spinigers and falcigers in anterior parapodia, with latter similar to supraacicular ones, and in median and posterior parapodia falcigers with short, triangular appendix, distally ending in curved tooth, with margin covered by one row of long spines (Fig. 1h).

Pygidium with pair of slender anal cirri. Anus terminal.

Epitokous stage.—Epitokous male, 8 mm long and 1.7 mm wide including parapodia, with 70 setigers, no coloration pattern. Body divided into 3 regions: pre-epitocal formed by two regions: anterior one, from

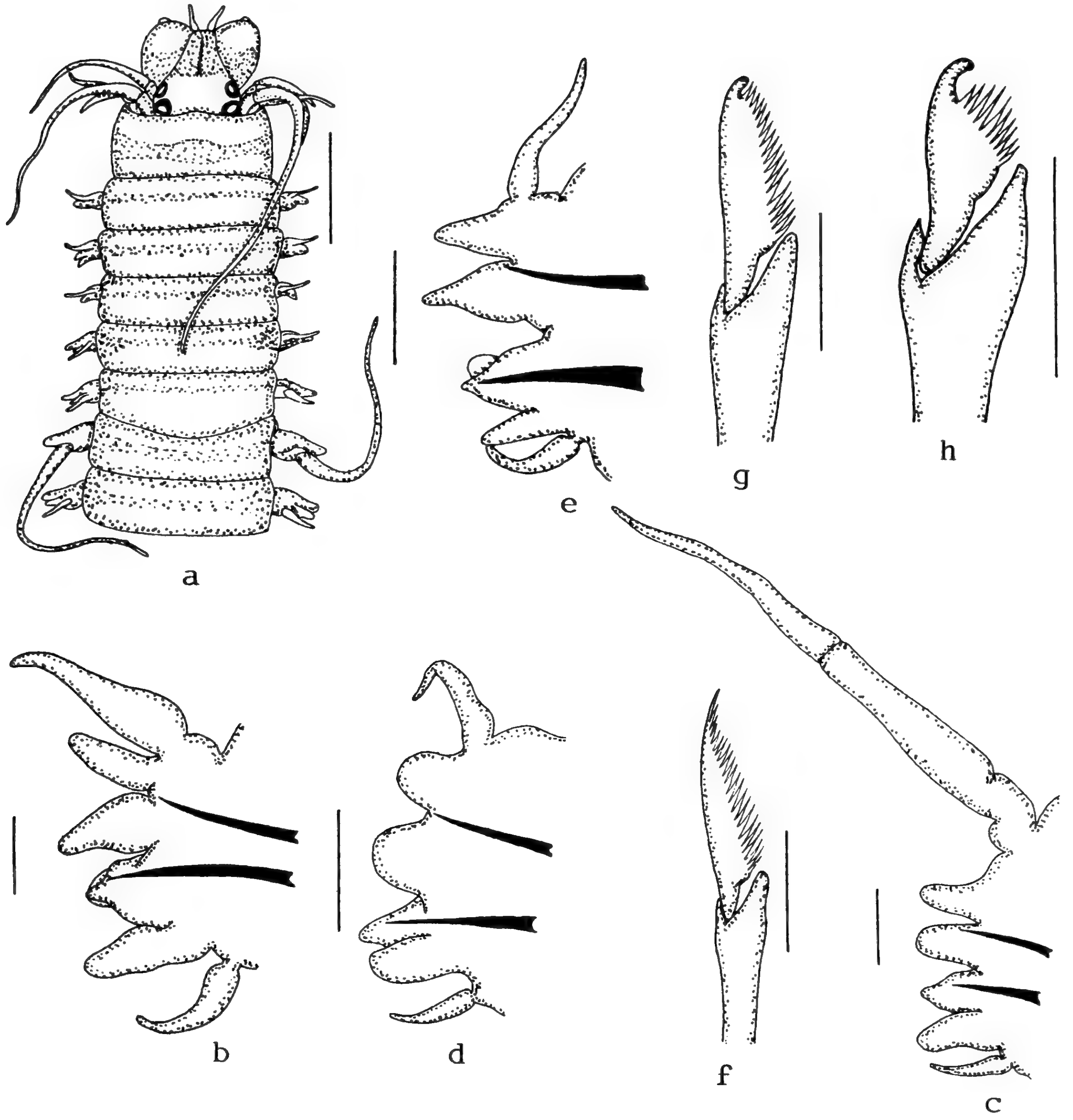

Fig. 1. *Neanthes egregicirrata* (atoke): a, Anterior end, dorsal view; b, 3rd seriger, anterior view; c, 6th setiger, anterior view; d, 10th setiger, anterior view; e, 32th setiger, anterior view; f, Neuropodial heterogomph spiniger of supraacicular position from setiger 3; g, Neuropodial heterogomph falciger of infraacicular position from setiger 10; h, Neuropodial heterogomph falciger of infraacicular position from setiger 32. Scale bars: a = 0.5 mm; b–e = 150 μm; f–h = 15 μm.

setigers 1 to 5, with notopodial and neuropodial ventral ligules digitate, neuropodial postsetal lobes conical. Dorsal cirrus enlarged, with a small cirrostyle attached near distal end (Fig. 2b). In setiger 6, as in atokous material, dorsal cirrus modified, wide proximally slender distally (Fig. 2a). From setigers 7 to 16, parapodia with notopodium formed by two triangular ligules, and a notopodial digitiform superior lobe (Fig. 2c). From setiger 17, parapodia modified for swimming, notopodia with one small lamella associated with dorsal cirrus, with crenulations. Neuropodia with elongate lamella associated with the postsetal lobe. Ventral cirri with two small lamellae (Fig. 2d).

In pre-epitokous setigers notosetae homogomph spinigers. First 5 setigers with supraacicular neurosetae homogomph spinigers and heterogomph falcigers with slender appendix (Fig. 2e); infraacicular spini-

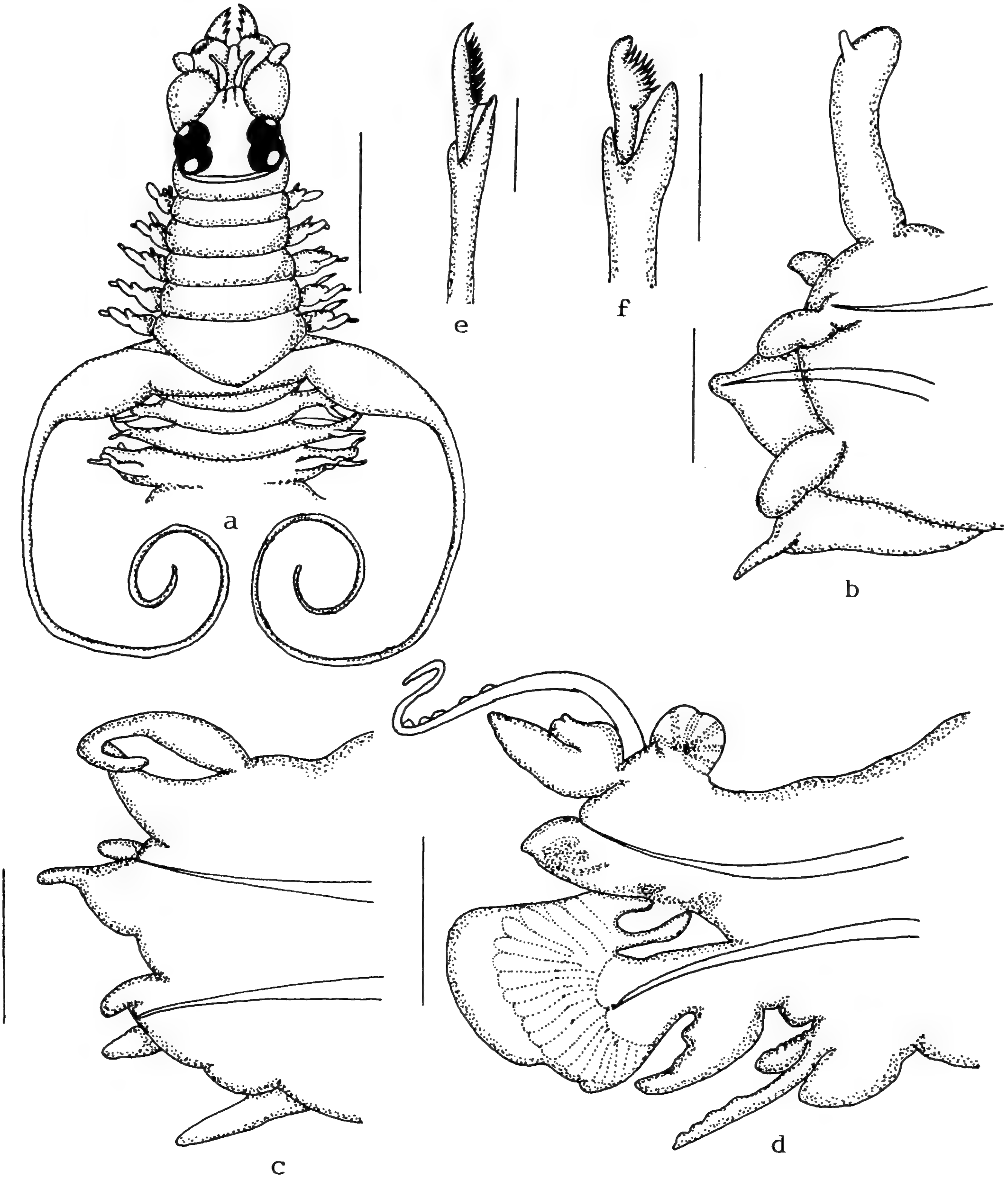

Fig. 2. *Neanthes egregicirrata* (epitokous male): a, Anterior end, dorsal view; b, 5th setiger, anterior view; c, 15th setiger, anterior view; d, 44th setiger, anterior view; e, Neuropodial heterogomph falciger of supraacicular position from setiger 5; f, Neuropodial heterogomph falciger of supraacicular position from setiger 15. Scale bars: a = 1 mm; b–d = 150 μm; e–f = 15 μm.

gers heterogomph. Parapodia posterior to modified setiger with supraacicular neurosetae homogomph spinigers and heterogomph falcigers with short and triangular appendix (Fig. 2f); only heterogomph falcigers in infraacicular position. Setae from epitocal region paleae with homogomph articulation, appendix oar-shaped.

Pygidium with pair of short anal cirri. Anus terminal.

Discussion.—The holotype of this species was described from an epitokous specimen. Before this study, the atokous form was unknown. When examining the atokous specimens, it was noted that no homogomph notopodial falcigers are present, which means that it should be included in the genus *Neanthes.* The dorsal elongate cirrus in the sixth setiger persists in the atokous phase and as previously thought, is not exclusive of the epitokes. F. Solís-Marín (pers. comm.) observed the epitokes in the water column and reported that they appeared to gyrate one around the other, until they stopped completely. Apparently, the modified dorsal cirri are used to hold the animals to each other during copulation.

In the type material examined from *Platynereis abnormis* Horst (1924) (ZMA Pol 730) it was noted that the dorsal cirri are modified as in *N. egregicirrata,* except that this happens on setiger 7, rather than on setiger 6.

Distribution.—Western Atlantic. Known from the Caribbean Sea, Quintana Roo, Mexico, Antigua Island, Puerto Rico, Barbados and Little Cayman Island. This is the first record for Mexico.

Habitat.—Atokous specimens collected among corals, epitokes collected close to the surface with zooplankton net attracting the organisms with a bright light.

Neanthes micromma (Harper, 1979)

Nereis (*Neanthes*) *micromma* Harper 1979: 91, figs. 1–11.
Neanthes micromma: Taylor, 1984:31.17, figs. 31.14a–h.—Hernández-Alcántara & Solís-Weiss, 1991:255.

Material examined.—*ICML-UNAM: Imca IV* expedition, Cayo Arcas, 3 Oct 1989 (4); 4 Oct 1989 (1); *Dinamo III* expedition, Cayo Nuevo, 24 Mar 1991 (1).

Distribution.—Amphi-American. Western coasts of Mexico, Gulf of Mexico.

Habitat.—Sandy muds, shallow waters down to 50 m.

Neanthes succinea (Frey & Leuckart, 1847)

Nereis (*Neanthes*) *succinea:* Pettibone, 1967:165, fig. 44a–e.—Day 1967:321, fig. 14a–e.—Hartmann-Schröder, 1971: 200, figs. 64–65.
Neanthes succinea: Hartman, 1945:17, pl. 3, figs. 1–2.—Rioja, 1946:205, pl. 1, figs. 1–2.—1962:165.—Imajima, 1972:108, fig. 32a–k.—Taylor, 1984:31.17, figs. 31.16a–h.

Material examined.—ZMUA: Margarita, Punta de Piedra, 21 Jan 1964 (2); Surinam, Suriname River, wreck of Goslar, 7 Mar 1964 (2); Jamaica, Kingston Harbour, inlet west of airport, 7 May 1973 (1).

Distribution.—Cosmopolitan in tropical to temperate waters. Atlantic from the North sea south to South Africa, and from Massachusetts south to Uruguay; Pacific Ocean from California south to Panama; Indian Ocean.

Habitat.—Among rhizoids of algae attached to rocks.

Nereis allene Pettibone, 1956

Nereis allene Pettibone, 1956:287, figs. 4b–f, 6a–h.

Material examined.—Puerto Rico, 15 Aug 1955 (Holotype, USNM 27778); Antigua, Jul 1918 (4 Paratypes USNM 27779). ZMUA: North Bimini, Bahamas, 17 Aug 1949 (56); 18 Aug 1949 (20).

Discussion.—The examined specimens are epitokes collected with a zooplancton net in the water column. Those are morphologically similar to the type specimens. However, in parapodia of setigers 1–6, the notopodium is slightly modified, with cylindrical dorsal cirri. In the original description, Pettibone mentioned that, in those specimens, paragnaths are present in both pharyngeal rings, but she does not detail their distribution. In the specimens collected in North Bimini the following pharyngeal arrangement is found: Area I: 1 cone, II: 13–15 cones in two rows; III: 18–22 small cones in an oval; IV: 25 cones in a crescent, with 3–4 rows; V: 0; VI: 3 cones in an irregular row; VII–VIII: 5 cones in a row. Jaws amber colored with 6 stout teeth.

Distribution.—Known only from the greater Caribbean region, Puerto Rico, Antigua, Barbados and Bahamas.

Habitat.—Undescribed for atokous specimens, epitokes collected with zooplankton net in the water column.

Nereis falsa Quatrefages, 1865

Nereis falsa: Fauvel, 1923:337, fig. 129e–m.—Day, 1967:317, fig. 14.7k–o (with synonymy).—Day 1973:41.
Nereis pelagica occidentalis Hartman, 1945:20, pl. 4, figs. 1–6.—1951:46.
Nereis (*Nereis*) *occidentalis:* Pettibone, 1956:291, fig. 7a–d, 8a–f.
Nereis occidentalis.—Dueñas, 1981:88, pl. 8, fig. a–f.

Material examined.—ZMUA: Bonaire, Lagoen Southeast, corner, 28 Oct 1930 (3); Bonaire, Lagoen south, 19 Sep 1967 (10); Curaçao, Piscadera Baai, N., 2nd buoy, 31 Oct 1963 (16); Curaçao, Ironbeam of mouth of sewer-pipe, 31 Oct 1963 (47); Curaçao, Piscadera Baai, northeast, 11 Oct 1963 (86); Curaçao, Piscadera Baai, northeast, 25 Nov 1963 (66); Curaçao, Piscadera Baai, northeast, 11 Dec 1963 (2); Curaçao, Piscadera Baai, central part, southeast, 31 Oct 1963 (10); Curaçao, Piscadera Baai, central part, southeast, 13 Dec 1963 (5); Curaçao, Piscadera Baai, central part, southeast, 18 Dec 1963 (1); Curaçao, St. Jorisbaai, northwest bay, 25 Feb 1970 (46); Curaçao, Piscadera Baai, inner bay north, islet, 26 Sep 1967 (20); Margarita, Puente de La Restinga, 11 Jan 1964 (1); Guadeloupe, Rivière Salée la Manche à Eau, 16 Jul 1967 (8); Jamaica, Kingston Harbour, inlet west of airport, 7 May 1973 (7).

Distribution.—Warm and tropical Atlantic from France to West Africa and North Carolina to the Gulf of Mexico; Mediterranean; South Africa to Madagascar.

Habitat.—Rocky bottoms, associated with algal mats and *Rhizophora* roots.

Nereis panamensis Fauchald, 1977
(Fig. 3a–g)

Nereis panamensis Fauchald, 1977:29, fig. 6d–i.—San Martín, 1994:6, fig. 2.—Salazar-Vallejo & Jiménez-Cueto, 1997: 374.

Material examined.—ZMUA: Klein Curaçao, west shore, 1 Oct 1948 (19); Anguilla, north sandy ground, 19 Apr 1949 (2); Anguilla, Cocus bay, north, 3 Aug 1973 (5); St. Barts, S. Public, near Gustaria, 4 Jun 1949 (21); Saba, East Fort Bay, 21 Jul 1949 (8) Saba, Covebay at flat point (tidal area), 5 Oct 1963 (22); Aruba, Matmok, Arasji, 14 Aug 1955 (5); St. Vincent, Calliwater Bay near Johnson Pt., 10 Jul 1967 (2); Jamaica, Drunkemans Key, 15 Jun 1973 (1);). ICML-UNAM: *Imca IV* expedition, Cayo Arcas, 3 Oct 1989 (27); 4 Oct 1989 (23); *Dinamo I, III* expeditions, Triangulos Oeste reef, East bay, 19 Mar 1990 (4); 19 Mar 1991 (5); Triangulos Oeste reef, West bay, 19 Mar 1991 (2); Triangulos Oeste reef, East bay, 19 Mar 1990 (1); Cayo Arcas, North bay, 10 Mar 1990 (12); 17 Mar 1991 (6); Cayo Arcas, South bay, 10 Mar 1990 (50); 17 Mar 1991 (12); Cayo Arcas, Southeast bay, 23 Mar 1991 (117), 10 Mar 1990 (2); Cayo Arcas, South bay, 17 Mar 1991 (166); Cayo Arcas, Northeast bay, 17 Mar 1991 (134); Cayo Arenas, Southwest bay, 21 Mar 1991 (1).

Diagnosis.—Best preserved specimen complete, 16.5 mm long, 1.5 mm wide, 71 setigers, no pigmentation pattern. Prostomium longer than wide, with pair of digitiform antennae extending from distal region of prostomium slightly past the palps. Two pairs of rounded eyes in rectangular arrangement, anterior pair clearly visible, posterior pair covered by peristomium. Palps long with conical palpostyle. Peristomium as long as first two setigers, with 4 pairs of tentacular cirri, longest pair extending to setiger 3 (Fig. 3a).

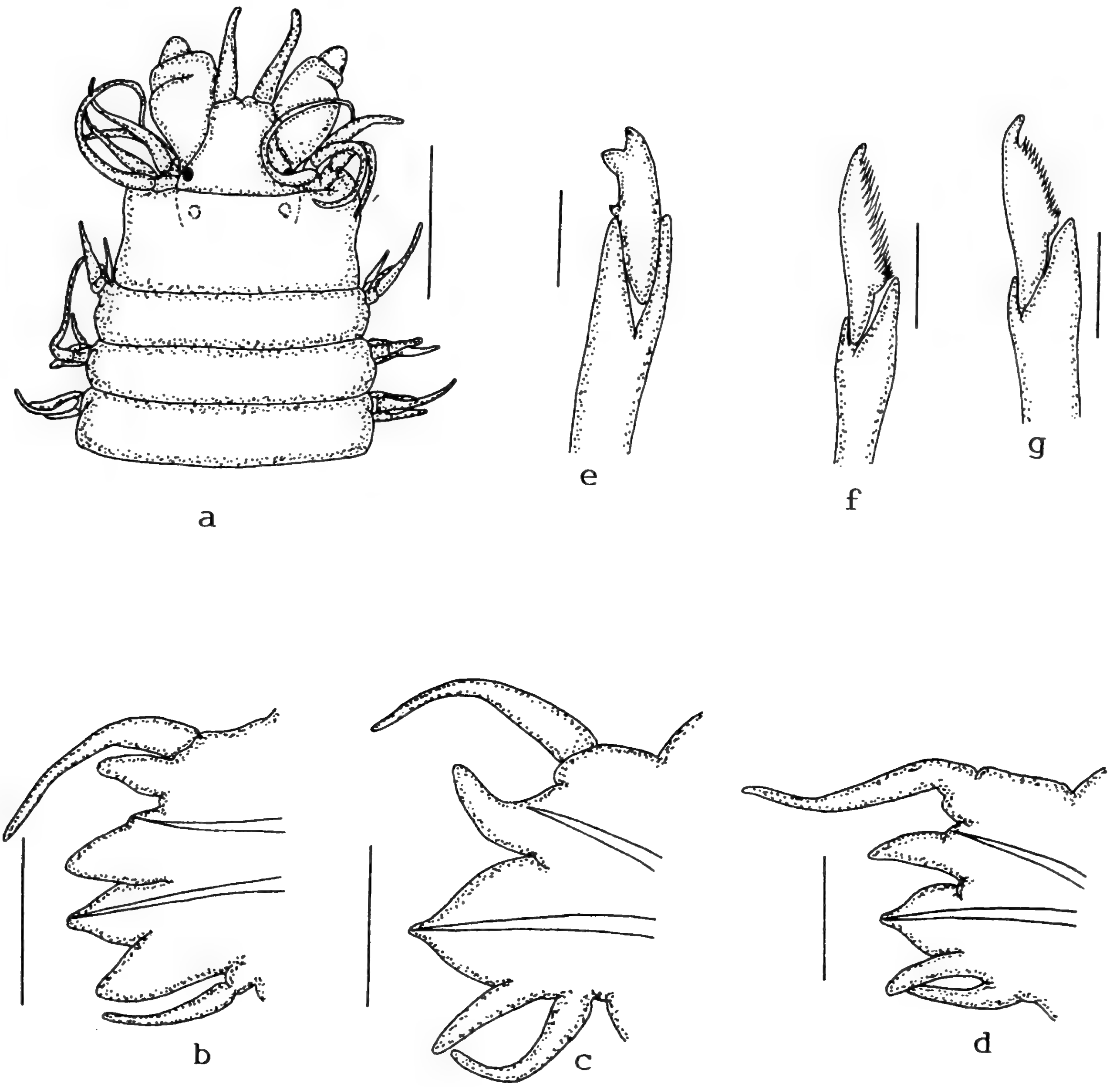

Fig. 3. *Nereis panamensis:* a, Anterior end, dorsal view; b, 10th setiger, anterior view; c, 30th setiger, anterior view; d, 58th setiger, anterior view; e, Notopodial homogomph falciger from setiger 30; f, Neuropodial heterogomph falciger of supraacicular position from setiger 10; g, Neuropodial heterogomph falciger of infraacicular position from setiger 58. Scale bars: a = 1 mm; b–d = 150 μm; e–g = 15 μm.

Paragnaths arranged on pharyngeal areas as follows: I: 0; II: 3 cones in a row; III: 3 in a row; IV: 9 3 in 2 rows; V: 0; VI: 3 in one row; VII-VIII: 6 in one row. Jaws dark brown with 8 teeth.

In anterior parapodia, notopodia with 2 ligules, dorsal one smaller, small flange representing the superior lobe present. Postsetal lobe of neuropodia conical distally, ventral ligule wide basally. Dorsal and ventral cirri subequal (Fig. 3b). Notopodial dorsal ligule in median and posterior parapodia represented only by small flange associated with basal region of dorsal cirrus, notopodial median ligule subulate. Neuropodia with postsetal lobe distally conical, ventral ligule slender (Fig. 3c–d).

Homogomph notopodial spinigers in anterior parapodia substituted in median and posterior parapodia by homogomph falcigers, appendage of latter with two blunt distal teeth, and small tooth on margin (Fig. 3e). Neuropodia with homogomph spinigers and heterogomph falcigers in supraacicular position in all parapodia, latter with slender appendix, strongly spinulate on margin in anterior parapodia (Fig. 3f); Infraacicular ones, including heterogomph spinigers and falcigers, appendix similar in anterior parapodia to these of supracicular falcigers, in posterior ones appendix somewhat smaller, and spinulation on the margin shorter (Fig. 3g).

Pygidium with pair of long anal cirri. Anus terminal.

Discussion.—Fauchald (1977) mentioned that in this species only one pair of eyes is present, but in the specimens examined for this study, a second pair was observed, covered by the anterior part of the peristomium.

Salazar-Vallejo & Jimenez-Cueto (1997) noted that San Martín's record (1994) for Cuba, could be *Nereis kauderni* Fauvel, but the absence of the notopodial superior lobes in posterior parapodia suggests that the Cuban record does belong to *N. panamensis,* since in *N. kauderni* two notopodial lobes in posterior parapodia are present.

Distribution.—Western Atlantic. Known from the Caribbean region, reported from Panama and Cuba as well as from Klein Curaçao, Anguilla, St. Barts, St. Vincent, Aruba, Jamaica and Saba. In this study its range is extended to the coral islands of the southern Gulf of Mexico, and it is the first record for Mexico.

Habitat.—In interstices of coralline rock fragments.

Nereis pelagica Linnaeus, 1758

Nereis pelagica: Fauvel, 1923:336, fig. 130a–f.—Imajima 1961:85.–1967:422.–1972:142, fig. 48a–m.—Imajima & Hartman, 1964:147.—Pettibone, 1963:179, fig. 42d–h.—Day, 1967:315, fig. 14.7f–j.—Taylor, 1984:31.42, fig. 31.40a–g.

Material examined.—ICML-UNAM: IMCA IV expedition, Cayo Arcas, 3 Oct 1989 (7); 4 Mar 1989 (1).

Distribution.—Cosmopolitan. Known from the Arctic, from Norway to the Mediterranean Sea, Azores, western coast of Africa, Atlantic coast of North America from Hudson Bay to the Gulf of Mexico, Behring Sea to Panama, Japan, Kerguelen Islands, Strait of Magellan, Mexican littoral areas, recorded from Baja California Norte, Baja California Sur, Sonora, Sinaloa, and Veracruz.

Habitat.—Rocky substrates, associated with algal mats, soft and hard bottoms from intertidal zone down to continental shelf.

Nereis riisei Grube, 1857

Nereis riisei Grube 1857:162.—Monro, 1933:43.—Hartman, 1940:221, pl. 33, fig. 37.—Fauchald, 1977:31, fig. 8c–e.—Taylor, 1984:31.38, fig. 31.36a–g.

Nereis (*Nereis*) *riisei:* Day, 1973:39, fig. 5g–j.—Gardiner, 1976:152; fig. 15o–r.

Material examined.—ZMUA: Bonaire, Kralendijk, near Pasanggrahan, Sep 1930 (1); Anguilla, north sandy ground, 19 Jun 1949 (1); St. Eustatius, south Tumble Down, Dick Bay, 10 Jul 1949 (1); St. Eustatius, Billy Gut, 13 Jul 1949 (8); Aruba, Seroe Colorado, Oostpunt, 2 May 1955 (8); Curaçao, Piscadera Baai, entrance east, 28 Sep 1963 (10); Curaçao, Piscadera Baai, north, 2nd buoy, 31 Oct 1963 (6); Curaçao, Piscadera Baai, central part, 3rd buoy, 31 Oct 1963 (26); Curaçao, Piscadera Baai, northeast, small bay, 25 Nov 1963 (2); Curaçao, Piscadera Baai, northeast, 11 Dec 1963 (13); Curaçao, Piscadera Baai, southeast part, 18 Dec 1963 (6); the Désirade, Grande Anse, near breadge, 23 Jan 1964 (1); Barbados, 0.5 mi. off Holetown, 19 Nov 1964 (3); St. Vincent, Calliwater bay, near Johnson Pt., 10 Jul 1967 (1); Grenada, Hog Island near Pt. Salines, 8 Jul 1967 (7); Barbuda, Great Lagoon entrance at Billy Pt., west, 22 Jul 1967 (2); Antigua, Dickinson Bay pier, 28 Aug 1967 (3); Curaçao, St. Joris Baai, south, shore, 23 Oct 1968 (40); Curaçao, St. Joris Baai, northwest bay, 25 Feb 1970 (6); Jamaica, Drunkemans Key, 15 Jun 1973 (2); F. Bonet coll., Alacran Reef, 18 Apr 1955 (2); USNM: Smithsonian-Bredin Caribbean Expedition IV, Stn. 52-60, Ascención Bay, just behind center of Nicchehabin Reef, east of Allen Point, 10 Apr 1960 (23); Stn. 67-60, Ascención Bay, behind central part of Nicchehabin Reef, 13 Apr 1960 (19); Stn. 72-60, Ascención Bay, central part of Nicchehabin Reef, 14 Apr 1960 (46); Stn. 77-60, north end of Ascención Bay, shore, just east of Halfway Point, 15 Apr 1960 (5); Stn. 83-60, Ascención Bay, mangrove inlet behind Allen Point light, 16 Apr 1960 (1); Stn. 82-60, behind central part of Nicchehabin Reef, 16 Apr 1960 (9); Stn. 87-60, north of Ascención Bay, southwest of Suliman Point, 17 Apr 1960 (2); Stn. 91-60, inner side Nicchehabin Reef, 18 Apr 1960 (1); Stn. 95-60, Ascención Bay, Suliman Point, 19 Apr 1960 (10); Stn. 100-60, north of Santa Maria Point, south end of Cozumel Island, 21 Apr 1960 (3); Stn. 118-60, San Miguel, Cozumel Island, 29 Apr 1960 (1). ICML-UNAM: *Imca IV* expedition, Cayo Arcas, 4 Oct 1989 (1); *Dinamo I, III* expeditions, 10 Mar 1990 (1); Alacran Reef, West bay, 18 Mar 1990 (10); 23 Mar 1991 (23); Alacran Reef, East bay, 23 Mar 1991 (4); Triangulos Oeste reef, 19 Mar 1991 (7); Cayo Nuevo, 24 Mar 1991 (1).

Distribution.—Amphi-American. Gulf of California to Panama, Gulf of Mexico down to the Caribbean Sea.

Habitat.—Soft bottoms, intertidal zone, under rocks, among sponges on mangrove roots, in the interstices of algae-sponges association, in algal rhizoids.

Perinereis anderssoni Kinberg, 1866

Perinereis anderssoni Kinberg, 1866:175; Fauchald, 1977:31, fig. 8a–b; Hartman, 1951 47, pl. 13, fig. 6; de León-González & Solís-Weiss, 1998:675, fig. 1a–g.

Material examined.—MZUA: Bonaire, Kralendijk, near Pasanggrahan, 5 Sep 1930 (1).

Distribution.—Amphi-American. From the Gulf of Mexico to Uruguay, and for Juan Fernández Island, Chile.

Habitat.—Rocky substrate, associated with algal mats.

Perinereis cariboea de León-González & Solís-Weiss, 1998

Perinereis cariboea de León-González & Solís-Weiss, 1998:677, fig. 3a–e.

Material examined.—ZMUA: Klein Bonaire, East coast at landing place, 13 Sep 1948 (1); St. Eustatius, Tumble Down, Dick Bay, 10 Jul 1949 (1).

Distribution.—Antilles and Mexican Caribbean area.

Habitat.—Among rocks and in sands, intertidal.

Perinereis cariacoensis Liñero-Arana, 1983

Perinereis cariacoensis Liñero-Arana 1983: 5, fig. a–e.

Material examined.—ZMUA: Bonaire, Kralendijk, near Pasanggrahan, 09/1930 (3).

Distribution.—Known only from Venezuela and Bonaire.

Habitat.—Rocky beaches, intertidal.

Perinereis elenacasoae Rioja, 1947

Perinereis elenacasoi: Rioja 1947:531.

Perinereis elenacasoae: Salazar-Vallejo, 1989:50.—de León-González & Solís-Weiss, 1998:680, figs. 4A–E, 5A–D.

Perinereis obfuscata: Berkeley & Berkeley, 1960:359 (in part).

Perinereis anderssoni: Rioja, 1961:295, figs. 12–15 (in part).

Material examined.—ZMUA: Bonaire, South of Kralendijk, near Hoop, May 1930 (3); Bonaire, Kralendijk, near Pasanggrahan, 5 Sep 1930 (57); Klein Bonaire, east coast at landing place, 13 Sep 1948 (2); Bonaire, Paloe Lechis of Salinja, 24 Feb 1949 (10); St. Eustatius, Tumble Down, Dick Bay, 10 Jul 1949 (1); Curaçao, Piscadera Baai, entrance east, 28 Sep 1963 (1); Curaçao, Piscadera Baai, north., 2nd buoy, 31 Oct 1963 (2); Curaçao, Piscadera Baai, central part, 3rd buoy, 31 Oct 1963 (3); Barbados, Conset Bay (St. John), 7 Jul 1967

(4); Curaçao, St. Joris baai, northwest bay, 25 Feb 1970 (14).

Distribution.—Amphi-American. Mexican Pacific from Puerto Peñasco, Sonora to Salina Cruz, Oaxaca; Gulf of Mexico, Caribbean Sea, Brazil.

Habitat.—Rocky substrates, among rhizoids of algae attached to rocks in breakwaters and in coral rocks.

Perinereis floridana (Ehlers 1868)

Nereis floridana: Ehlers, 1868:503.
Perinereis floridana: de León-González & Solís-Weiss, 1998:683, figs. 6a–e, 7a–e.

Material examined.—ZMUA: St. Barts, South Public, near Gustaria, 4 Jun 1949 (1); Klein Bonaire, east coast of landing place, 13 Sep 1948 (1); Klein Curaçao, west shore, 1 Oct 1948 (2); Barbados, Conset Bay (St. John), 7 Jul 1967 (2).

Distribution.—Western Atlantic. Known from the greater Caribbean region.

Habitat.—Associated with coral rocks, intertidal.

Platynereis dumerilii (Audouin & Milne-Edwards, 1834)

Platynereis dumerilii: McIntosh, 1885:224, pl. 35, figs. 7–9, pl. 16A, figs. 14–16.—Day, 1967:306, figs. 14.4d–k.—Fauchald, 1977:31, fig. 4d–f.

Material examined.—ZMUA: Bonaire, Kralendijk, near Pasanggrahan, 5 Sep 1930 (2); Margarita, Punta Mozquito, near Porlomar, 4 Jun 1936 (10); Klein Bonaire, east coast at landing place, 13 Sep 1948 (3); Klein Bonaire, west shore, 1 Oct 1948 (5); Bonaire, Paloe Lechis of Salinja, 24 Feb 1949 (1); St. Barts, South Public, near Gustaria, 4 Jun 1949 (5); St. Eustatius, South Tumble Down, Dick Bay, 10 Jul 1949 (25); St. Eustatius, Billy Gut, 13 Jul 1949 (84); Florida, east of Soldier Key, 5 Sep 1963 (7); Puerto Rico, Parguera, Mata de the Gata, 12 Sep 1963 (5); Curaçao, Piscadera Baai, central Part, 3rd buoy, 31 Oct 1963 (2); Curaçao, Piscadera Baai, north, 2nd buoy, 31 Oct 1963 (1); Curaçao, Piscadera Baai, northeast, 11 Oct 1963 (1); Margarita, Puente de La Restinga, 11 Jan 1964 (2); Barbados, Conset Bay (St. John), 7 Jul 1967 (34); Guadeloupe, Rivière Salée, La Manche à Eau, 16 Jul 1967 (1); Antigua, Dickinson Bay pier, 28 Jul 1967 (2); Bonaire, Lac entrance, 200m west of Cai, 11 Aug 1967 (3); Curaçao, St. Jorisbaai, northwest bay, 25 Feb 1970 (3); Jamaica, Drunkemans Key, 15 Jun 1973 (15); Anguilla, Cocus Bay, north, 3 Aug 1973 (14); USNM: Smithsonian-Bredin Caribbean Expedition IV, Stn. 34-60, San Miguel, Cozumel Island, near anchorage northwest of main dock, 03 Apr 1960 (3); Stn. 35-60, Espiritu Santo Bay, 5 Apr 1960 (9); Stn. 44-60, north end of Ascención Bay, small inlet behind Allen Point, 7 Apr 1960 (2); Stn. 52-60, Ascención Bay, just behind center of Nicchehabin Reef, east of Allen Point, 10 Apr 1960 (2); Stn. 60-60, Allen Point, Ascención Bay, where last sand beach adjoins mangroves, 12 Apr 1960 (1); Stn. 61-60, near Allen Point, 12 Apr 1960 (1); Stn. 72-60, Ascención Bay, central part of Nicchehabin Reef, 14 Apr 1960 (2); Stn. 82-60, behind central part of Nicchehabin Reef, 16 Apr 1960 (2); Stn. 87-60, north of Ascención Bay, 200–300 yds. southwest of Suliman Point, 17 Apr 1960 (2); Stn. 91-60, inner side, Nicchehabin Reef, 18 Apr 1960 (10); Stn. 95-60, Ascención Bay, Suliman Point, 19 Apr 1960 (11); Stn. 100-60, north of Santa Maria Point, Cozumel Island, 21 Apr 1960 (1). ICML-UNAM: *Dinamo I* expedition, Cayo Arcas, North bay, 10 Mar 1990 (1).

Distribution.—Cosmopolitan in tropical and subtropical waters.

Habitat.—Associated with hard substrates between algal mats. Specimens forming mucous tubes were collected in brown algal fronds.

Pseudonereis gallapagensis Kinberg, 1866

Pseudonereis gallapagensis: Hartman, 1940:231.—Fauvel, 1953:215, fig. 110a–

c—Rioja 1961:297.—Wesenberg-Lund, 1962:84, fig. 32.—Imajima, 1972:97, fig. 28a–j.—Fauchald, 1977:32, fig. 4g–h.—Rozbaczylo & Bolados, 1980.—219, fig. a–d.—Wu et al., 1985:220, fig. 124a–f.—Bastida-Zavala, 1993:30.

Material examined.—ZMUA: Bonaire, Lagoen, southeast corner, 28 Oct 1930 (1); Margarita, Punta Mozquito, near Porlamar, 4 Jun 1936 (1); Klein Curaçao, west shore, 1 Oct 1948 (2); St. Eustatius, South Tumble Down, Dick Bay, 10 Jul 1949 (34); Saba, East Fort Bay, 21 Jul 1949 (36); Aruba, Seroe Colorado, Oostpunt, 2 May 1955 (14); Saba, Covebay at flat point, 5 Oct 1963 (9); Curaçao, Piscadera Baai, central part, 3rd buoy, 31 Oct 1963 (1); Grand Cayman, south of Jackson's Point, 9 Jun 1973 (33).

Distribution.—Cosmopolitan in tropical to temperate waters Galapagos Islands, Peru, Chile, Panama, Hawaii Islands, Marshall Islands, Samoa, New Caledonia, China, Japan, India, Sri Lanka, Madagascar, Cape of Good Hope, Cameroon, Brazil and Gulf of Mexico.

Habitat.—Associated with rocky bottoms, and coral substrates.

Stenoninereis martini Wesenber-Lund, 1958

Stenoninereis martini Wesenberg-Lund, 1958:9, fig. 2–4.—Pettibone, 1971:39, figs. 23–24.—Williams et al., 1976:83.—Hartmann-Schröder, 1977.—Gardiner & Wilson, 1979:165.—Hernández-Alcántara & Solís-Weiss, 1991:251.–1995: 117.—de León-González & Solís Weiss, 1998:199, fig. 1a–d.

Material examined.—ZMUA: St. Martin, Devils Hole Swamp, 14 Oct 1963 (32).

Distribution.—Western Atlantic greater Caribbean region (type locality St. Martín Island and Sarasota, Florida), western Gulf of Mexico (Texas), Cuba, North Carolina and Laguna de Términos, Campeche.

Habitat.—Soft bottoms, associated with roots of grassbeds.

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A new stygobitic Calanoida (Crustacea: Copepoda) of the genus *Stygodiaptomus* Petkovski, 1981 from the Balkan Peninsula

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Abstract.—A new species of the genus *Stygodiaptomus* Petkovski, 1981 is described. The genus now includes three species, all endemic to the Balkan Peninsula: *S. kieferi* Petkovski, 1981, *S. petkovskii* Brancelj, 1991, and *S. ferus* n. sp. The male of *S. ferus* can be distinguished from males of the other species by the setation of swimming legs 1–4, and morphology of the exopodite and endopodite of leg 5. The diagnosis for the genus *Stygodiaptomus* is revised.

There are only a few true stygobitic species of calanoid copepods. Most reports of calanoid copepods from freshwater subterranean habitats are of one or a few specimens of epygean species, which are collected in subterranean habitats accidentally. Bowman (1986) cited only eight stygobitic freshwater calanoids of the world. In Europe, until now, five species have been described. Borutzky (1962) described *Speodiaptomus birsteini* from Crimea as a new species and new genus in a new subfamily, Speodiaptominae. Dussart (1970) described *Spelaeodiaptomus rouchi* from southern France as a new species and new genus in the recognized subfamily Diaptominae, and Kiefer (1978) redescribed the species. Three other stygobitic species of freshwater calanoids are known from the Dinaric Alps. Petkovski (1978) described *Troglodiaptomus sketi* as a new species and genus in the subfamily Speodiaptominae. Subsequently it has been recorded by Stoch (1984), Petkovski (1984), and Brancelj (1987, 1991) from other localities in the northern and central Dinaric Alps. Petkovski (1981) described *Stygodiaptomus kieferi* as a new species and new genus in the subfamily Diaptominae. Brancelj (1991) collected it again from the type locality in central the Dinaric Alps, and described *Stygodiaptomus petkovskii* as a new species from two caves in northern Dinaric Alps. During an investigation of the copepod fauna in Montenegro, one male specimen of a new species of the genus *Stygodiaptomus* was collected in Skadar Lake Valley (southern Dinaric Alps).

In the description, standard abbreviations of the characters are used as follows: A1, antennule; A2, antenna; Md, mandible; Mxp, maxilliped; P1–4, first to fourth swimming legs; P5, fifth leg.

Family Diaptomidae Baird, 1850
Subfamily Diaptominae Kiefer, 1932
Genus *Stygodiaptomus* Petkovski, 1981
Stygodiaptomus ferus, new species

Material examined.—One male (Holotype) from a small lake in the cave Sutimska Jama (42°25′50″N, 19°10′40″E), near the town Podgorica, Montenegro, coll. T. Karanovic, 18 Sep 1997. The specimen is completely dissected, mounted on a slide in Faure's medium, and deposited in the author's collection (No. 8/60/0584/c) at the Institute of Marine Biology, Kotor, Montenegro.

Description.—Male (Holotype): Length, including furcal rami (excluding furcal setae), 1.18 mm. Body colorless; without integumental windows, or paired sensila on the lateral extensions of thoracic somite 6 or on the right side of the genital somite). Naupliar eye absent. Cephalothorax subcylindrical; about 1.4 times as long as wide, equaling 36.5% of body length (Fig. 9). Five thoracic somites of unequal width and length. Urosome cylindrical, 5-segmented, and dorsoventrally symmetrical (Fig. 10). Genital somite small. Caudal rami smooth, subcylindrical, and about 2.6 times longer than wide.

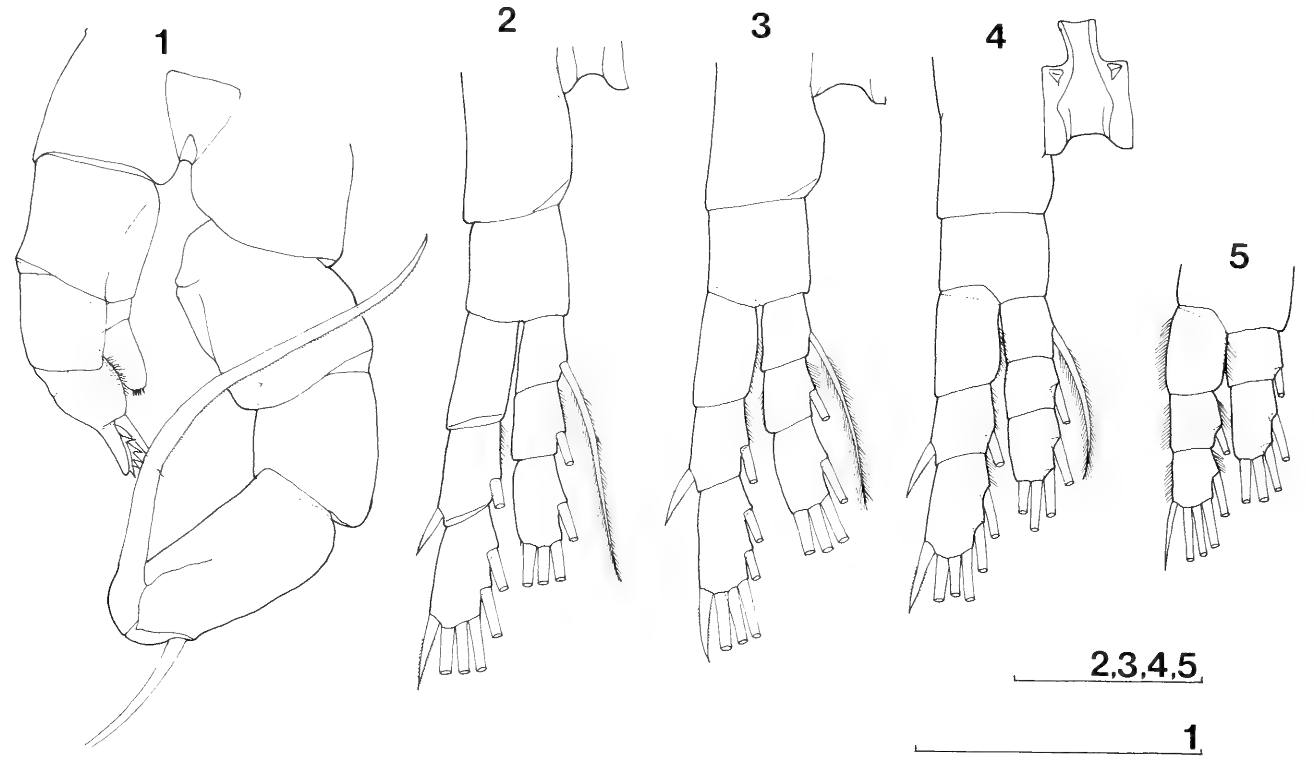
Left A1 25-segmented, reaching to middle of the furca, with cylindrical aesthetascs on articulating segments 1, 2, 3, 5, 9, 12, 14, and 19 (Fig. 12). Right A1 23-segmented (Figs. 6, 7, and 8), prehensile, with aesthetascs on articulating segments 1, 2, 4, 5, 7, 9, 12, 14, 18, and 23. Strong spines on segments 10, 11, and 13, as well as small ones on segments 7 and 12 (Fig. 6). Segments 15 and 16 with an attenuation on inner margin (Fig. 7). A2 with 2-segmented endopodite, and 7-segmented exopodite (Fig. 13). Md with 2-segmented endopodite, and 4-segmented exopodite (Fig. 14). Basis bears 4 setae; coxa with a sharp tooth separated from a number of small teeth. Maxillule and maxilla typical for the subfamily. Maxilliped slender, with 3 plumose setae on the basis, and 8 naked setae (2 long, and 6 small) on the coxa (Fig. 11).

All swimming legs without setae on the inner margin of the coxa. P1 with 3-segmented exopodite, and 2-segmented endopodite (Fig. 5). Exopodite of P1 with outer spine only on distal segment; first exopodite segment without inner seta. P2–4 almost identical (Figs. 2, 3, and 4); exopodite with outer spines on middle and distal segments; proximal segment unarmed. Middle endopodite segment of P2 without Schmeil's organ. Spine and setal formula on exopodite and endopodite of P1–P4 as follows (number to left of first slash refers to the inner spines or setae; number to right of second slash refers to the outer spines or setae; number between two slashes refers to the apical spines or setae):

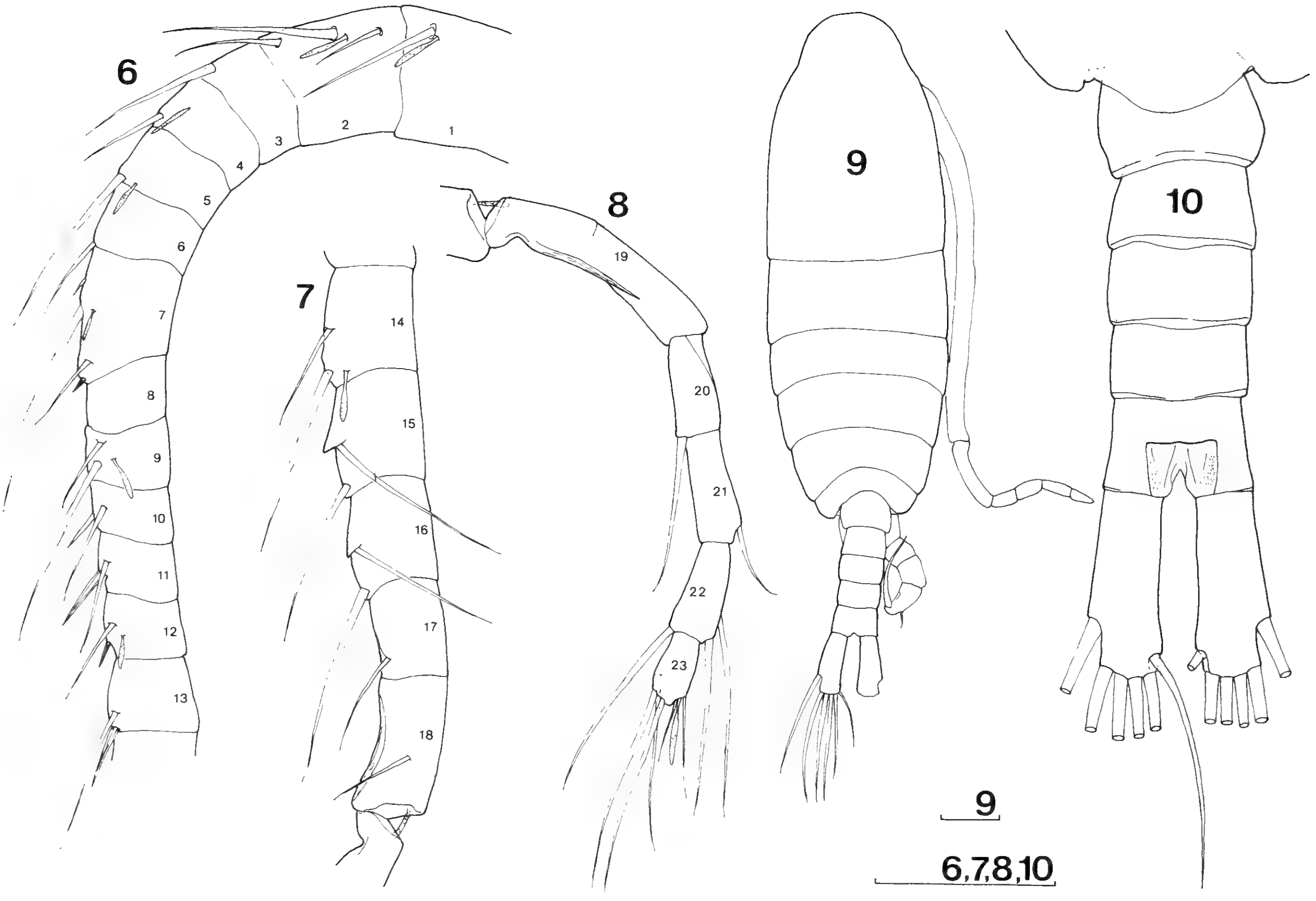
	exopodite			endopodite		
segments	1	2	3	1	2	3
P1	0/0	1/0	2/2/1	1/0	2/2/0	—
P2	0/0	1/1	2/2/2	1/0	1/0	2/2/0
P3	0/0	1/1	2/2/2	1/0	1/0	2/2/0
P4	0/0	1/1	2/2/2	1/0	1/0	2/2/0

Right P5 basis without hyaline membrane and almost as long as wide (Fig. 1). Proximal segment of exopodite as long as wide and with rounded distal-lateral corner. Distal segment of exopodite about 2 times longer than wide, with long lateral spine at 3/4th of its length, and a very long apical claw. Endopodite of right P5 undifferentiated. Left P5 with quadriform basis and 2-segmented rami. Distal exopodite segment bears 2 digitiform processes. The inner process is naked and longer than outer, while the outer one has 5 teeth on inner margin (Fig. 1).

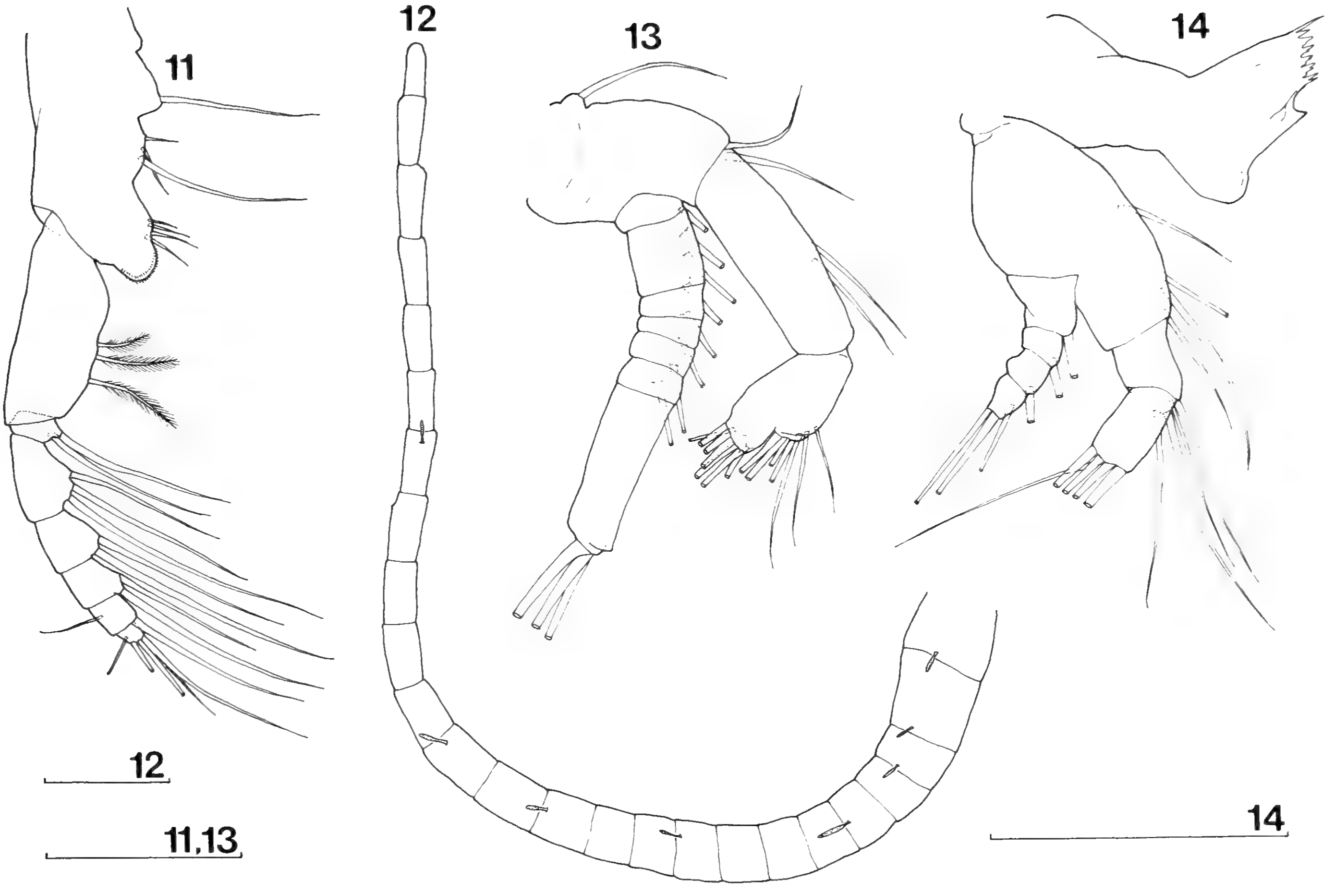
Remarks.—*Stygodiaptomus ferus* is clearly distinguished from the other two species in the genus *Stygodiaptomus* by the following: absence of armature elements on the first exopodite segment of P1–P4; presence of an outer spine on the second exopodite segment of P2; undifferentiated endopodite on male right P5; and basal segment of the exopodite on male right P5 with rounded distal-lateral corner. Other differences between *S. kieferi* Petkovski, 1981, and *S. ferus* n. sp. are: 2-segmented exopodite of P1 in *S. kieferi* (in *S. ferus* 3-segmented); inner margin of basis on male right P5 in *S. kieferi* with a strong spine (not developed in *S. ferus*); and completely fused 22nd and 23rd segments of the male right A1 in *S. kieferi* (not fused in *S. ferus*). *Stygodiaptomus ferus* n. sp. is more similar to *S. petkovskii* Brancelj, 1991; in addition to the differences noted above they differ only in details in armature of the male right A1, and male P5. A close relationship among these three species is suggested by the shape of male P5, A1, and identical armature of the P1–P4 endopodites.



Figs. 1–5. *Stygodiaptomus ferus,* n. sp., Holotype: 1, P5; 2, P4; 3, P3; 4, P2; 5, P1. Scale bars = 0.1 mm.



Figs. 6–10. *Stygodiaptomus ferus,* n. sp., Holotype: 6, right A1 (segments 1–13); 7, right A1 (segments 14–18); 8, right A1 (segments 19–23); 9, habitus, dorsal view; 10, abdomen, dorsal view. Scale bars = 0.1 mm.



Figs. 11–14. *Stygodiaptomus ferus,* n. sp., Holotype: 11, Mxp; 12, left A1; 13, A2; 14, Md. Scale bars = 0.1 mm.

Etymology.—The specific name is from the Latin adjective *ferus,* which means wild, agreeing in gender with the masculine generic name.

Geographic distribution.—The new species is known only from the type locality. We presume that it inhabits a wide area of Skadar Lake Valley in southeastern Montenegro and northwestern Albania.

Habitat notes.—Samples collected on two other occasions (3 Feb 1997, and 10 Aug 1998) from the type locality and earlier from more than 300 other localities in Montenegro did not yield additional specimens of the new species, or any other stygobitic calanoid. This suggests that either *S. ferus* is a very rare species, or that a cave environment is not the optimal habitat for it. We believe that its optimal habitat may be the large artesian reservoir which is located under Skadar Lake Valley. Unfortunately artesian waters have not yet been investigated in Montenegro.

Revised diagnosis for the genus Stygodiaptomus.—Diaptomids with 2- or 3-segmented endopodite of P1. Second segment of P2–P4 endopodites each with only 1 seta on the inner margin. Terminal segments on exopodites P2–P4 with 5 setae and 1 spine. Terminal segments of endopodites P2–P4 with 4 setae. All swimming legs without setae on the inner margin of the coxa. Male right P5 with 1-segmented, very small, or completely reduced endopodite. Male right A1 with short and strong spines on segments 10, 11, and 13, as well as a smaller one on 12th segment. This diagnosis separates the genus *Stygodiaptomus* from the most similar genus *Spelaeodiaptomus,* as well as from all other genera in the subfamily Diaptominae.

Key to the species of *Stygodiaptomus*

1. Right male P5 with smooth inner margin on basis 2

Right male P5 with a strong spine on inner margin of basis . . . . *S. kieferi* Petkovski, 1981
2. First exopodite segment of P2–P4 with spine on outer margin . . . . *S. petkovskii* Brancelj, 1991
First exopodite segment of P2–P4 without spine on outer margin . . *S. ferus* n. sp.

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The freshwater centropagid *Osphranticum labronectum* Forbes, 1882 (Crustacea: Copepoda: Calanoida) in Mexico with description of a new subspecies

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Abstract.—From a zooplankton survey carried out during January 1998 in several ponds of the Mexican state of Tabasco, southern Gulf of Mexico, several specimens of the freshwater centropagid copepod *Osphranticum labronectum* Forbes, 1882 were collected. This is a widespread species in North America. There is a single record south of 25°N, in Guatemala (ca. 15°N). The species has not been reported from the large area lying between these records, mostly represented by Mexico. This finding in southeast Mexico is helpful to understand the distributional range of the species. It is also the first record of a freshwater species of the Centropagidae for Mexico. The Mexican specimens show morphological differences when compared with previously described material, mainly on the armature of male and female fifth legs, and in their size. These differences, and the assumed isolation of the Mexican populations from the species main distribution area in the Nearctic region, suggest that the Mexican population is a new subspecies, *O. labronectum mexicanum.* Taxonomic illustrations, including structures not depicted or described before for the species, are also provided herein.

The calanoid copepod family Centropagidae is represented in the Americas by six freshwater genera (*Parabroteas* Mrázek, 1901; *Limnocalanus* Sars, 1863; *Osphranticum* Forbes, 1882; *Boeckella* De Guerne & Richard, 1889; *Neoboeckella* Bayly, 1992a; *Sinodiaptomus* Kiefer, 1932). The genus *Pseudoboeckella* Mrázek, 1901 is now considered a synonym of *Boeckella* (Bayly, 1992b). However, only *Limnocalanus, Sinodiaptomus,* and *Osphranticum* are known to be distributed in North America (Williamson 1991, Bayly 1992a, Reid & Pinto-Coelho 1994).

Osphranticum labronectum, the only species of this genus, is one of the most widely distributed freshwater centropagids in the United States and Canada (Wilson & Yeatman 1959, Williamson 1991). This species was described originally by Forbes (1882) from material collected in Lake Michigan. It is mainly a Nearctic copepod, reported from several localities of the United States and Canada (Marsh 1933; Wilson & Yeatman 1959; Dussart & Defaye 1983, 1985; Bayly 1992a). Its southernmost record in North America is in the Everglades, Florida (Reid 1992). South of this, there is one record from Guatemala (Juday 1915, Reid 1990) which was overlooked by Fernando & Smith (1982) in their revision of the Central America freshwater copepod fauna.

From a zooplankton survey carried out to investigate the copepod diversity of freshwater environments of the state of Tabasco, southeastern Mexico, several specimens of this copepod were recorded. A geographic record of this species is presented along with illustrations of the material examined, and the description of a new subspecies, *O. labronectum mexicanum.*

Zooplankton was collected 12 January

1998, during a survey of several aquatic environments in the state of Tabasco, southeastern Mexico. Samples were collected using a standard plankton net with a 0.072 mm mesh, deployed in near–shore plankton trawls. The zooplankton specimens were fixed in 4% formalin, and then processed for identification. The taxonomically relevant structures for the identification of these copepods, and those not previously depicted were illustrated with the aid of a camera lucida. Descriptions are provided of the cephalic appendages. Specimens were deposited in the collection of the National Museum of Natural History (USNM), Washington, D.C., in the the Muséum National d' Histoire Naturelle (MNHN), and in the zooplankton collection of El Colegio de la Frontera Sur, Chetumal (ECO-CHZOO).

Family Centropagidae
Osphranticum labronectum Forbes, 1882
O. labronectum mexicanum, new subspecies
Figs. 1–13

Material examined.—Holotype: One adult female, ethanol-preserved. Laguna Matillas, Tabasco, Mexico, 12 Jan. 1998, USNM 288458. Paratypes: Six adult females from same site, deposited in MNHN-Cp1777. One adult male in the same institution (MNHN-Cp1776). One adult female and three adult males from same locality, 12 Jan 1998, ethanol-preserved, access number ECOCH-ZOO-00463. Two adult males from same locality, USNM 288459.

Type locality.—Laguna Matillas, Tabasco, southeastern Mexico: 17°53′45.8″N, 92°31′19.6″W, 12 Jan 1998. Environmental conditions of the sampling site associated with this record were: temperature: 27.7°C; pH: 6.32; oxygen: 7.2 ppt.

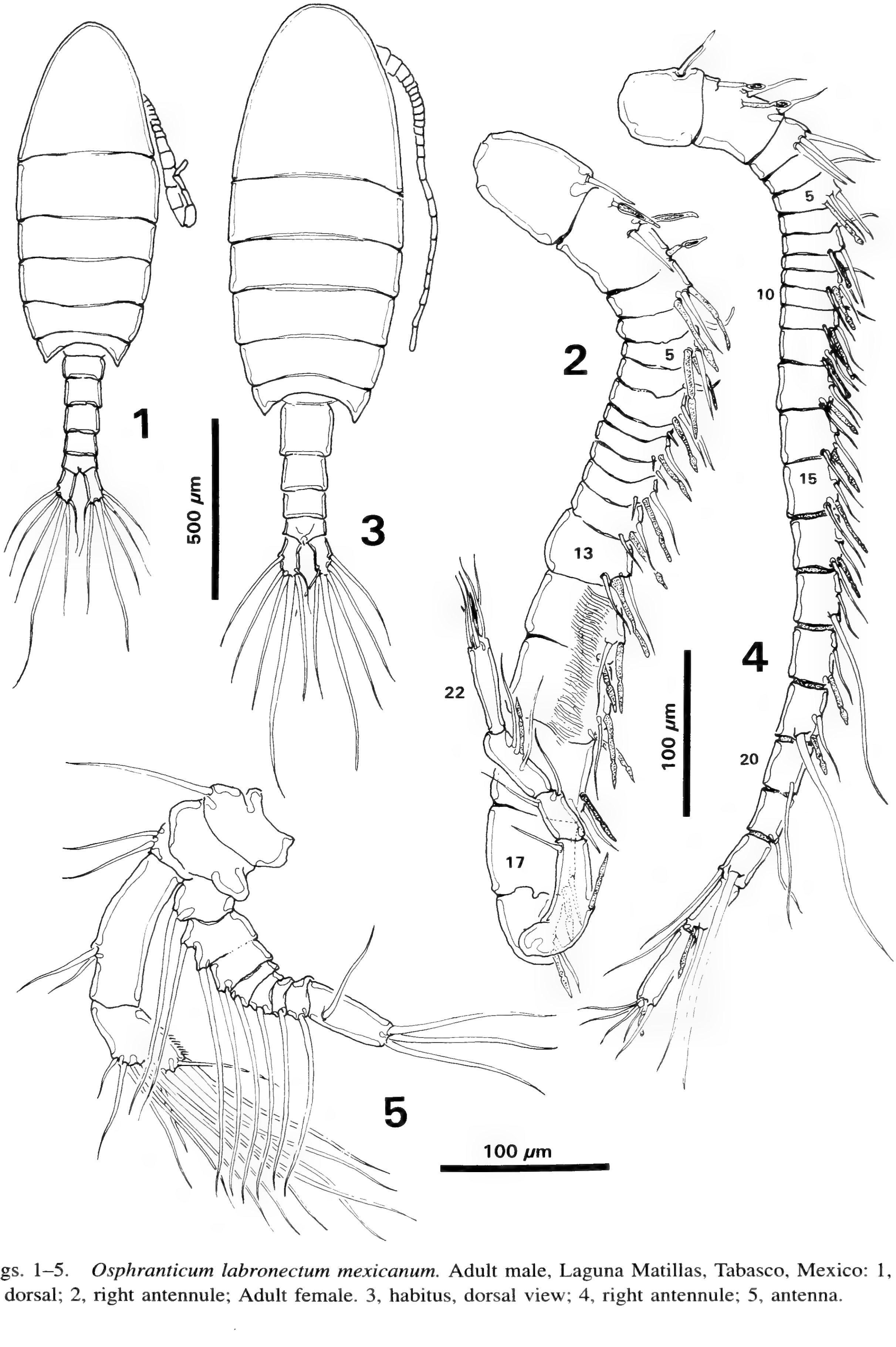
General description.—Body shape and proportions as described and depicted by Marsh (1933) and Dussart & Defaye (1995). Average length (n = 5) of females: 1.44 mm, cephalothorax 0.97 mm long, 0.15 mm wide. Antennule length 1.06 mm. Genital somite 0.14 mm long, 0.15 mm wide. Average length (n = 5) of males: 1.26 mm, cephalothorax 0.85 mm long, 0.34 mm wide. Antennules 0.79 mm. Genital somite 0.07 mm long, 0.09 mm wide.

Description of cephalic appendages.—Female: Antennules (Fig. 4) relatively short, 24-segmented, reaching posterior margin of third pediger (Fig. 3), longer in some specimens. Spiniform seta on first segment long, stout. Long setae on segments 17, 19, and 22. Appendages per segment as follows (numerals = segment, numerals between brackets = number of setae, ae = aesthetasc, sp = spine): 1(sp), 2(2+2ae), 3(3), 4(1), 5(2+ae), 6(1), 7(2+ae), 8(1), 9(2+ae), 10(1), 11–16(2+ae), 17(2), 18(1+ae), 19(2+ae), 20(1), 21(1), 22(2), 23(2+ae), 24(5+ae) (Fig. 4).

Male: Antennules 22-segmented, left antennule as in female, right antennule (Fig. 2) geniculated between segments 18–19, segments 13–17 relatively wider. Strong muscular striation on segments 14 and 15. Appendages per segment as follows: 1(sp), 2(1+3ae), 3(1+2ae), 4(1), 5(1+2ae), 6(1), 7(2+ae), 8(1), 9(2+ae), 10(1), 11–13(2+ae), 14 and 15(1+2ae), 16(2+ae), 17 and 18(1+ae), 19(1+ae), 20(2), 21(2+ae), 22(5+ae).

Antennae with exopod longer than endopod (Fig. 5). Coxa with one long seta. Basis wide, with two subequal setae on outer distal margin. Endopod with two segments, proximal with two setae on distal 1/3. Distal portion of terminal endopodal segment with two lobes, internal with row of hairlike spinules, with five setae, one smaller than others. External lobe with one short and seven long setae. Exopod 8-segmented, with one seta on first segment, two on second, and one seta each on segments 3–7. Distal segment with one short seta on proximal 1/3, and three long terminal subequal setae.

Mandible (Fig. 6) with seven bluntly-pointed teeth on gnathobase and a movable tooth at the tip. Basis with three setae; endopod of two segments, proximal segment



Figs. 1–5. *Osphranticum labronectum mexicanum.* Adult male, Laguna Matillas, Tabasco, Mexico: 1, Habitus, dorsal; 2, right antennule; Adult female. 3, habitus, dorsal view; 4, right antennule; 5, antenna.

with four setae on distal portion of outer margin; distal segment slightly longer, with 7 subequal terminal setae plus one posterior seta. Exopod 5-segmented, with a 1,1,1,1,2 setation pattern.

Maxillule (Fig. 7) with praecoxal arthrite with 15 spiniform setae, two anterior, nine terminal, four posterior. Coxal epipodite with nine setae, inner two smaller and thinner than the others, coxal endite with four setae. Basis with one internal lobe bearing four setae, basal exite with one seta. Basal endite with five setae. Endopod 3-segmented, articulating with basis, setation pattern as: 4,4,7. Exopod with 12 setae, three of five proximalmost larger, plumose.

Maxilla (Fig. 8) indistinctly segmented, with two praecoxal and two coxal lobes, and a well developed basal lobe. Setation pattern of five lobes as: 4, 3 (first and second praecoxal endites), 3, 3 (first and second coxal endites), 3 (basal endite); endopod 4-segmented, with setation pattern: 1,1,2,3.

Maxilliped (Fig. 9) well developed. Coxa fused with praecoxa, with anterior protuberance projecting over next segment, with row of short spinules surrounding process. Coxa with 3 distinct lobes, proximalmost low, with two setae, second with three, third with four. Basis with group of three setae on middle of inner margin. Endopod 6-segmented, with first segment partially fused to basis, bearing two subequal setae. Second and third endopodal segments with four subequal setae, fourth with three, fifth with four; terminal segment with four subequal setae.

Caudal rami (Fig. 10) structure and proportions as described and depicted by Marsh (1933), furcal seta relatively long, length of ramus/setal length ratio: 1.75. Other caudal seta as depicted by Marsh (1933).

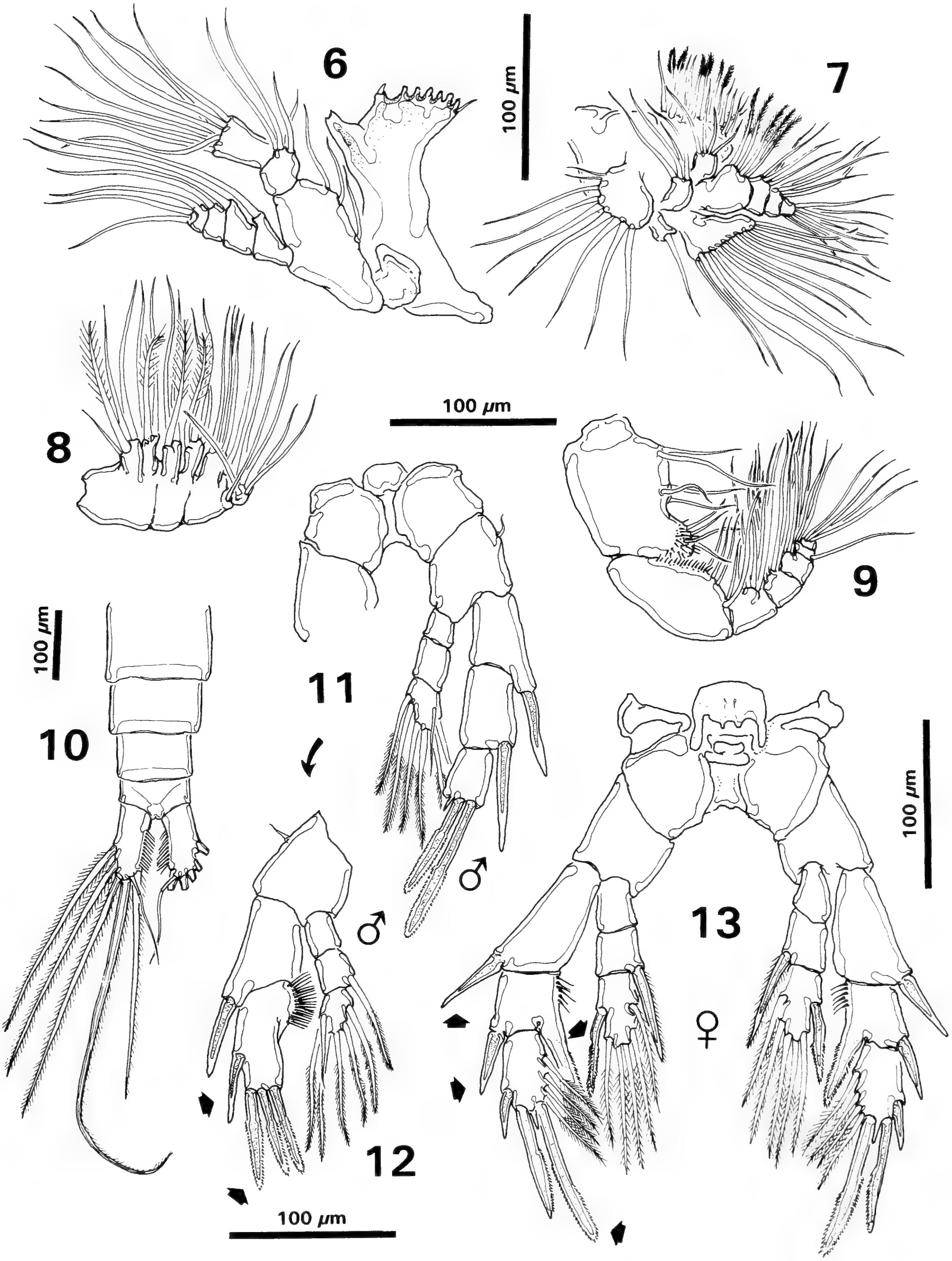
Male fifth legs (Figs. 11, 12).—As described by Marsh (1933), Bayly (1992a), and Dussart & Defaye (1995). Relative length ratios of lateral spine on terminal exopodal segment, and of the outermost terminal spine of same segment as presented in Table 1. Inner rounded protuberance on terminal exopodal segment relatively low and not pronounced.

Female fifth legs (Fig. 13).—As described by Marsh (1933), Bayly (1992a), and Dussart & Defaye (1995) but differs in the relative length of the spines on first and second exopodal segments, the innermost apical spine, and the spine on third endopodal segment (see Table 1).

Etymology.—The subspecific epithet refers to the country in which the specimens were collected and for which they represent the first record of a freshwater centropagid. The gender of the genus and species names is neuter, and so is the corresponding Latin form used on the subspecies name.

Remarks.—The species can be readily distinguished from most genera of freshwater Centropagidae by having, in the fifth legs, 3-segmented endopodites on both sides in males and females. Additionally, the male left distal exopodal segment has an inner rounded protuberance at its base (Fig. 12). The caudal rami in both sexes are less than 2.5 times as long as maximum width (Wilson & Yeatman 1959, Bayly 1992a). The right caudal ramus has the second inner terminal seta clearly wider and longer than the others (Williamson 1991). Several structures, including the antennules, antennae, and mouthparts (Figs. 2, 4–9) are illustrated here; some of these appendages have not been depicted before.

We detected some differences in the Mexican specimens with respect to the illustrations of the species by Marsh (1933), Wilson & Yeatman (1959), Dussart & Defaye (1995), and Bayly (1992a), all from material of the Nearctic region. The relative length of the spines of both the female and male fifth legs are different in both groups of specimens (see arrowed spines on Figs. 12, 13), as shown in Table 1. The antennule relative length is 70.8% of the total body length and 89.5% of the cephalothorax length in Wilson & Yeatman (1959, fig. 20.29). It is 63.5%, and 85.7%, respective-



Figs. 6–13. *Osphranticum labronectum mexicanum.* Adult female, Laguna Matillas, Tabasco, Mexico: 6, mandible; 7, maxilla; 8, maxillule; 9, maxilliped; 10, urosome, dorsal view; 11, male right fifth leg; 12, male left fifth leg; 13, female fifth leg.

Table 1.—Comparison of length ratios of some morphological features described for *Osphranticum labronectum* in the Nearctic region, and *O. labronectum mexicanum* from Tabasco, Mexico. P5 = fifth leg.

Features	Wilson & Yeatman (1959)	Dussart & Defaye (1995)	Marsh (1993)	Specimens from Tabasco
Female P_5: Re 1 spine/Re2	0.87	0.77	0.85	1.37
Female P_5: Re 2 outer spine/Re 2	0.78	0.74	0.69	1.11
Female P_5 : apical inner spine/Re 3	1.87	1.26	1.78	2.1
Female P_5 : spine on Ri 3/Ri 3	1.0	0.83	0.6	1.23
Female furca : dorsal seta/furcal ramus	0.40	0.75	0.41	1.75
Male P_5 Re 2 lateral spine/Re 2	0.53	0.52	0.56	0.68
Male P_5 Re: apical outer spine/apical medial and inner spines	1	1	1	1.15
Male P_5 Re : process on inner margin	high, pronounced	high, pronounced	high, pronounced	low, not pronounced

ly, in Dussart & Defaye (1995, fig. L7). Although relatively shorter in the figure by Dussart & Defaye (1995), in both, antennules do not reach beyond the posterior margin of the fourth pediger. In our specimens the corresponding relative lengths are ca. 67% (60–73.9%), and ca. 95% (78.9–more than 100%). Antennules are relatively longer in our specimens, reaching at least the posterior margin of the third pediger, but in some they reach the second urosomite. However, the variability of this character seems to make it taxonomically unimportant.

The dorsal furcal setae are much longer in the Tabasco specimens (1.6–1.7 the length of the furcal rami versus 0.4–0.7) than in the North American material. This character is not as variable as the antennule length and could be used to recognize the subspecies.

Both, our female and male specimens body size (1.4 mm, 1.26 mm, respectively) seem to be well below the species range when compared with the measurements reported by Wilson & Yeatman (1959) for specimens from the United States (total length: females 1.7–2.5 mm; males: 1.4–2.3 mm). As found in the Tabasco material, males tend to be smaller than females.

The Tabasco specimens show consistent but slight differences when compared with illustrations of North American material. These differences, which include secondary sexual structures such as the male and female fifth legs, the smaller size, the relative length of the dorsal furcal seta, and the geographic isolation of the Mexican population (and probably that of Guatemala), seem to be enough evidence to justify the erection of a new subspecies of *O. labronectum.* Of course, further studies on comparative morphology and even interbreeding experiments should be carried out in order to determine the status of the neotropical populations of *O. labronectum.*

The species record permits a southward extension of the known latitudinal distribution of this species into the tropical zone of Middle America (17°N), from the subtropical Florida area (30°N). It also represents a modest northwards range extension from the two localities in which it was recorded in two localities of Guatemala, Los Amates (15°16′N, 89°05′) and Puerto Barrios (15°43′N, 88°36′W), both close to the Gulf of Honduras, on the Atlantic coast (Juday 1915). The present record consolidates the regional distributional range of this species in the region (Fig. 14).

The present record of *O. labronectum* represents the first report of a freshwater representative of the family Centropagidae in Mexico (see Suárez-Morales & Reid 1998). *Osphranticum labronectum* can be collected in littoral areas, contrasting with

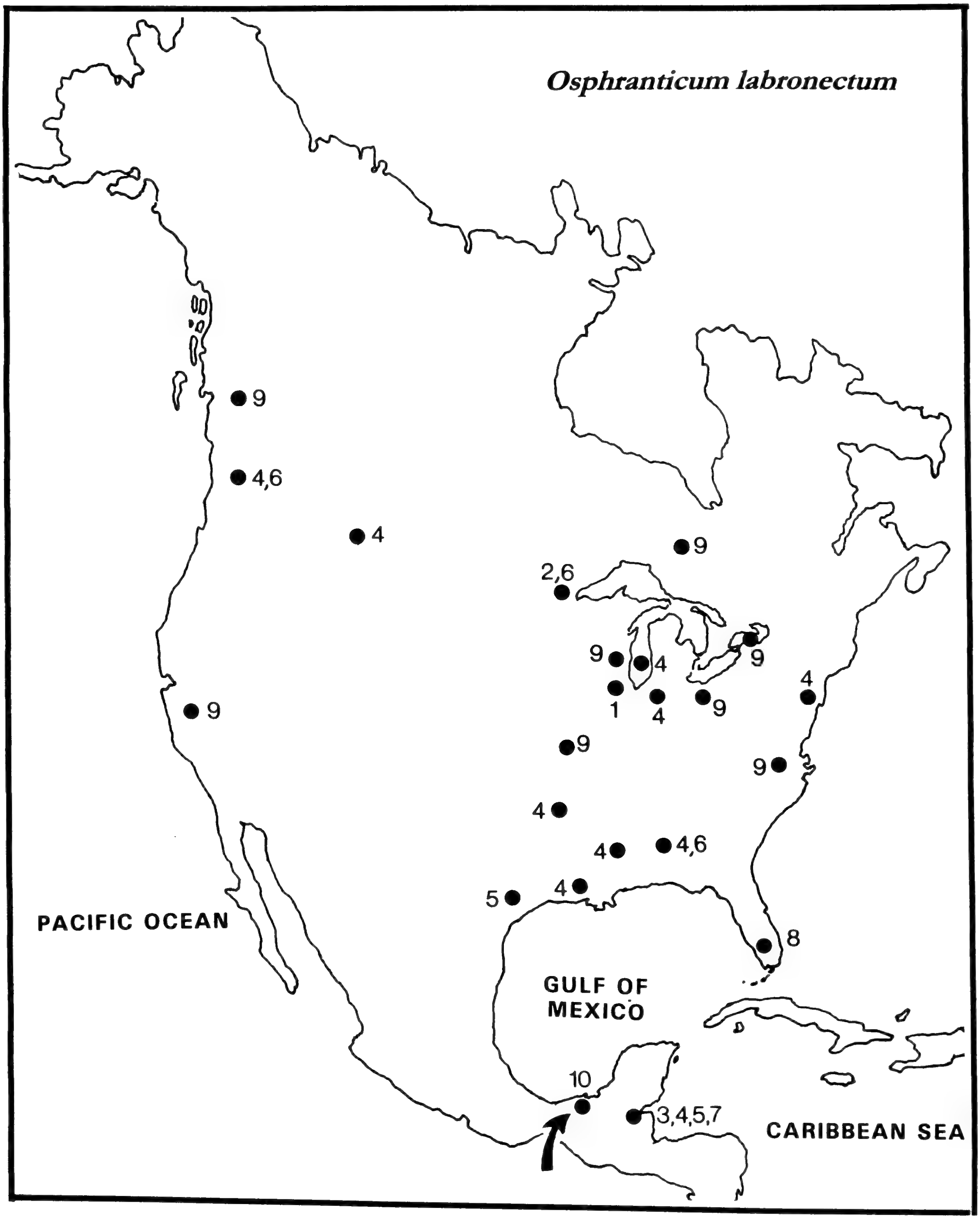


Fig. 14. Records of *O. labronectum* and authors reporting the species from different areas of North America. 1. Forbes (1882); 2. Herrick (1895); 3. Juday (1915); 4. Marsh (1933); 5. Wilson & Yeatman (1959); 6. Dussart & Defaye (1983); 7. Reid (1990); 8. Reid (1992); 9. other records from data of the Wilson Copepod Library, Washington, D.C.; 10. record in this paper (arrowed).

the diaptomid calanoid copepods which tend to prefer open waters.

Acknowledgments

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New records of isopods from the Indian River Lagoon, Florida (Crustacea: Peracarida)

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Abstract.—Fifteen species of isopod are recorded for the first time as occurring in the Indian River Lagoon. Two species are described as new: the janirid asellote *Iais floridana,* n. sp., which occurs commensally with *Sphaeroma terebrans* in low salinity water, and the sphaeromatid flabelliferan *Sphaeromopsis sanctaluciae,* n. sp., which is also recorded from the Orange River, Lee County, Florida, and from Islas de Juventud, Cuba. A brief discussion of protogyny in the sphaeromatid *Paradella dianae* is included.

The Indian River Lagoon, Florida, is the most biologically diverse estuarine system on the east coast of North America. As part of the Intra-coastal Waterway, it is subject to heavy usage by commercial and sport/recreational water traffic, and has seen heavy residential development along its shores. Given its important mixed-use resources, intensive study of the lagoon has been carried out for some time (see Richards 1995). Ongoing investigations by the authors of the crustacean fauna of the lagoon have revealed a number of isopod species not recorded in earlier studies (e.g., Kensley, Nelson, & Schotte 1995), although some of these may be known from the wider Florida region (see Camp, Lyons, & Perkins 1998). In part, these new records are the result of sampling in a wide variety of habitats, both in the main lagoon as well as in its tributary rivers and in the inlets that open to the sea. Twenty-five marine isopod species had previously been recorded from the IRL. The present paper documents 15 additional species and adds to the knowledge of the biodiversity of the Indian River Lagoon. Restricted synonymies, which include the original description plus any Florida records, and references that contain fuller synonymies are provided for most species. Collecting stations designated 'FTP' are those of the authors'. Unless otherwise stated, all material is deposited in the collections of the National Museum of Natural History, Smithsonian Institution.

Suborder Anthuridea

Family Anthuridae

Cyathura polita (Stimpson, 1855)

Anthura polita Stimpson, 1855:393.—Harger, 1880:398–402, pl. XI, figs. 68–69.
Cyathura polita: Burbanck, 1959:507.—Kruczynski & Subrahmanyam, 1978: 93.—Camp et al., 1998:132.

Material examined.—1 ♀, FTP-1, St. Lucie River, rotten wood in mangroves, 0.5 m, salinity 15–20 ppt., 29 May 1995.—1 ♀, FTP-22, Fort Pierce, Taylor's Creek near Rt. 1, rotten wood on muddy bank with cattails and *Spartina,* intertidal, 10 ppt., 25 Apr 1996.

Previous records.—East coast of America from the Gulf of Mexico to Canada.

Mesanthura pulchra Barnard, 1925

Mesanthura pulchra Barnard, 1925:145, fig. 9e.—Kensley & Schotte, 1989:49, fig. 19b; 52–53.—Camp et al., 1998:132.
Mesanthura decorata Menzies & Glynn, 1968:26, fig. 8a–i.

Mesanthura floridensis Menzies & Kruczynski, 1983:28–30, fig. 9a–i.

Material examined.—1 ♀, 1 ♂, FTP-4, Fort Pierce Inlet, south of South Jetty, mixed algal turf on sand bag barrier on beach, intertidal, 30 May 1995.—1 ovigerous ♀, FTP-89, Sebastian Inlet State Park, 100 ft inside south jetty, encrusting orange sponge with red branching alga on jetty rocks, 0.5 m, 19 Sep 1996.—1 ♀, 1 juv., FTP-51, Sebastian Inlet State Park, south side, algal clumps on granite boulders on shore inside bridge, 0.5 m, 25 Jun 1997.

Previous records.—Belize; Puerto Rico; Florida; intertidal to 36 m.

Ptilanthura tenuis Harger, 1878
Fig. 1

Ptilanthura tenuis Harger, 1878:377.—Kensley, 1996a:763, figs. 1, 2.—Kensley, 1996b:278, fig. 5B–D.—Camp et al., 1998:132.

Material examined.—5 ♀, Indian River Lagoon, south of Sebastian Inlet, 27°49.64′N, 80°27.04′W, 1.6 m, salinity 30.15 ppt., 1995, coll. R. Heard.

Previous records.—Florida, Alabama, to Maine; intertidal to 253 m.

Remarks.—The material from the region of Sebastian Inlet had a distinctive and persistant color pattern, which is recorded here.

Suborder Asellota
Family Janiridae
Carpias algicola (Miller, 1941)

Janira algicola Miller, 1941:318–320, fig. 4a–n.

Bagatus algicola.—Pires, 1982:247–250, fig. 47–55.

Carpias algicola.—Kensley & Schotte, 1989:82–83, fig. 38a–g.—Camp et al., 1998:133.

Material examined.—1 ♂, 4 ♀, FTP-38, Sebastian Inlet State Park, gravel and pebbles in pockets around boulders, infratidal, 0–0.8 m, 19 Sep 1996.—2 ♂, 1 ovigerous ♀, 11 immature, FTP-40, Sebastian Inlet State Park, clumps of *Caulerpa racemosa* and branching red alga on granite boulders inside inlet, 0.5–1.0 m, 19 Sep 1996.—2 ♂,

Fig. 1. *Ptilanthura tenuis:* Female in dorsal view, showing persistent color pattern. Scale = 1 mm.

4 ♀, 2 immature, FTP-42, Sebastian Inlet State Park, off south jetty about 50 yds. west of bridge, on *Caulerpa* 0.25 m, 19 Sep 1996.—18 specimens, FTP-51, Sebastian Inlet State Park, south side, granite boulder shore inside bridge, algal clumps on boulders, 0.5 m, 25 Jun 1997.—3 ♂, 7 ovigerous ♀, 60+ immature, FTP-53, same locality, algal clumps and sponge on boulders outside of bridge, 0.5–1.0 m, 26 Jun 1997.—3 specimens, FTP-65, Sebastian Inlet State Park, orange sponge on rocks inside of inlet, low tide level, 0–50 cm, 18 Aug. 1998.—1 ovigerous ♀, 5 immature, FTP-68, Sebastian Inlet State Park, gravel rubble, empty shells in pockets between rocks inside inlet, 0–20 cm, 18 Aug 1998.—12 ovigerous ♀, 8+ immature, FTP-69, Sebastian Inlet State Park, algal turf and hydroids on granite boulders inside inlet, 0–50 cm, 18 Aug. 98.

Previous records.—Venezuela; Jamaica; Yucatan, Mexico; Belize; Looe Key, Florida; intertidal to 2 m.

Carpias triton (Pires, 1982)

Bagatus triton Pires, 1982:251–254, figs. 72–84.

Carpias triton.—Kensley & Schotte, 1989: 83, 87, fig. 39e–f.

Material examined.—20+ specimens, FTP-5, Ft. Pierce Inlet, large barnacle clumps with orange sponge and algal turf on boulders inside inlet, shallow infratidal, 30 May 1995.

Previous records.—Belize, intertidal.

Iais floridana, new species

Figs. 2, 3

Material examined.—Holotype, USNM 243843, 1 ♂ tl 1.35 mm, Paratypes, USNM 243844, 10 ♂ tl 1.26–1.40 mm, 12 ovigerous ♀ tl 1.71–1.82 mm, 10 non-ovigerous ♀, 50+ juveniles, sta FTP-22, on *Sphaeroma terebrans* in rotten wood, Taylor Creek near Rt. 1, intertidal, 10 ppt., 25 Apr 1996.

Additional material.—10 specimens, sta FTP-2, on *Sphaeroma terebrans* in rotten wood, Port St. Lucie, Florida, 29 May 1995.—100+ specimens, sta FTP-12, on *Sphaeroma terebrans* in rotten wood, Riverside Park at Port St. Lucie Boulevard, intertidal–1 m, 10 ppt., 1 Jun 1995.—1 specimen, sta FTP-13, on *Sphaeroma terebrans* in dead wood, north fork of St. Lucie River, at Prima Vera Boulevard, 2.5 ppt, 0.1 m, 1 Jun 1995.—2 specimens, sta FTP-17, on *Sphaeroma terebrans* in rotten wood, Riverside Park on St. Lucie River, 0 ppt, 0.1–0.5 m, 23 Apr 1996.—3 specimens, sta FTP-27, on *Sphaeroma terebrans* in rotten wood, near mouth of St. Sebastian River, 15 ppt, 0.5 m, 17 Sep 1996.—2 specimens, sta FTP-29, on *Sphaeroma terebrans* in rotten wood, island in mouth of St. Sebastian River, 15 ppt., 0.5 m, 17 Sep 1996.—14 specimens, Estero River mouth, Lee County, Florida, 26°26′05″N, 81°50′52″W, coll. A. S. Walton.—1 specimen, Hendry Creek, off Estero Bay, Lee County, Florida, coll. A. S. Walton, 14 Apr 1993.

Description.—Male: Body about 2.5 times longer than greatest width at pereonite 4. Cephalon about twice wider than long, anterolateral corners rounded. Anterolateral corners of pereonites, especially of 3–5, rounded, setose, coxae visible on all pereonites in dorsal view. Pleon consisting of short anterior pleonite lacking free lateral margins, plus subcircular pleotelson. Eye consisting of 2 ommatidia. Antennular flagellum of 3 articles, terminal and subterminal articles each bearing single aesthetasc. Antennal flagellum of 13 articles. Mandibular palp of 3 articles, article 2 with 2 stout setae, article 3 with distal row of 7 setae; incisor of about 6 sclerotized cusps; spine row of 4 or 5 setae; lacinia of 2 cusps; molar distally truncate with 2 distomesial setae. Maxilla 1, inner ramus with 4 distal setae, outer ramus with about 10 pectinate distal setae. Maxilla 2, 2 outer lobes each with 4 distal fringed setae. Maxilliped; endite broad, distolaterally convex, with about

7 fringed setae and 8 simple setae; palp articles setose on mesial margins.

Pereopod 1, dactylus bearing 2 claws; pereopods 2–3, 5–7, dactyli each with 3 claws. Pereopod 4 considerably shorter than 3 or 5, dactylus with 2 claws, propodus with single stout distal claw. Pleopod 1, rami fused for about 4/5 of total length, distal lobes rounded, bearing 9 setae distally per side. Pleopod 2, protopod semicircular, canula not reaching beyond distal angle of protopod. Uropodal rami both longer than protopod, exopod about 1/3 longer than endopod, each with 4 elongate distal simple setae.

Female: Brood pouch containing up to 8 eggs. Pleonal operculum ovate, midlength about 2/3 greatest width, with 4 or 5 fine marginal setae.

Remarks.—Of the eight described species of *Iais* (see Wilson & Wägele 1994), at least three occur commensally with sphaeromatid isopods, as does the present species, which is found in association with *Sphaeroma terebrans.* Several species (e.g., *I. aquilei* Coineau, 1977; *I. elongata* Sivertsen & Holthuis, 1980; see Kensley 1994) also perform mate-guarding as is seen in the present material, with the male clasping a manca female with the shortened specialized pereopod 4.

Given that some species of *Sphaeroma,* especially those that bore into mangroves, have wide distributions, and have been implicated in introductions along with their commensals (Rotramel 1972, 1975), it is necessary to compare the present material closely with *I. californica* (found on *Sphaeroma quoyanum*), in case the present species was somehow introduced to the east coast of the United States, where *Sphaeroma terebrans* is the available host. However, *Iais floridana* more closely resembles *I. singaporensis* Menzies & Barnard, 1951 (see Müller & Brusca 1992) especially in the general habitus and in possessing rounded anterolateral lobes on the pereonites, than *I. californica* (Richardson, 1904). Comparison with recently collected material of both *I. californica* and *I. singaporensis* reveals several differences that reinforce the view that the Florida material represents an undescribed species. The two distal articles of the antennule differ in proportions, the penultimate articles especially being more slender and elongate on the two previously described species. The antennal flagellum has fewer articles in the Florida material (13) than in *I. californica* (20) and *I. singaporensis* (24). The distal propodal spine of pereopod 4 in the male of *I. californica* is noticeably more elongate than in the Florida and Asian material. *Iais californica* is a larger species (♂ 2.49 mm mean length, $n = 15$; ovigerous ♀ 2.55 mm mean length, $n = 11$) than either the Florida species (♂ 1.34 mm mean length, $n = 10$; ovigerous ♀ 1.76 mm mean length, $n = 10$) or *I. singaporensis* (♂ 1.3–1.7 mm, ovigerous ♀ 1.4–1.7 mm). The stylet of pleopod 2 of the male is more slender and elongate in the Florida species than in *I. singaporensis.*

Etymology.—The specific name derives from Florida, from whence the species is recorded.

Family Joeropsidae

Joeropsis coralicola Schultz & McCloskey, 1967

Joeropsis coralicola Schultz & McCloskey, 1967:103–107, figs. 1–39.—Kensley & Schotte, 1989:88, fig. 40g.—Camp et al., 1998:133.

Material examined.—11 specimens, sta FTP-5, Fort Pierce Inlet, on large barnacle clumps with orange sponge and algal turf on boulders inside inlet, shallow infratidal, 30 May 1995.

Previous records.—North Carolina to Florida Middle Grounds, Gulf of Mexico, 25–33 m.

Joeropsis tobagoensis Kensley & Schotte, 1994

Joeropsis tobagoensis Kensley & Schotte, 1994:482, 486, fig. 1a–o.

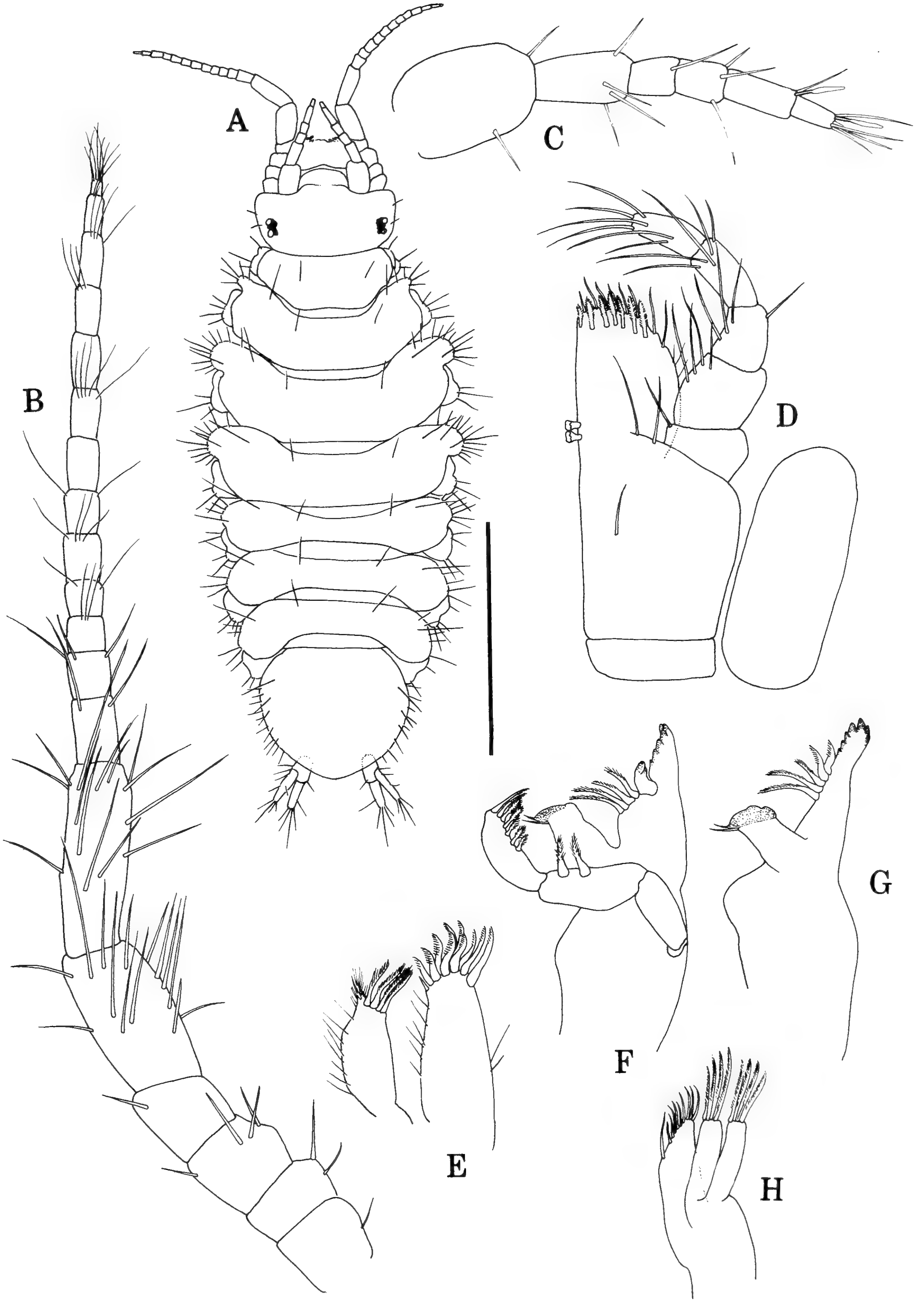

Fig. 2. *Iais floridana,* new species: A, habitus, dorsal view, scale = 0.5 mm; B, antenna; C, antennule; D, maxilliped; E, maxilla 1; F, left mandible; G, right mandible (palp omitted); H, maxilla 2.

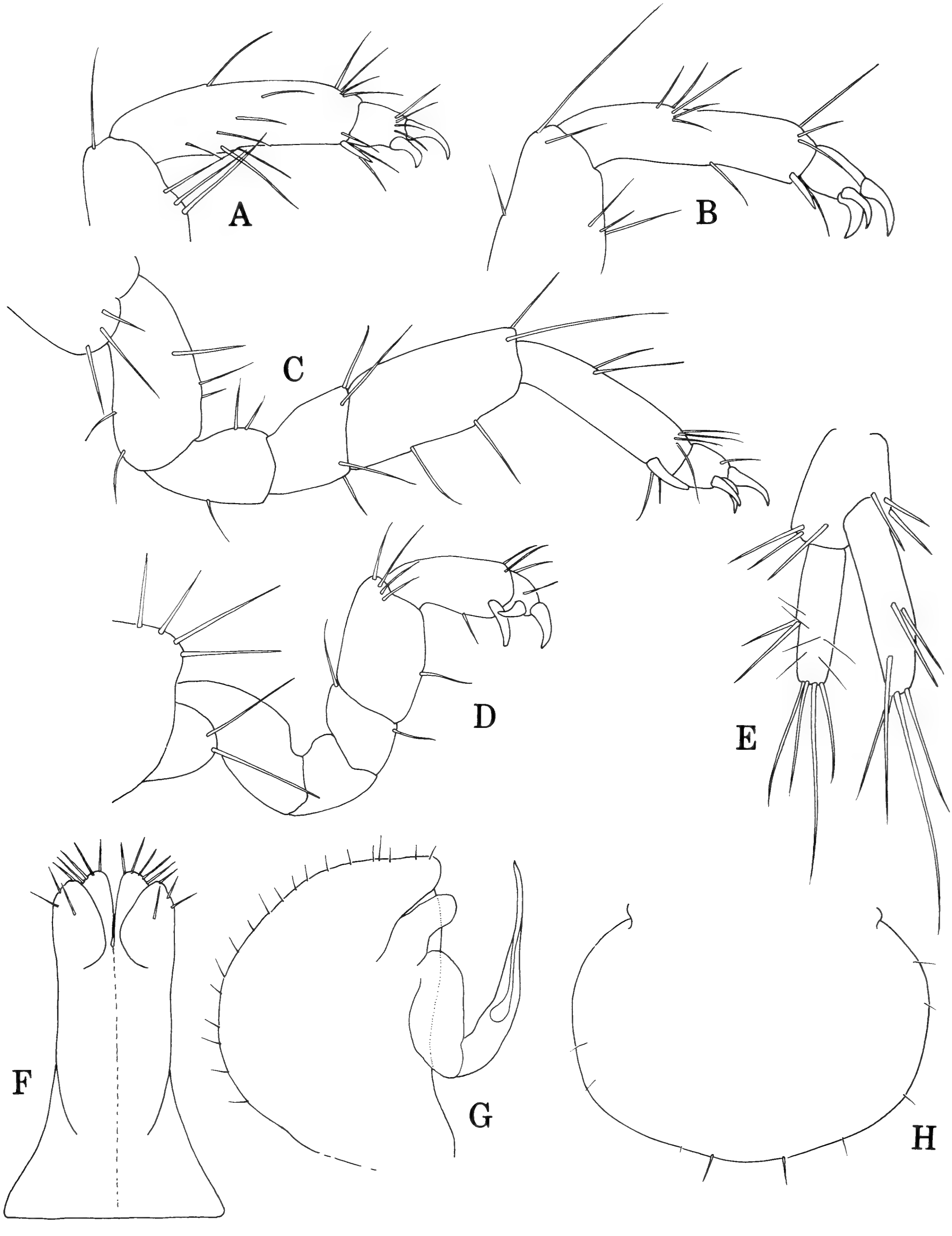

Fig. 3. *Iais floridana,* new species: A, pereopod 1 propodus and dactylus; B, pereopod 2, propodus and dactylus; C, pereopod 3; D, male pereopod 4; E, uropod; F, male pleopod 1; G, male pleopod 2; H, female operculum.

Material examined.—18 specimens, sta FTP-5, Fort Pierce Inlet, on large barnacle clumps with orange sponge and algal turf on boulders inside inlet, shallow infratidal, 30 May 1995.

Previous records.—Tobago, intertidal to 5 m.

Suborder Flabellifera

Family Cirolanidae

Anopsilana jonesi Kensley, 1987

Anopsilana jonesi Kensley, 1987:565–568, fig. 5a–j, 6a–h.—Camp et al., 1998:135.

Material examined.—1 ♀, sta FTP-12, North Fork St. Lucie River at Riverside Park on Port St. Lucie Blvd., rotten wood around dock, intertidal to 1 m, salinity 10 ppt., 1 Jun 1995.—1 ♂, 1 juv., sta FTP-27, Indian River Lagoon near mouth of Sebastian River, rotten submerged wood on small island, in low turf of *Enteromorpha* and *Ceramium,* 0.5 m, salinity 15 ppt., 17 Sep 1996.—1 ♂, 1 ♀, sta FTP-29, Sebastian River, first island inside mouth, on rotten wood at shore, salinity 15 ppt., 17 Sep 1996.

Previous records.—Belize; Florida; in estuarine mangroves.

Cirolana parva Hansen, 1890

Cirolana parva Hansen, 1890:340–341, pl. II, fig. 6–6b, pl. III, fig. 1–1d.—Bruce & Bowman, 1982:325–333, figs. 1, 2.—Kensley & Schotte, 1989:135, fig. 59d–e, 60.—Camp et al., 1998:135.

Material examined.—2 ♀, sta FTP-38, Sebastian Inlet State Park, gravel and pebbles in pockets around granite boulders, infratidal, 19 Sep 1996.—1 ♀, 1 juv., sta FTP-51, Sebastian Inlet State Park, south side of inlet, algal clumps on granite boulders, 0.5 m, 25 Jun 1997.—1 juv., sta FTP-52, Sebastian Inlet State Park, south side, shallow embayment at campsite in State Park, 1/2 mile from mouth in lagoon, 0.5 m, 25 Jun 1997.—1 juv., sta FTP-57, Sebastian Inlet State Park, lagoon near Coconut Point, sweep through *Syringodium* on Inlet side, 0.5–1 m, 26 Jun 1997.—1 juv., sta FTP-60, Wabasso Causeway Park, submerged rotten wood, 20–40 cm, 26 Jun 1997.

Previous records.—Panama; Belize; Cozumel, Mexico; Antilles to Florida Keys; Gulf of Mexico; N. & S. Carolina; intertidal to 55 m.

Family Corallanidae

Excorallana sexticornis (Richardson, 1901)

Corallana sexticornis Richardson, 1901: 518, fig 9.

Excorallana sexticornis: Delaney, 1989: 38.—Kensley & Schotte, 1989:165, figs. 75e–f, 76d–f.—Camp et al., 1998:135.

Material examined.—1 ♀, sta FTP-14, Ft. Pierce Inlet, barnacles, sponges, algal turf on blocks in inlet, intertidal, 23 Apr 1996.—1 ovigerous ♀, sta FTP-15, Ft. Pierce State Recreational Area, rotten wood piles with encrusting algae, intertidal, 23 Apr 1996.—1 ♀, 3 juvs., sta FTP-17, North Fork St. Lucie River, Riverside Park, rotten submerged wood on mud with numerous barnacles and shells, 10–50 cm, 23 Apr 1996.—2 ♀, sta FTP-33, Jim Island near Ft. Pierce Inlet, dead submerged wood at edge of mangrove island, with algal mat, 0.–0.5 m, 18 Sep 1996.—1 ♀, sta FTP-38, Sebastian Inlet State Park, gravel inlet, south side, east of bridge, algal clumps, sponge on boulders, strong wave and wash action, 0.5–1.0 m, 26 Jun 1997.—1 ♀, sta FTP-61, North Hutchinson Island, near causeway, rocks with algal turf, 0.1 m, 27 Jun 1997.—1 ♂, 1 ♀, 1 juv., sta FTP-71, Ft. Pierce Inlet, north bank, algal turf on boulders, low tide level, 19 Aug 1998.

Previous records.—Belize; Puerto Rico; Cuba; Florida; shallow infratidal.

Family Sphaeromatidae

Cassidinidea ovalis (Say, 1818)

Naesa ovalis Say, 1818:484–485.—Richardson, 1900:224, 1901:537.

Cassidena lunifrons: Richardson, 1900: 222.

Cassidina lunifrons: Richardson, 1901:533, fig. 14.

Cassidisca lunifrons: Richardson, 1905: 273, figs. 283–284.—Schultz, 1969:115, fig. 158.

Cassidinidea lunifrons: Hansen, 1905: 130.—Menzies & Frankenberg, 1966:44, fig. 20.—Kussakin, 1979:336, figs. 199–200.—Bruce, 1994:1151.

Cassidinidea ovalis: Schultz, 1969:115, fig. 159.—Kensley & Schotte, 1989:208, fig. 92b–e.—Bruce, 1994:1151, fig. 45.—Camp et al., 1998:136.

Dies arndti Ortiz & Lalana, 1980:161–164, figs. 1–8.

Dies barnardi Carvacho, 1977:14–17, figs. 4a–f, 5a–i.

Material examined.—1 ♀, FTP-1, North Fork St. Lucie River, rotten wood in mangroves, 0.5 m, salinity 1–20 ppt., 29 May 1995.—3 specimens, FTP-12, North Fork St. Lucie River at Riverside Park, Port St. Lucie Boulevard, rotten wood around dock, intertidal, salinity 10 ppt., 1 Jun 1995.—specimen, FTP-13, North Fork St. Lucie River at marina on Prima Vera Boulevard, dead submerged wood in shore grass at river's edge, 0.1 m, salinity 2.5 ppt., 1 Jun 1995.—4 specimens, FTP-17, Riverside Park on North Fork St. Lucie River, rotten submerged wood on mud with numerous barnacles and shells, 10–50 cm, salinity 0 ppt., 23 Apr 1996.—30+ specimens, FTP-23, mouth of North Fork St. Lucie River at U.S. Rt. 1 and Fern Rd., oysters shells and rocks on muddy bank, intertidal, salinity 0 ppt., 25 Apr 1996.—1 ovigerous ♀, FTP-29, Sebastian River, first island west of mouth, rotten submerged wood at shore, salinity 15 ppt., 17 Sep 1996.—1 specimen, FTP-30, same locality as above, in organic detritus, intertidal, 17 Sep 1996.—1 specimen, FTP-31, Sebastian River, island opposite MacDonald State Campground, submerged leaf litter, *Typha* and *Crinum* in shallow water, salinity 0 ppt., 17 Sep 1996.

Previous records.—Panama; Belize; Trinidad; Dominica; Cuba; Gulf of Mexico; Florida to New Jersey; intertidal–1 m.

Paradella dianae (Menzies, 1962)
Figs. 4, 5

Dynamenopsis dianae Menzies, 1962:341, fig. 3.

Paradella dianae: Harrison & Holdich, 1982:103, fig. 6.—Kensley & Schotte, 1989:224, fig. 98a–c.

Material examined.—3 ♂, FTP-14, Ft. Pierce Inlet, barnacles, sponges, algal turf on blocks in inlet, intertidal, 23 Apr 1996.—6 ♂, 14 ovigerous ♀, 30+ immature, FTP-15, Ft. Pierce Recreational Area, rotten wood piles with encrusting algae, intertidal, 23 Apr 1996.—6 ♂, 4 ovigerous ♀, 25+ immature, FTP-17, Riverside Park on North Fork St. Lucie River, rotten submerged wood on mud with barnacle shells, salinity 0 ppt., 10–50 cm, 23 Apr 1996.—1 ♂, 2 ovigerous ♀, 15+ immature, FTP-19, Jack Island near Ft. Pierce Inlet, *Caulerpa* and empty shells near oyster bank, 0.5 m, 24 Apr 1996.—100+ specimens, FTP-38, Sebastian Inlet State Park, gravel and pebbles in pockets around granite boulders lining inlet, infratidal, 0–32″, 19 Sep 1996.—92 specimens, FTP-39, same locality, on encrusting orange sponge with red branching algae on jetty rocks ca. 100 ft from end of south jetty, 0.5 m, 19 Sep 1996.—2 ♂, 1 immature, FTP-42, same locality, 50 m west of bridge off south jetty, in Caulerpa, depth 6″, 19 Sep 1996.—38 specimens, FTP-44, same locality, 50 ft inland from bridge, mixed algae on sandy/shelly bottom with rocks and boulders, 0.5 m, 19 Sep 1996.—1 ♂, 7 ♀, 2 juvs., FTP-45, same locality, red filamentous alga on rocks and south jetty wall, 30 cm, 19 Sep 1996.—1 ♂, 4 ovigerous ♀, 3 immature, FTP-46, Sebastian Inlet State Park, north side, gravel and pebbles among granite boulders ca. 100 m inside inlet, 10–50 cm, 20 Sep 1996.—12 ♂, 11 ovigerous ♀, 73 ♀, 40 juvs., FTP-48, Sebastian Inlet State

Park, south side, rubble and stones in 3″ pools at top of shore, with blue-green alga, 25 Jun 1997.—1 ♂, 5 ♀, 1 juv., FTP-50, same locality, granite boulder shore inside of bridge, stones and rubble with low algal turf, at bottom of shore with strong wave and wash action, 25 Jun 1997.—6 subadult ♂, 3 ovigerous ♀, 4 ♀, 6 juvs., FTP-51, same locality, algal clumps on boulders inside of bridge, 0.5 m, 25 Jun 1997.—2 ♀, FTP-53, same locality, outside of bridge, algal clumps and sponge on boulders in strong wave and wash action, 26 Jun 1997.—1 ♂, 1 subadult ♂, FTP-54, same locality, boulders outside bridge, chunks of reef worm rock, 26 Jun 1997.—7 ovigerous ♀, 14 juvs., FTP-56, Sebastian Inlet State Park, lagoon near Coconut Point, *Enteromorpha*/*Ulva* mats exposed at low tide on boulders at top of shore, surface, 26 Jun 1997.—1 ♂, 4 ovigerous ♀, FTP-63, large boat canal at Smithsonian Marine Station, in floating *Sargassum,* at surface, 25 Jun 1997.—1 ♂, 4 ovigerous ♀, FTP-66, Sebastian Inlet State Park, chunks of reef worm tubes on rocks at low tide level, inside inlet, 0–50 cm, 18 Aug 1998.—4 subadults, 1 ovigerous ♀, FTP-68, same locality, gravel rubble and empty shells in pockets between rocks, inside inlet, 0–20 cm, 18 Aug 1998.—3 ovig ♀, FTP-69, same locality, algal turf with hydroids on granite boulders inside inlet, 0–50 cm, 18 Aug 1998.—3 ovigerous ♀, FTP-70, Ft. Pierce Inlet, north bank, reef worm tubes on boulders in inlet, low tide, surface, 19 Aug 1998.—2 ovigerous ♀, FTP-71, same locality, algal turf at low tide level on boulders, surface, 19 Aug 1998.

Previous records.—Baja California, Mexico; Queensland, Australia; Western Australia; Marshall Islands; Hong Kong; Puerto Rico; Florida; intertidal.

Remarks.—While *Paradella dianae* has previously been recorded from the IRL, an aspect of its biology has come to light that demands mention.

Fifty-one ovigerous females out of 182 examined (about 28%) were observed to possess penes, suggesting that a protogynous sex change occurs in *P. dianae.* In Fig. 4C, a scanning electron micrograph, the ovigerous female shows both the opening of the marsupium between the fourth pereopod bases, and penes that are characteristic of a subadult male. The penes of the adult male are long, very slender in the distal half, tapering to acute apices and extending beyond the endopod of pleopod 1 by nearly 50%. The ovigerous hermaphrodites show no retention of either appendix masculina or adult penes, which suggests that protandry is not the condition here. This would seem to be the first record of protogyny in the sphaeromatid subfamily Dynameninae. Among the Isopoda, protandrous sex change is well known in the families Anthuridae (Wägele 1979), Cymothoidae (Brusca 1981), several families of the suborder Epicaridea (Kozloff 1987), and in at least one oniscidean (Brook et al. 1994). Members of the Sphaeromatidae known to exhibit protogyny are members of other subfamilies: *Gnorimosphaeroma oregonense* (Dana, 1853), *G. luteum* Menzies, 1954 (both Sphaeromatinae), and *Paraleptosphaeroma glynni* Buss & Iverson, 1981 (Cassidininae). Bruce (1994:1132) further mentions observing hermaphroditism in *Paracassidina munna,* having "developed male characters in . . . pleopod 2" as well as oostegites in the same specimen. Pleopod 2 in the ovigerous females of *P. dianae* did not display any male characters. The proportion of ovigerous females with penes in *G. oregonense* (31% of females collected in the field) is comparable to that of *P. dianae* recorded here. Brook et al. (1994) provide a discussion of the adaptive value of protogyny as compared to protandry, the commoner reproductive strategy in Crustacea.

Paradella quadripunctata (Menzies & Glynn, 1968)

Fig. 6

Dynamenella quadripunctata Menzies & Glynn, 1968:60–61, fig. 28a–n.

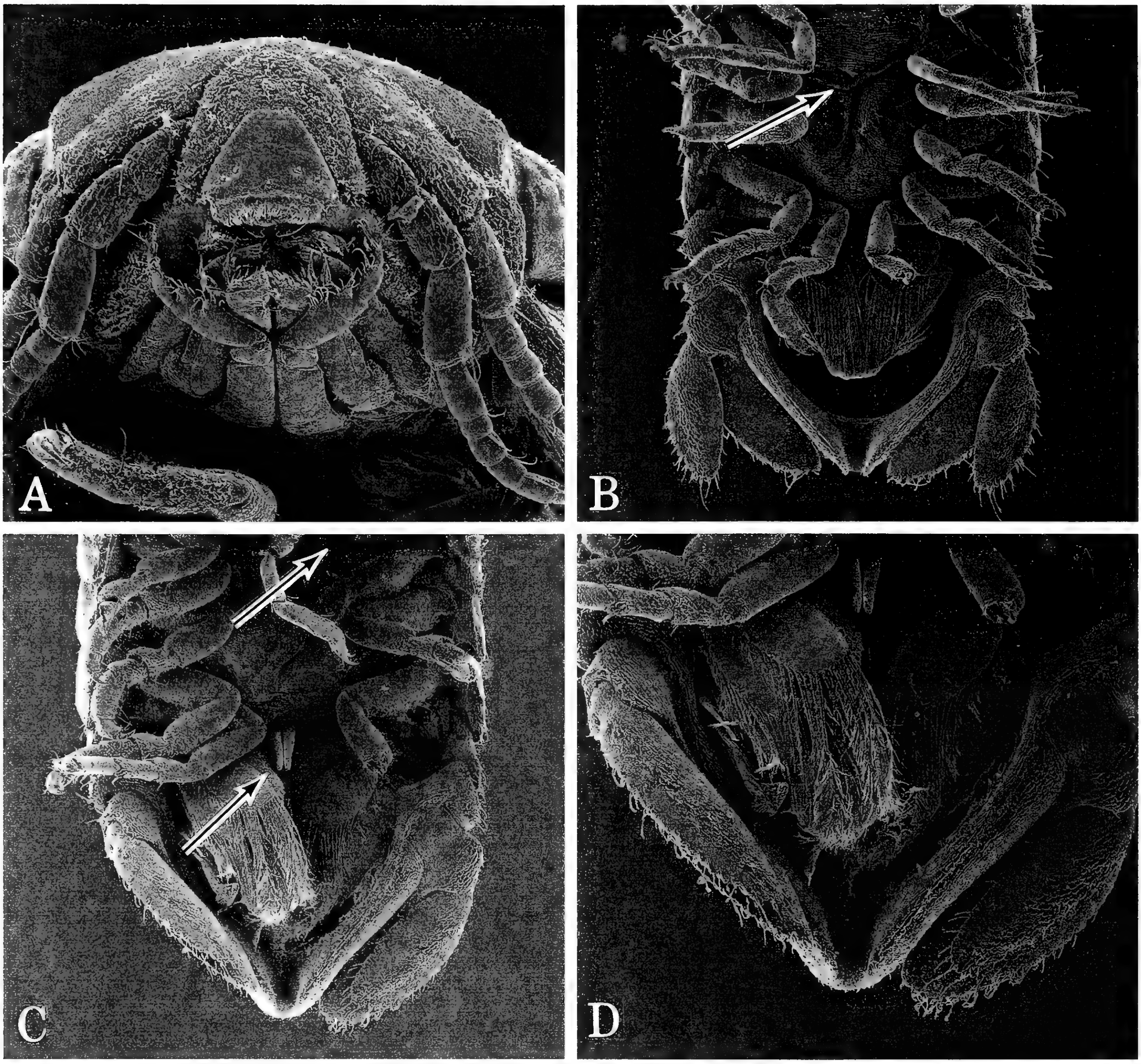

Fig. 4. *Paradella dianae:* A, ventral cephalon; B, ovigerous female, ventral view, arrow indicating opening of brood pouch between fourth pereopods; C, ovigerous female with brood pouch opening and penes; D, ovigerous female, close-up of ventral pleotelson and penes.

Paradella quadripunctata: Harrison & Holdich, 1982:101.—Kensley & Schotte, 1989:224–225, fig. 98f–g.—Camp et al., 1998:136.

Material examined.—1 ovigerous ♀, FTP-38, Sebastian Inlet State Park, gravel and pebbles in pockets around granite boulders lining inlet, infratidal, 0–32″, 19 Sep 1996.—1 immature, FTP-50, Sebastian Inlet State Park, south side, granite boulder shore inside of bridge, in stones and rubble with algal turf at bottom of shore with strong wave action, 25 Jun 1997.—24 immature, FTP-51, same locality, algal clumps on boulders, 0.5 m, 25 Jun 1997.—25+ immature, same locality, FTP-53, south side, outside bridge, algal clumps and sponge on boulders in strong wave and wash action, 0.5–1.0 m, 26 Jun 1997.—1 subadult ♂, 80+ immature, FTP-54, same locality, south side, boulders in inlet, outside of bridge, in chunks of reef worm rock, 26 Jun 1997.—5 immature, FTP-59, Sebastian Inlet State Park, lagoon near Coconut Point, 26 Jun 1997.—25+ immature, FTP-62, North Hutchinson Island, Recreation Park,

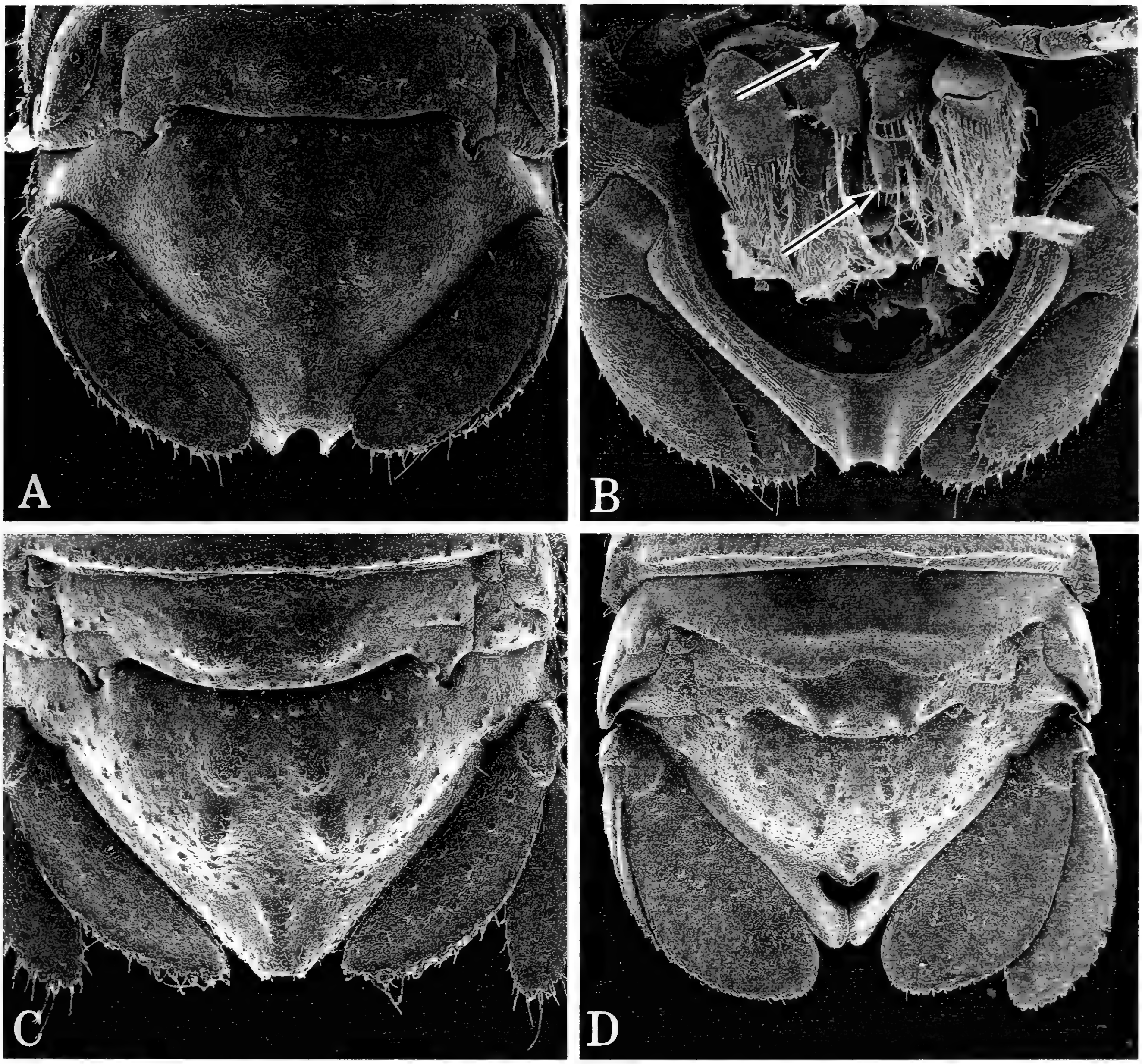

Fig. 5. *Paradella dianae:* A, sub-adult male, dorsal pleotelson; B, sub-adult male, ventral pleotelson, arrows indicating immature penes and appendix masculina; C, ovigerous female, dorsal pleotelson; D, mature male, dorsal pleotelson.

rotten wood in shallow water, < 1 m, 27 Jun 1997.—8 subadult ♂, FTP-66, Sebastian Inlet State Park, chunks of reef worm tubes on rocks at low tide, inside inlet, 0–50 cm, 18 Aug 1998.—1 ovigerous ♀, FTP-67, same locality, algal turf at low tide inside inlet, 0.5–1 m, 18 Aug 1998.—1 ovigerous ♀, FTP-68, same locality, gravel rubble, empty shells between rocks inside inlet, 0–20 cm, 18 Aug 1998.—1 ovigerous ♀, 3 immature, FTP-69, same locality, algal turf mixed with hydroids on granite boulders inside inlet, 0–50 cm, 18 Aug 1998.—2 subadult ♂, 1 ovigerous ♀, FTP-70, Ft. Pierce Inlet, north bank, reef worm tubes on boulders in inlet, low tide, 19 Aug 1998.—2 subadult ♂, 2 immature, FTP-71, same locality, algal turf on boulders at low tide level, 19 Aug 1998.—2 subadult ♂, 3 ovigerous ♀, FTP-72, Warton Beach rocks off Rt. A1A, algal turf growing on beach rock at bottom of shore, 0–50 cm, 20 Aug 1998.

Previous records.—Dominican Republic; Puerto Rico; U.S. Virgin Is.; Florida; Bermuda; intertidal–1 m.

Remarks.—Although no adult males were collected, identification was based on

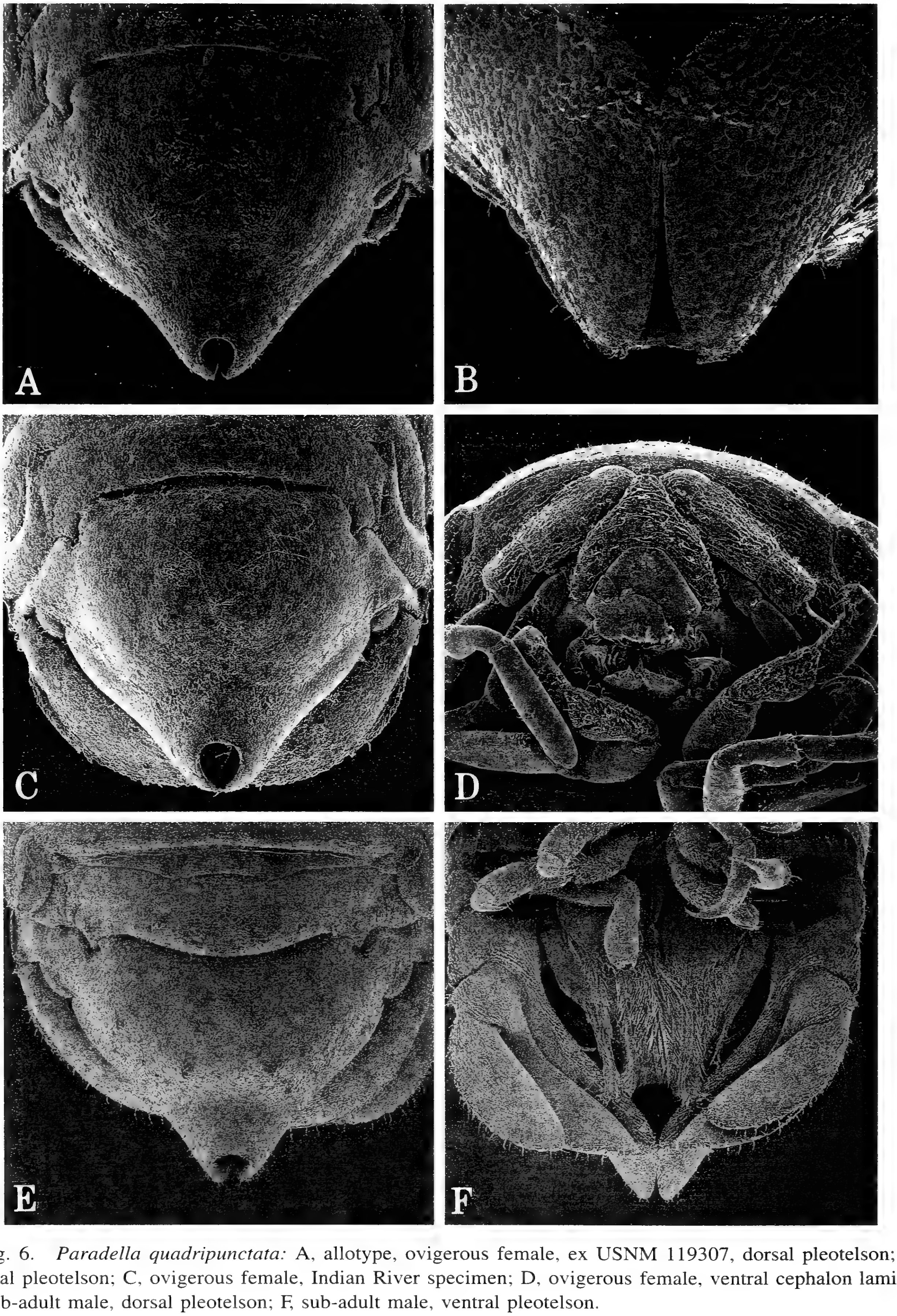

Fig. 6. *Paradella quadripunctata:* A, allotype, ovigerous female, ex USNM 119307, dorsal pleotelson; B, ventral pleotelson; C, ovigerous female, Indian River specimen; D, ovigerous female, ventral cephalon lamina; E, sub-adult male, dorsal pleotelson; F, sub-adult male, ventral pleotelson.

comparison of ovigerous females and subadult males to the ovigerous allotype (Fig. 6A–F).

Sphaeromopsis sanctaluciae, new species
Figs. 7–9

Material examined.—Holotype, USNM 285356, 1 ♂ tl 3.1 mm, Allotype USNM 285357, 1 ♀ tl 2.0 mm, Paratypes, USNM 285358, 45 ♂, 29 ♀, 39 juvs., sta FTP-13, North Fork of St. Lucie River at Prima Vera Boulevard, Port St. Lucie, Florida, in dead, submerged wood, 0.1 m, 1 Jun 1995.

Additional material.—USNM 285359, 2 ovigerous ♀, 2 ♀, 1 juv., sta K-CUBA-64, Islas de Juventud, Ensenada de la Siguanea, Cuba, in algal carpet on *Rhizophora* roots, 0.5 m, 9 Jun 1995.—USNM 285360, 5 ♀, 1 juv., sta FTP-8, Merritt Island at boat ramp, Indian River Lagoon, on dead wood, 0.5 m, 31 May 1995.—USNM 285361, 1 ♀, 3 juvs., sta FTP-11, on ring of metal plates in Banana River off Merritt Island, Indian River Lagoon, amongst encrusting oysters, barnacles and algal turf, 0.5 m, 31 May 1995.—USNM 285362, 1 ♀, 2 juvs., sta FTP-24, mouth of North Fork of St. Lucie River at US 1 and Fern Rd., in algal turf with *Enteromorpha* on boulders, intertidal, 25 Apr 1996.—USNM 285363, 1 ♀, Indian River Lagoon at Jensen Beach, in algae in mangrove roots, 29 May 1995.—USMN 285364, 3 ♂, 1 ovigerous ♀, 1 ♀, Orange River, Lee County, Florida, coll. A. Walton, 15 Aug 1994.—USNM 285365, 1 ♂, Orange River, Lee County, Florida, coll. A. Walton, 18 Jan 1995.

Diagnosis.—Sexes similar, cephalon and pereon smooth, pigmented; pleotelson domed, smooth, apex broadly truncate. Margins of uropodal rami entire. Appendix masculina of male broad proximally, tapering to narrowly rounded apex. Rami of penes elongate, widening in proximal half before tapering to narrowly rounded apices.

Description.—Adult male: Body length about 1.9 times greatest width. Cephalon broader than long, frontal margin undulating, rostral point small and acute. Frontal lamina narrowly truncate distally. Brown pigment pattern somewhat variable, strong in fresh specimens, densest on pleotelson. Pleon with two short suture lines reaching posterior margin. Pleotelson broadly triangular, domed, with apex broadly truncate in posterior view.

Antennule with basal article equal in length to articles 2 and 3 combined; flagellum of 9 articles; articles 5–8 each bearing single aesthetasc. Antenna with articles 1 and 2 subequal in length; article 3 shorter than 2; article 4 somewhat shorter than 2 and 3 together; article 5 longest; flagellum of 13 articles. Mandible having incisor of 3 cusps, spine row of 5 spines, 3 of which fringed, molar process with numerous small teeth; palp, article 2 having 4 fringed setae, terminal article with 7 fringed setae. Maxilla 1, inner ramus with 4 fringed setae, outer ramus with 4 stout spines and 4 slender, fringed spines. Maxilla 2 bearing 3 unarmed and 4 fringed spines on inner ramus; outer ramus having 4 fringed spines on each lobe. Maxillipedal endite with 1 coupling hook on mesial margin; dense, fine setae distally; distal margin with 5 blunt spines and several fringed setae; palp of 5 articles, articles 2 and 3 with distomesial lobe bearing several setae, article 4 longer and more slender than 3, article 5 short with terminal setae.

Pereopods with fringe of short setae on posterior margins of propodus, carpus and merus, very sparse on merus of pereopod 5. Pereopod 1, propodus and carpus each with single plumose seta at anterodistal margins; merus with anterodistal lobe bearing 3 long setae. Pereopod 2 slender, longer than 1; propodus with single plumose seta anterodistally; carpus with single plumose setae on posterodistal margin; merus having anterodistal lobe bearing 4 long setae; ischium with several long setae on anterior margin. Pereopods 3–7 equally robust, increasing in length posteriorly. Pereopod 3 shorter than 2; propodus with 2 fringed posterodistal spines; carpus triangular with

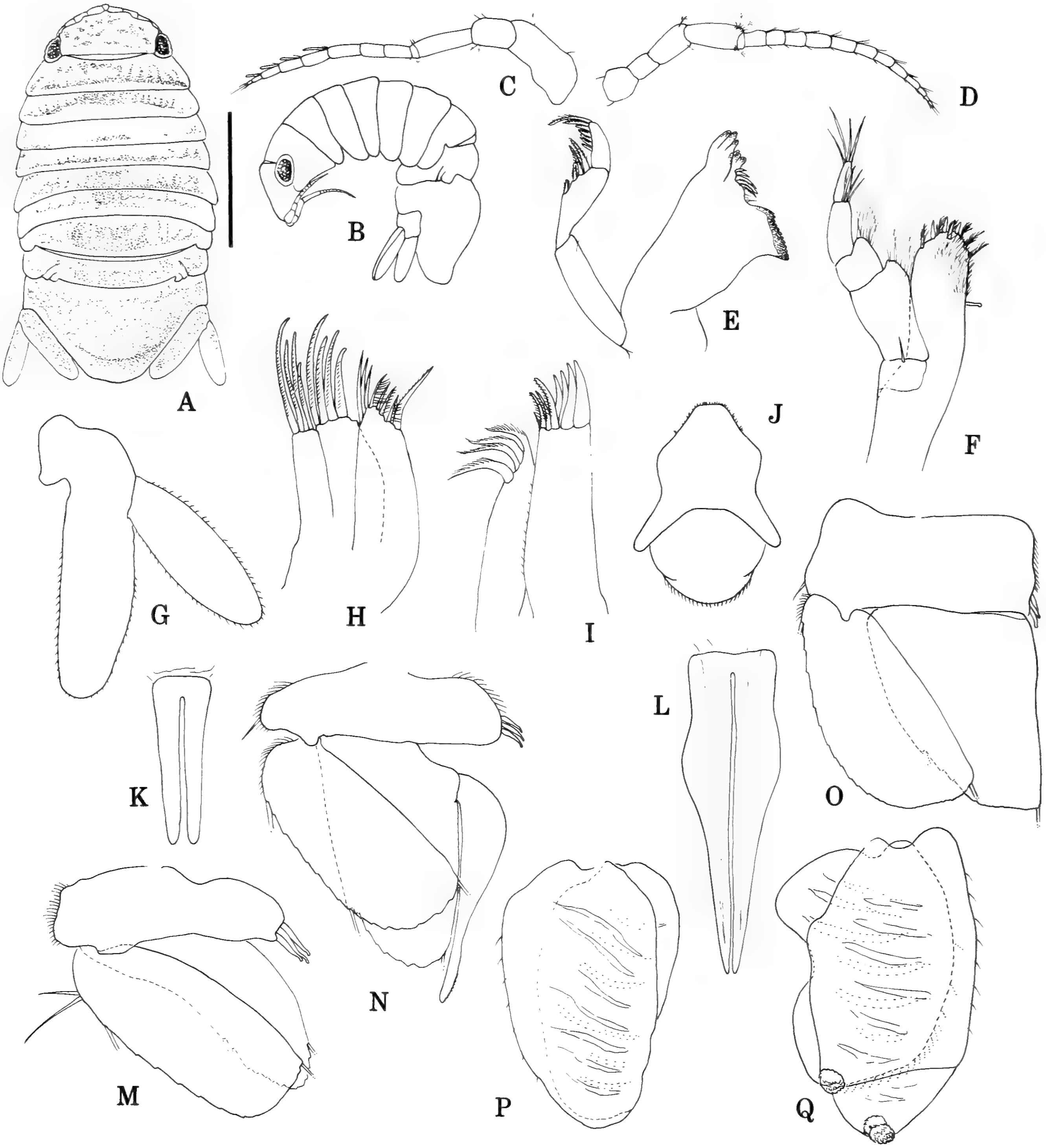

Fig. 7. *Sphaeromopsis sanctaluciae,* new species: A, adult male, habitus. Scale = 1 mm; B, lateral view; C, antennule; D, antenna; E, mandible; F, maxilliped; G, uropodal rami; H, maxilla 2; I, maxilla 1; J, ventral cephalon; K, penes of sub-adult male; L, penes of adult male; M, pleopod 1; N, pleopod 2; O, pleopod 3; P, pleopod 4; Q, pleopod 5.

fringed spine at posterodistal corner; merus with small anterodistal lobe and single fringed, posterodistal spine. Pereopod 4, propodus having single plumose seta at anterodistal angle; carpus with single plumose seta at each distal margin; merus with anterodistal lobe bearing several long setae. Pereopod 5, carpus with single stout fringed spine at posterodistal margin; anterodistal lobe of merus having several long setae. Pereopod 6, carpus with plumose seta and stout fringed spine at antero- and poster-

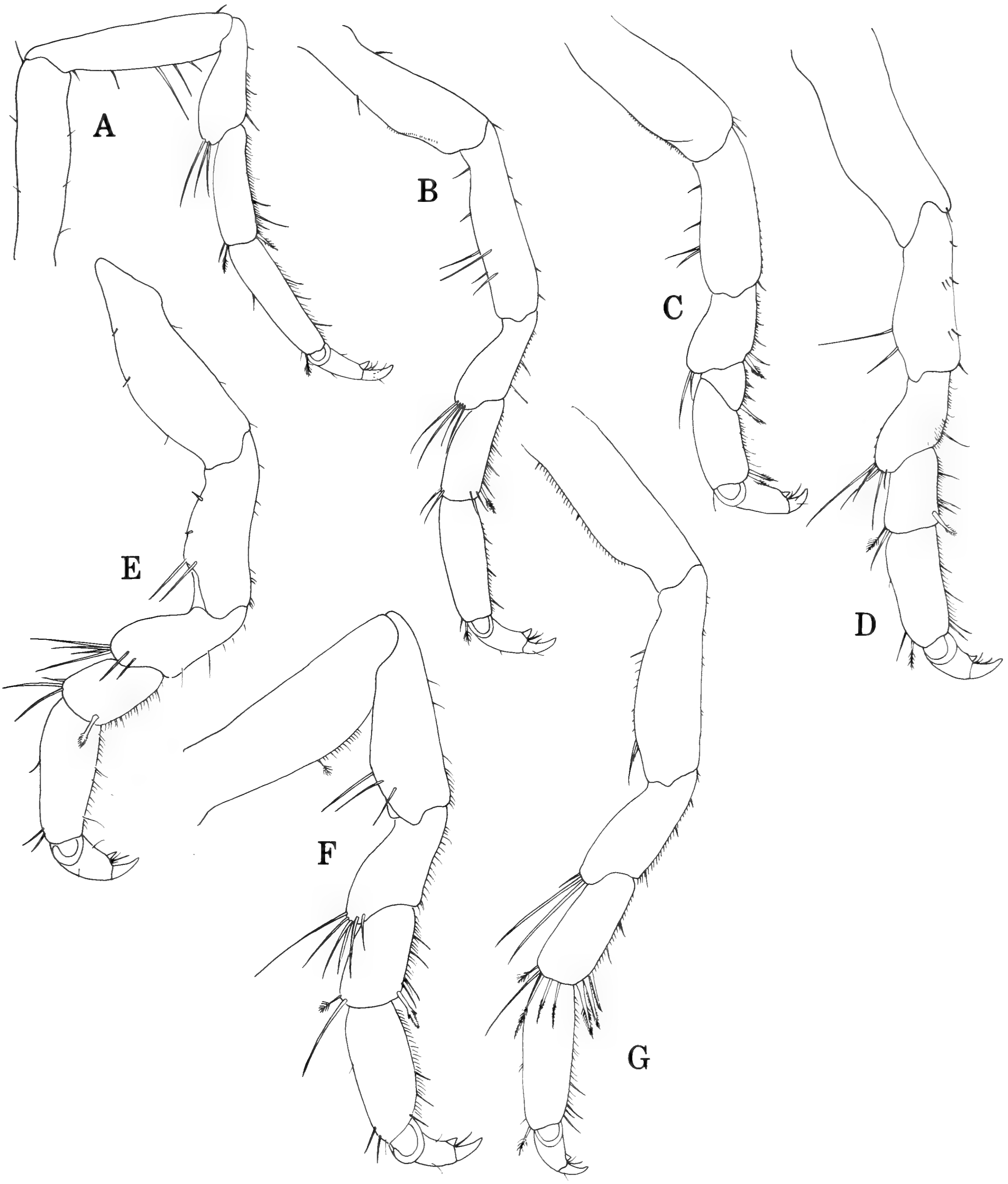

Fig. 8. *Sphaeromopsis sanctaluciae,* new species: A, pereopod 1; B, pereopod 2; C, pereopod 3; D, pereopod 4; E, pereopod 5; F, pereopod 6; G, pereopod 7.

odistal margins respectively; anterodistal lobe of merus with several long setae; ischium bearing 3 long setae on anterodistal margin. Pereopod 7, propodus with single plumose seta at anterodistal corner; distal margin of carpus with 3 fringed spines, 3 fringed, 2 unarmed, and 1 plumose setae; anterodistal margin of merus with 2 long and 1 short setae; ischium and basis with several setae on anterior margins.

Penial rami basally fused, elongate, widening at 1/3 length and tapering to narrowly

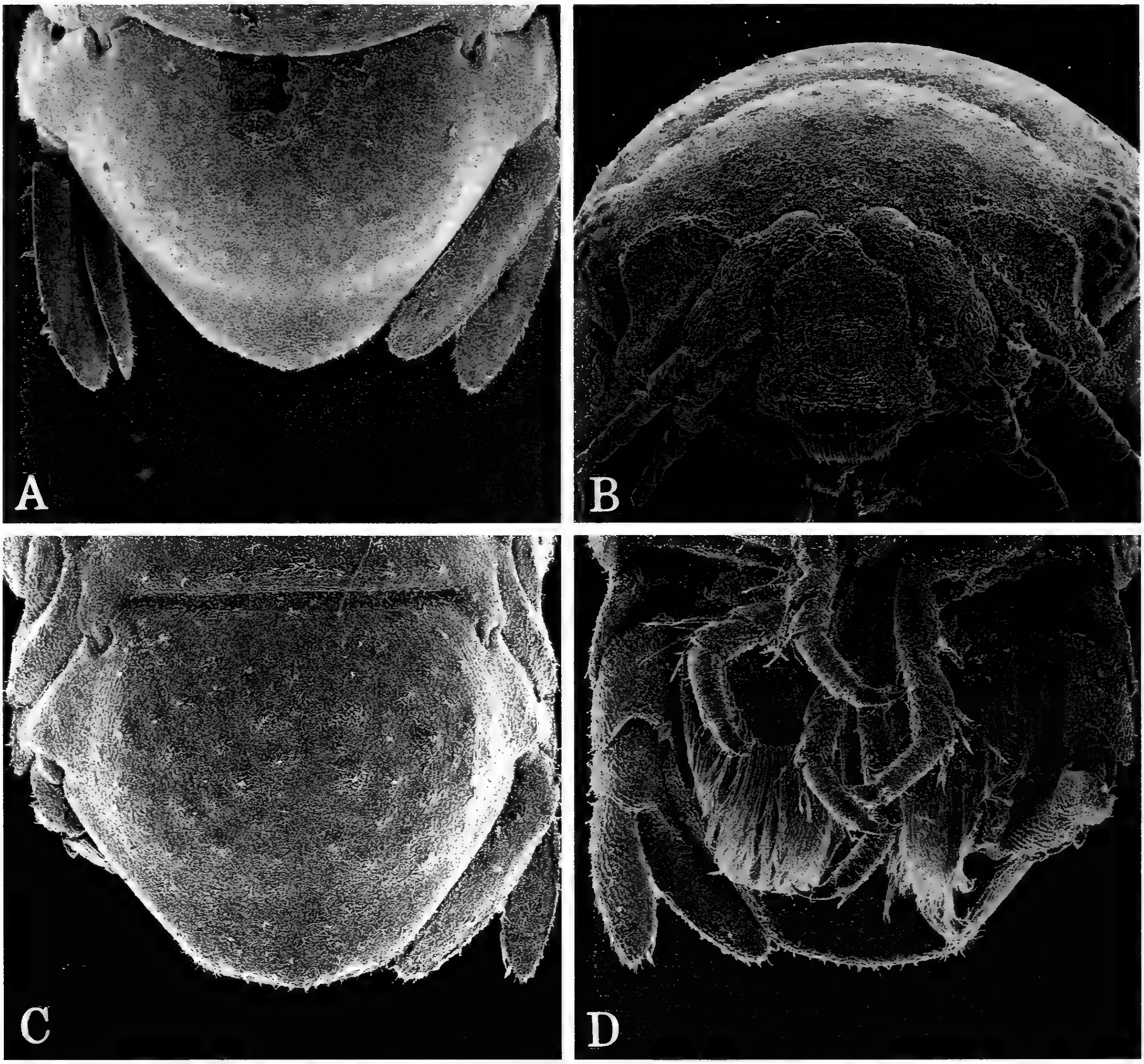

Fig. 9. *Sphaeromopsis sanctaluciae,* new species: A, adult male, dorsal pleotelson; B, ventral cephalon; C, adult female, dorsal pleotelson; D, adult female, ventral pleotelson.

rounded apices. In subadult male, penial rami fused basally with subparallel margins and rounded apices. Pleopod 1, basis with 3 coupling hooks; exopod subrectangular in shape, slightly broader than endopod. Pleopod 2, basis and exopod as in pleopod 1; endopod broad, subrectangular; appendix masculina articulating basally, broad proximally, tapering to narrow apex extending somewhat beyond apex of endopod. Pleopod 3, basis broadly rectangular with 3 coupling hooks; endopod triangular without articulation; exopod somewhat ovate. Pleopod 4, both rami broad with transverse pleats. Pleopod 5, both rami with transverse pleats and setae on mesial margins; exopod with transverse suture and 3 spinulose bosses. Rami of uropods subequal in length, margins entire, bearing short setae.

Female: As in male except in secondary sexual characters; generally smaller.

Remarks.—The new species is the seventh member of the genus to be described and the third from the western hemisphere, following *S. mourei* Loyola e Silva, 1960 and *S. heardi* Kensley & Schotte, 1994. Like *S. minutus* Javed & Yousef, 1995, it lacks the "dense pads of setae" on posterior margins of the pereopods, previously thought to be a generic character (Holdich

& Harrison 1981). The comparatively sparse nature of the setal fringe plus morphological details of the appendix masculina and penes serve to separate *S. sanctaluciae* from *S. mourei* and *S. amathitis* Holdich & Jones, 1973, both of which it superficially resembles. In contrast to the other two species, the appendix masculina in *S. sanctaluciae* is markedly inflated near the base and extends beyond the apex of the pleopod endopod.

Whereas almost all cogeners have been collected from sandy beaches and intertidal habitats (Holdich & Harrison 1981), *S. sanctaluciae,* like *S. serriguberna* Holdich & Harrison 1981, can also tolerate low salinity, e.g., 2.5 ppt. in the St. Lucie River.

Etymology.—The species is named for its type locality, St. Lucie River.

Suborder Valvifera
Family Idoteidae
Erichsonella filiformis (Say, 1818)

Stenosoma filiformis Say, 1818:424.
Erichsonella filiformis: Kensley & Schotte, 1989:258, fig. 108c.—Camp et al., 1998: 137.

Material examined.—7 specimens, 1 ovigerous ♀, FTP-40, Sebastian Inlet State Park, clumps of *Caulerpa racemosa* and branching red alga on granite boulders inside of inlet, 0.5–1.0 m, 19 Sep 1996.—1 ♀, FTP-41, Sebastian Inlet State Park, south side, sheltered cove ca. 1/2 mile from mouth, small boulders with clumps of algae, 0.5–1 m, 19 Sep 1996.—3 ♀, 2 juvs., FTP-42, same locality, 50 yds. west of bridge, in *Caulerpa* sp., depth 6″, 19 Sep 1996.—1 ♀, 1 juv., FTP-44, same locality, 50 ft west of bridge, mixed algae on sandy/shelly/rocky bottom, 0.5 m, 19 Sep 1996.—1 ♀, 4 juvs., FTP-51, Sebastian Inlet State Park, south side, granite boulder shore inside of bridge, algal clumps on boulders, 0.5 m, 25 June 1997.—2 ♂, 4 ♀, 7 juvs., FTP-52, same locality, south side, shallow embayment at camp site 1/2 mile from mouth in lagoon, algal clumps on stones and rocks, 25 Jun 1997.—1 ♀, 1 juv., FTP-53, same locality, south side, boulders outside of bridge, algal clumps and sponge on boulders in strong wave and wash action, 0.5–1.0 m, 26 Jun 1997.—3 ovigerous ♀, 1 ♀, FTP-55, Sebastian Inlet State Park, lagoon near Coconut Point, algal clumps in shallow embayment, 1 m, 26 Jun 1997.—1 juv., FTP-65, Sebastian Inlet State Park, orange sponge on rocks at low tide level, inside of inlet, 0–50 cm, 18 Aug 1998.—1 ♀, FTP-68, same locality, gravel rubble, empty shells between rocks inside inlet, 0–20 cm, 18 Aug 1998.—1 ♂, FTP-69, same locality, algal turf mixed with hydroids on granite boulders inside inlet, 0–50 cm, 18 Aug 1998.

Previous records.—Brazil; Yucatan, Mexico; Puerto Rico; Turks & Caicos Is.; Bahamas; Gulf of Mexico; shallow infratidal–109 m.

Acknowledgments

We are grateful to the staff of the Smithsonian Marine Station, and especially Woody Lee and Sherry Reed for assistance with this project in the field, and for providing ideal working conditions at the lab. We thank Dr. David Camp, late of the Florida Marine Research Institute, and Dr. A. S. Walton of the Florida Department of Environmental Regulation for making material available for study. Susann Braden assisted with the SEM's, for which we are grateful.

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112(4):714–721. 1999.

A new species of *Pseudostegias* Shiino, 1933 (Crustacea: Isopoda: Bopyridae: Athelginae) parasitic on hermit crabs from Bali

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Abstract.—A single male and female bopyrid pair was collected in Sanur, Bali, Indonesia in August 1997, from the abdomen of a hermit crab, *Calcinus gaimardii* (H. Milne Edwards). Examination of these specimens showed that they belong to the athelgine genus *Pseudostegias* Shiino, but cannot be placed into any described species. We describe this new species as *P. macdermotti* and compare it to *P. dulcilacuum* Markham, which it most closely resembles. This is the first record of a *Pseudostegias* from the genus *Calcinus*. A list and key of all described *Pseudostegias* species are provided.

Bopyrid isopods of the subfamily Athelginae are obligate parasites found on the abdomen of hermit crabs and lithodids (Decapoda: Paguroidea). The seven genera in this subfamily are defined primarily on the combination of lateral plates and pleopods on the pleomeres of the female. The genus *Pseudostegias* is distinguished by the presence of long uniramous lateral plates on pleomeres 1–4, and biramous pleopods. The lateral plates on pleomere 5 are reduced to a dorsally produced globular or bifurcated lobe.

One of us (JDW) collected a series of hermit crabs in Sanur, Bali, Indonesia during August 1997. One of these crabs was found to bear an immature female bopyrid with a male inside her brood plates. The specimens belong to the genus *Pseudostegias* and represent a new species most similar to *P. dulcilacuum* Markham, 1982. A list of the species of *Pseudostegias,* with their known localities and hosts, and a key to their identification are provided.

Methods

Hermit crabs inhabiting gastropod shells were collected intertidally in Sanur, Bali, Indonesia on 5–6 August 1997. Specimens were relaxed in 3% magnesium chloride, fixed in 10% formalin-seawater solution and stored in 70% ethanol. The shells were cracked using a hammer and pliers and the crabs removed and examined for parasites.

Camera lucida sketches made of specimens were scanned into a Macintosh™ computer. Images were then prepared using the programs Adobe Photoshop™ and Adobe Illustrator™.

Shield length (SL) is provided as an indicator of size for the host crabs. Isopod size is given as total body length (anterior margin of head to posterior margin of pleotelson). Measurements were made to 0.01 mm using an ocular micrometer.

Specimens are deposited in the Department of Invertebrates, American Museum of Natural History, New York, U.S.A. (AMNH).

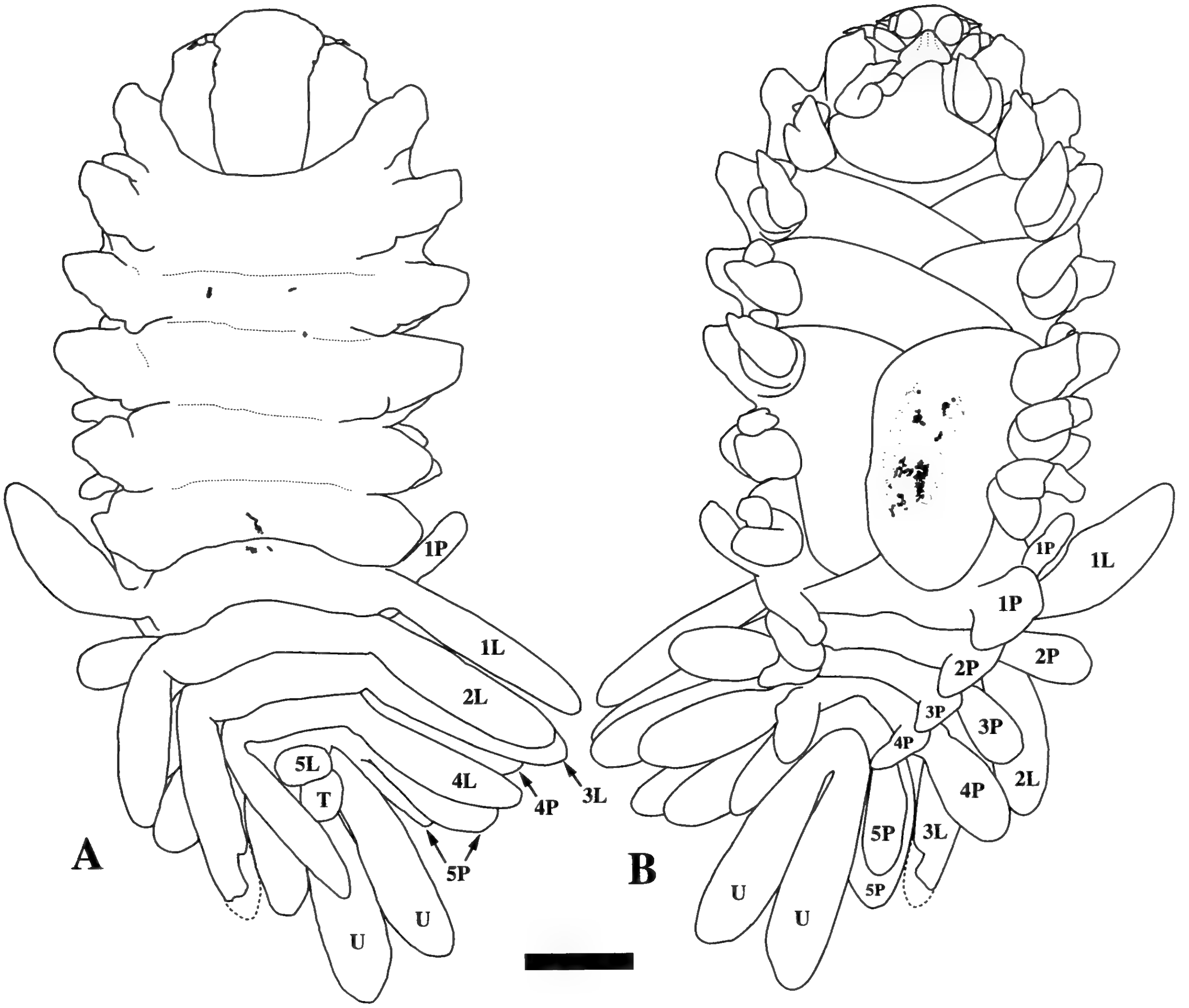

Fig. 1. *Pseudostegias macdermotti,* new species. Female, 3.6 mm, AMNH 17877, holotype. A, dorsal view; B, ventral view. L = lateral plate; P = pleopod; T = telson; U = uropod; numbers indicate pleon segment. Scale = 0.5 mm.

Family Bopyridae Rafinesque, 1815
Subfamily Athelginae Codreanu and Codreanu, 1956
Genus *Pseudostegias* Shiino, 1933
Pseudostegias macdermotti, new species
Figs. 1–4

Material examined.—Holotype: female (3.6 mm), infesting male *Calcinus gaimardii* (H. Milne Edwards) (2.66 mm SL; AMNH 17879), inhabiting shell of *Drupella cornus* (Röding), 08°41′S, 115°15′E, Sanur, Bali, Indonesia, intertidal, coll. J. D. Williams, 6 Aug 1997 (AMNH 17877). Allotype: male (1.06 mm), same data as holotype (AMNH 17878).

Type locality.—Sanur, Bali, Indonesia, Pacific Ocean.

Description.—Female (Figs. 1–2). Body length 3.60 mm, maximal width 1.83 mm, head length 0.75 mm, head width 0.44 mm, pleon length 1.64 mm. Pereon not distorted due to immaturity; pleon deflected to the right. Body outline narrow and elongated. All body regions and most pereomeres distinctly segmented (Fig. 1A, B).

Head not produced due to immaturity. Eyes present approximately 1/4 distal from anterior margin. Antenna (Fig. 2C) of 7 articles; antennule (Fig. 2C) of 3 articles, distal margins of segments with setae. Maxilliped (Fig. 2E) with low rounded spur; palp absent; posterior margin setose. Barbula undeveloped.

Pereon composed of 7 pereomeres,

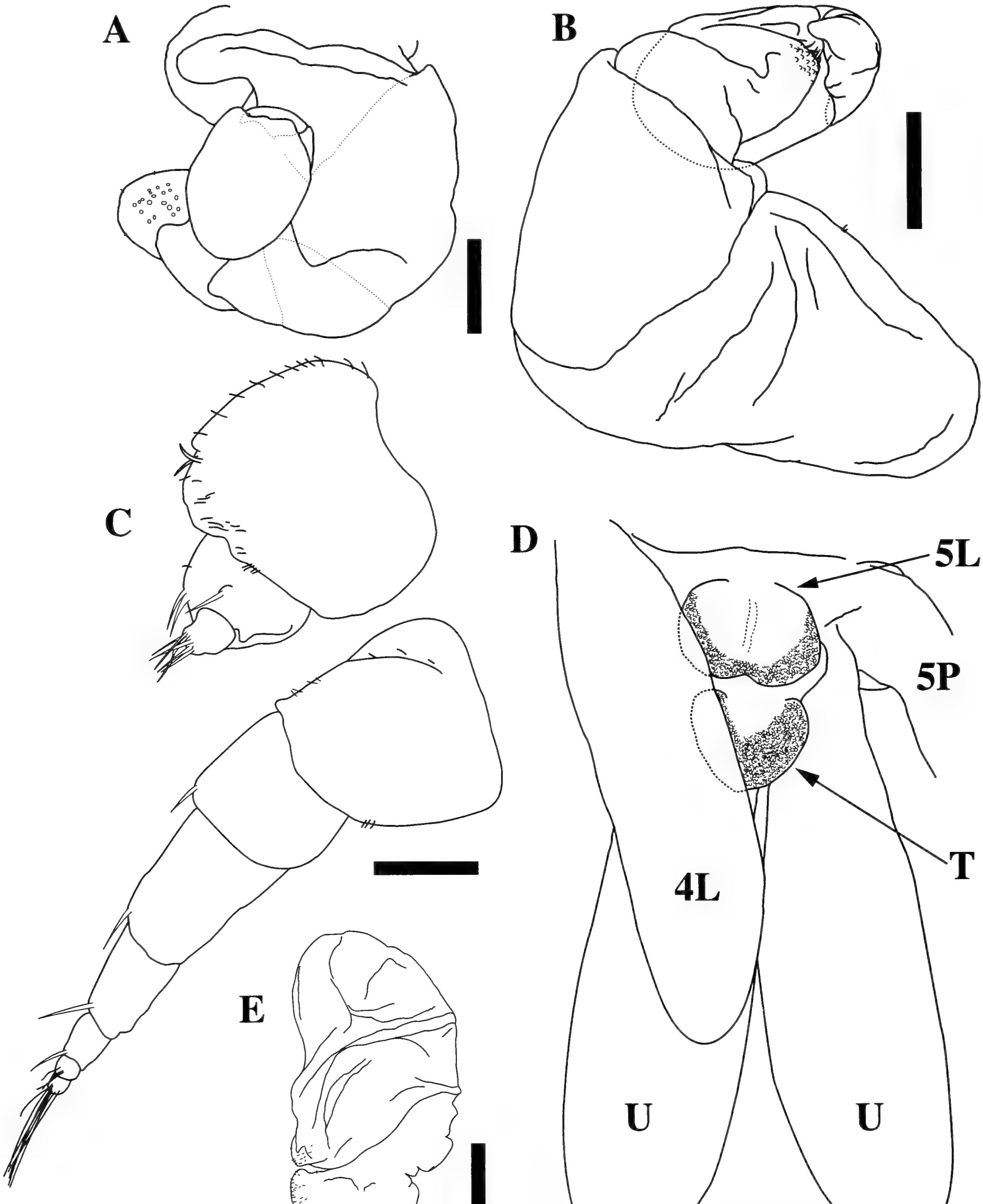

Fig. 2. *Pseudostegias macdermotti,* new species. Female, 3.6 mm, AMNH 17877, holotype. A, right pereopod 1; B, left pereopod 7; C, right antenna and antennule; D, dorsal view of fifth lateral plates, pleotelson, and uropods (L = lateral plate; P = pleopod; T = telson; U = uropod; numbers indicate pleon segment); E, left maxilliped. Scale = 0.1 mm (A, B, D), 0.05 mm (C), and 0.02 mm (E).

broadest across pereomeres 4 and 5, tapering anteriorly and posteriorly. Pereomeres 2–7 incompletely fused. Coxal plates on sides of pereomeres all similar. Oostegites completely enclosing brood pouch; posteriormost oostegite with fringe of setae on posterior margin. Pereopods 1–4 (Fig. 2A) of about same size, pereopods 5–7 (Fig. 2B) slightly smaller and shorter. Propodus of all pereopods with distally-directed medioventral projection (Fig. 2B); distal region of projection with small, rounded tubercles; short setae at distal tip. First 2 pereopods surrounding head region; no large gaps between any pereopods.

Pleon with 6 distinct pleomeres. Pleomeres 1–4 with extended lanceolate, distally rounded, biramous pleopods and uniramous lateral plates (Fig. 1B); pleomere 5 (Figs. 1A, 2D) with biramous pleopods and dorsally produced globular plate, only slightly bifurcated posteriorly and with papillate surface; pleotelson (Fig. 2D) with pair of large lanceolate, distally rounded, uniramous uropods and rounded, dorsally produced, papillate pleotelson.

Male (Figs. 3–4). Length 1.06 mm, head length 0.09 mm, head width 0.21 mm, pleon length 0.33 mm. Occurring under oostegites of female (Fig. 1B); directed anteroposteriorly.

Head suboval, widest posteriorly, incompletely fused with 1st segment of pereon. Large eyes near posterolateral margin. Antenna (Fig. 4C) of 7 articles, distally setose; extending posterolaterally from head; antennule of 3 articles (Fig. 4C).

Pereomeres 2–6 broadest, tapering anteriorly and posteriorly. Pereomeres 1–4 directed laterally; 5–7 directed posterolaterally. All segments of body except for head with irregular dark pigmentation pattern. All pereopods (Fig. 4A, B) of equal size, all articles distinctly separated.

Pleon tapering posteriorly, pleomeres directed laterally and fringed with setae. First segment incompletely fused to 2nd segment; all other segments fused. No midventral tubercles; 5 pairs of tuberculiform pleopods (Fig. 3A). Pleotelson (Fig. 4D) notched medially, produced distolaterally, distal ends of lobes with setae; uropods absent.

Distribution.—Found on hermit crab, *Calcinus gaimardii* from Sanur, Bali, Indonesia; intertidal.

Etymology.—This species is named in honor of Dr. John J. McDermott (Franklin and Marshall College, Pennsylvania, U.S.A.) for his considerable contributions to the biology and systematics of numerous marine invertebrates, including bopyrids. The specific name is spelled to conform to the ICZN Recommendations on the Formation of Names, Appendix D 21(a) (ICZN 1985: 197).

Remarks.—Pseudostegias macdermotti most closely resembles females of *P. dulcilacuum* Markham, 1982 from Hong Kong, Thailand and South Korea, in the number of segments in the antennae, shape of pleopods, and presence of a papillate pleotelson. *Pseudostegias macdermotti* differs from females of *P. dulcilacuum* in the degree of subdivision of the 5th pleomere lateral plate. In *P. macdermotti,* the undivided globular 5th pleomere lateral plate has only a hint of a medial seam, while *P. dulcilacuum* has a strongly bifurcated 5th pleomere lateral plate. The only other species in the genus which has an undivided 5th pleomere lateral plate is *P. otagoensis* Page, 1985, from New Zealand. *Pseudostegias otagoensis* differs from *P. macdermotti* in both the shape of its 5th pleomere lateral plate, which is extended anteroposteriorly rather than mesiolaterally as in *P. macdermotti,* and in the distally pointed shape of the pleopods which are rounded in *P. macdermotti.* Some authors (Shiino 1933, Lemos de Castro 1965) have incorrectly described species of *Pseudostegias* as lacking 5th pleomere lateral plates, although all species in this genus possess such plates (Markham 1982). We consider the shape of the 5th pleomere lateral plate to be diagnostic in species of *Pseudostegias,* since it has been shown to be constant

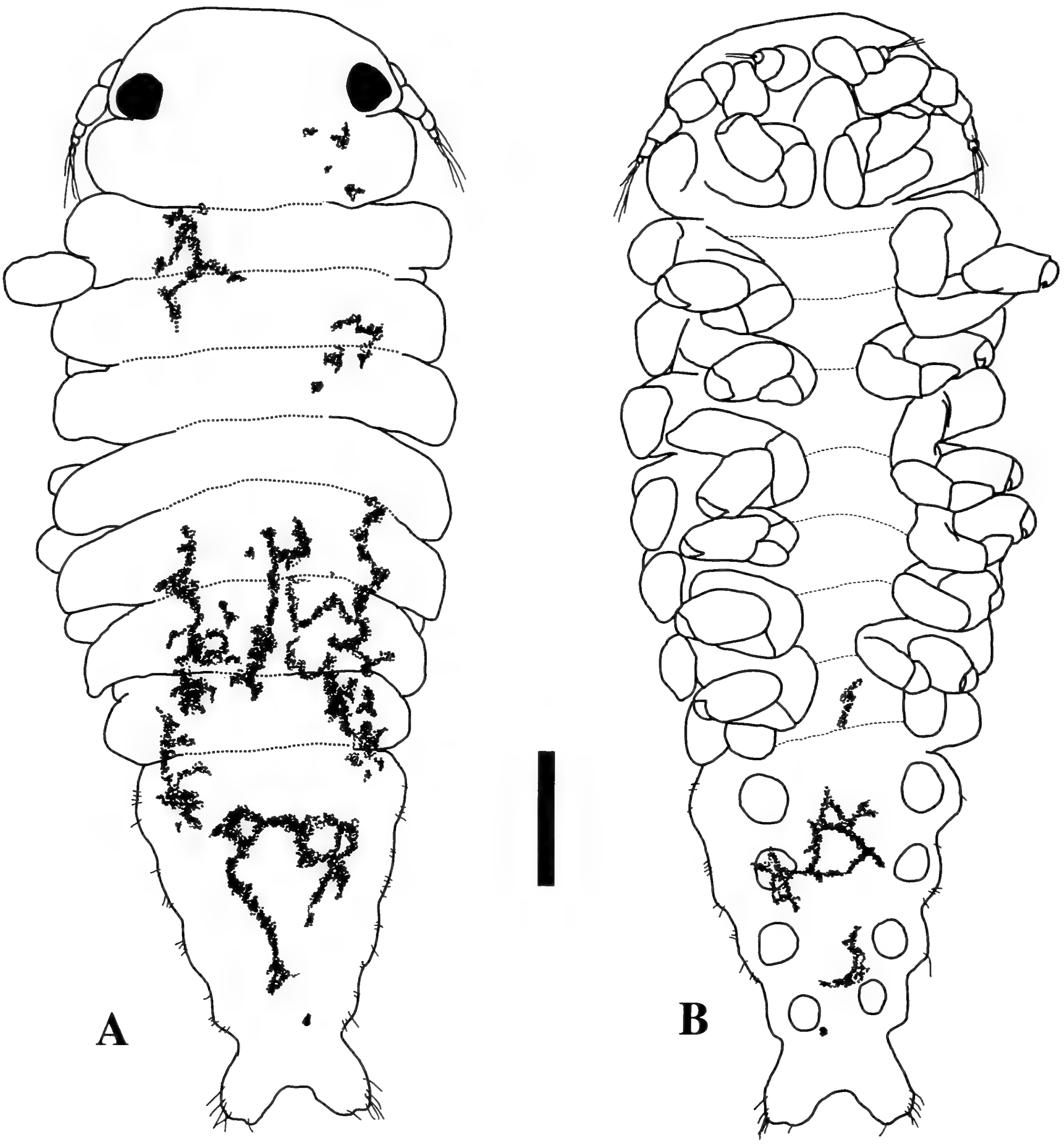

Fig. 3. *Pseudostegias macdermotti,* new species. Male, 1.06 mm, AMNH 17878, allotype. A, dorsal view; B, ventral view. Scale = 0.1 mm.

within species, including *P. dulcilacuum,* between juveniles and adults (Lemos de Castro 1965: figs. 2–4, Markham 1985: figs. 26–27). The key given below provides additional characters for separating the species of *Pseudostegias* based on females.

Male *P. macdermotti* differ from those of *P. dulcilacuum* in having a fused head with the first pereon segment and in pleotelson shape. The pleotelson of the male *P. macdermotti* is notched medially and produced distolaterally while *P. dulcilacuum* possesses a pleotelson which tapers to a blunt point. Male *P. macdermotti* differ from those of *P. otagoensis* in posessing eyes and in pleotelson shape. *Pseudostegias otagoensis* lacks eyes and has a tapered, pointed pleotelson. The location of the male inside the brood plates of the female is consistent with other reports for this genus (Shiino 1933, Markham 1982), although the male of *P. hapalogasteri* was found outside

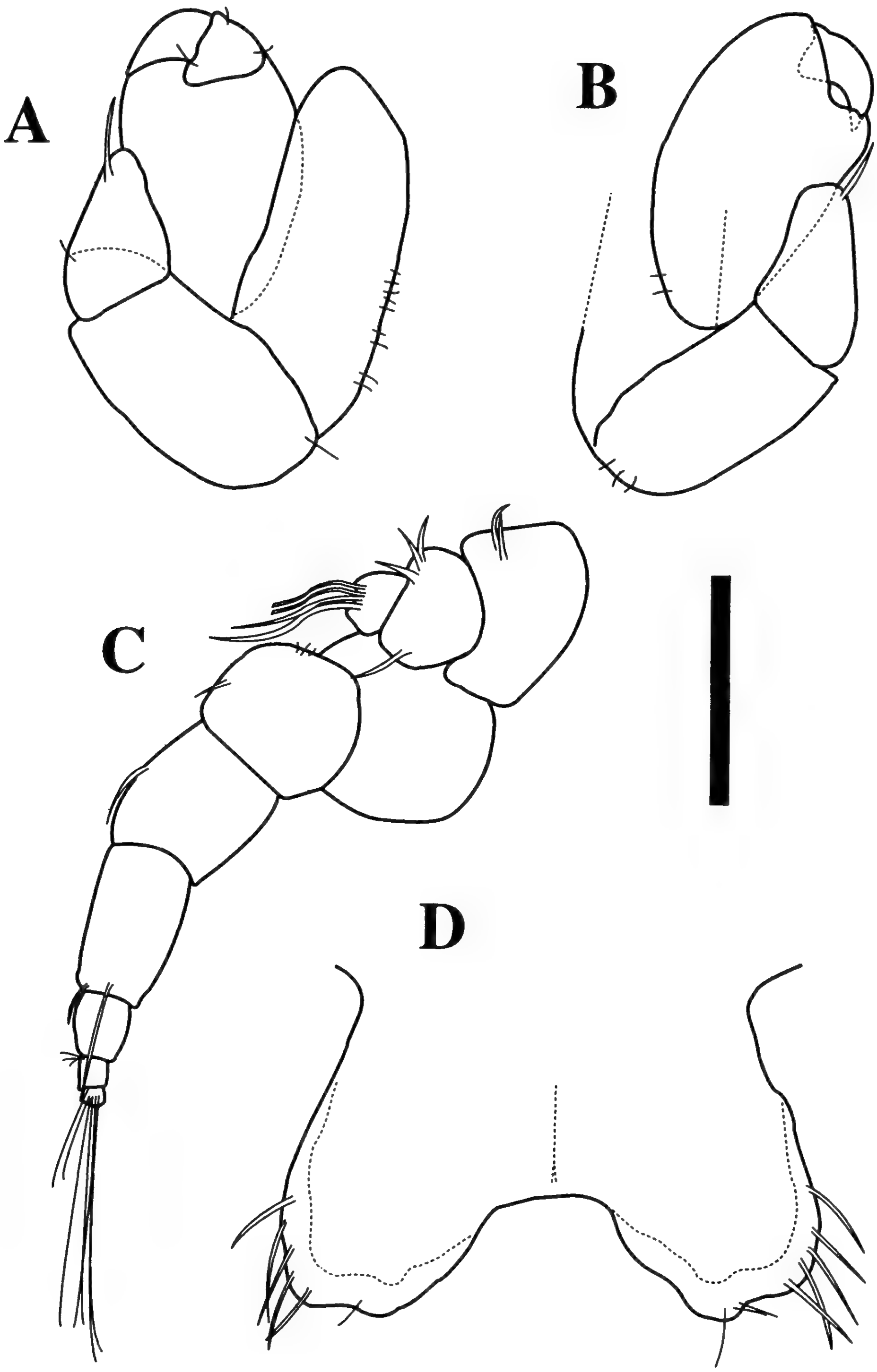

Fig. 4. *Pseudostegias macdermotti,* new species. Male, 1.06 mm, AMNH 17878, allotype. A, left pereopod 1; B, left pereopod 7; C, right antenna and antennule; D; Dorsal view of pleon. Scale = 0.05 mm.

the brood plates on the posterior end of the female (Shiino 1950).

Ecology.—A total of 43 hermit crabs were collected from Sanur, Bali on Aug. 5–6, 1997. The majority were *Calcinus gaimardii* (34 specimens) and only a single specimen of this crab was found with a bopyrid parasite (3% prevalence). This is the first report of a species of *Pseudostegias* on a species of *Calcinus.* The other crabs collected were *Calcinus latens* (Randall) (4 specimens), *Clibanarius* sp. (1 specimen), *Dardanus* sp. (2 specimens), and 2 unidentified hermits. No specimens of any of these other species were parasitized. The overall rate of bopyrid occurrence was 2.3%, which is comparable to rates found in large (1000+) sample sizes (Thompson 1901, Pike 1961).

The species of Pseudostegias.—The genus *Pseudostegias* now contains the following six species:

P. atlantica Lemos de Castro, 1965, Brazil, on *Clibanarius* sp. (Lemos de Castro 1965).

P. dulcilacuum Markham, 1982, Hong Kong, on *Diogenes* aff. *edwardsii* (de Haan) (Markham 1982); Thailand, on *Clibanarius merguiensis* de Man (Markham 1985); South Korea, on *Diogenes* sp. (Kim & Kwon 1988).

P. hapalogasteri Shiino, 1950, Japan, on *Hapalogaster dentata* (de Haan) (Shiino 1950).

P. macdermotti, n. sp., Bali, Indonesia, on *Calcinus gaimardii* (H. Milne Edwards).

P. otagoensis Page, 1985, New Zealand, on *Paguristes barbatus* Heller (Page 1985).

P. setoensis Shiino, 1933, Japan, on *Clibanarius bimaculatus* (de Haan) (Shiino 1933); Taiwan, on *C. striolatus* Dana (Shiino 1958); Hong Kong, on *C. bimaculatus* (de Haan) and *C. ransoni* Forest (Markham 1982); Thailand, on *C. padavensis* de Man (Markham 1985); New Caledonia, on "*Trizopagurus*" sp. (Markham 1994) =*Striopagurus boreonotus* Forest, 1995.

Discussion.—There is a strong possibility that the material reported as *Pseudostegias setoensis* by Shiino (1933), Markham (1985), and Markham (1994) actually represents three distinct species. Based on the published illustrations and descriptions, the 5th pleomere lateral plates on each specimen are quite different, the number of pereopods found overlapping the head region is not identical, and the shape of the pleopods is more variable than has been demonstrated for other athelgine species. Specimens would need to be examined to make a final determination on their status. However, neither *P. setoensis* sensu Markham (1985) or Markham (1994) closely resembles our specimens of *P. macdermotti* n. sp. The key below contains only *P. setoensis* sensu Shiino (1933).

All available evidence indicates that species of *Pseudostegias,* like all athelgine bopyrids, are obligate abdominal parasites and records from hermit crab branchial cavities (e.g., Kim & Kwon 1988: p. 215) should be regarded as erroneous.

Key to the species of *Pseudostegias* (based on females)

1. Pleomere 5 lateral plate undivided 2
– Pleomere 5 lateral plate divided 3
2. Pleomere 5 lateral plate extended anteroposteriorly, pleopods pointed distally .. .. *P. otagoensis*
– Pleomere 5 lateral plate extended mesiolaterally, pleopods rounded distally ... . *P. macdermotti*
3. Pleomere 5 lateral plate posteriorly separated .... *P. atlantica*
– Pleomere 5 lateral plate wholly separated 4
4. Pleomere 5 lateral plate lobes large, papillate .... *P. dulcilacuum*
– Pleomere 5 lateral plate lobes small, widely separated 5
5. Pleotelson large, uropods shorter than pleopods .... *P. hapalogasteri*
– Pleotelson small, uropods longer than pleopods .. *P. setoensis* sensu Shiino, 1933

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Drs. Paul Cassidy (Western Washington University) and Alan Harvey (Georgia Southern University) kindly assisted in the identification of hermit crabs. Two anonymous reviewers contributed greatly to the final product. This work was supported by a grant from the Lerner-Gray Fund for Marine Research (American Museum of Natural History) and a Libbie Hyman Memorial Scholarship (Society for Integrative and Comparative Biology) to JDW.

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Caprella kuroshio, a new species (Crustacea: Amphipoda: Caprellidae), with a redescription of *Caprella cicur* Mayer, 1903, and an evaluation of the genus *Metacaprella* Mayer, 1903

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Abstract.—A new species of *Caprella, C. kuroshio,* is described based on the specimens collected from the Pacific coast of central Japan. *Caprella cicur* Mayer, 1903, closely related to the new species, is redescribed based on the type material. The new species differs from *C. cicur* in the shape of the pereonites and the second gnathopod. The female of the new species has a pair of abdominal appendages, which is a diagnostic character of the genus *Metacaprella* Mayer, 1903. However, the abdominal appendage is considered to be a polymorphic and symplesiomorphic character in *Caprella* and *Metacaprella.* Therefore, the genus *Metacaprella* is not recognised, and the new species is assigned to the genus *Caprella.*

In 1991, during a study of the caprellid fauna of the west coast of Shikoku, western Japan, numerous specimens of a caprellid species were collected by the author from the red algae, *Gelidium elegans* Kützing, at Kashiwajima Island, Kochi Prefecture. Afterward, many individuals of the same species also were found on *G. elegans* in Kushimoto and Shirahama, Wakayama Prefecture, in 1992 and 1996 respectively. Furthermore, a single specimen of the species was collected from the drifting brown algae, *Sargassum* sp., in Suruga Bay in 1993. Detailed examination revealed that all of these specimens belong to a new species. The description of the species is presented here.

The type series is deposited in the Seto Marine Biological Laboratory, Kyoto University (SMBL).

Caprella kuroshio, new species
Figs. 1–5

Type material.—Holotype (SMBL Type No. 391): male, 26 Apr 1991, on *Gelidium elegans,* 2 m in depth, Sankaku-bae, Kashiwajima Island (32°46′N, 132°38′E), Kochi Prefecture, Japan. Paratypes (SMBL Type No. 392): 10 males, 10 females, collected together with holotype.

Additional material examined.—10 males, 10 females, 4 Jun 1992, on *Gelidium elegans,* 1 m in depth, Sabiura, Kushimoto (33°28′N, 135°46′E), Wakayama Prefecture, Japan; 1 male, 10 Apr 1993, on drifting *Sargassum* sp., off the mouth of Fuji River, Suruga Bay (35°04′N, 138°39′E), Shizuoka Prefecture, Japan; 5 males, 5 females, 16 Jun 1996, on *Gelidium elegans,* depth unrecorded, Rinkai, Shirahama (33°42′N, 135°21′E), Wakayama Prefecture, Japan.

Description of holotype.—Body (Fig. 1A) 9.65 mm long, smooth. Head with blunt triangular projection directed straight forward; pereonite 1 shorter than head; pereonite 2 longer than pereonite 3, with single acute projection on ventral surface between insertions of second gnathopods (Fig. 1B).

Antenna 1 (Fig. 1A) longer than a half of the body length; flagellum consisting of 14 segments, shorter than peduncle. Antenna 2 (Fig. 1A) shorter than peduncle of antenna 1; peduncular segments 3–5 with 2

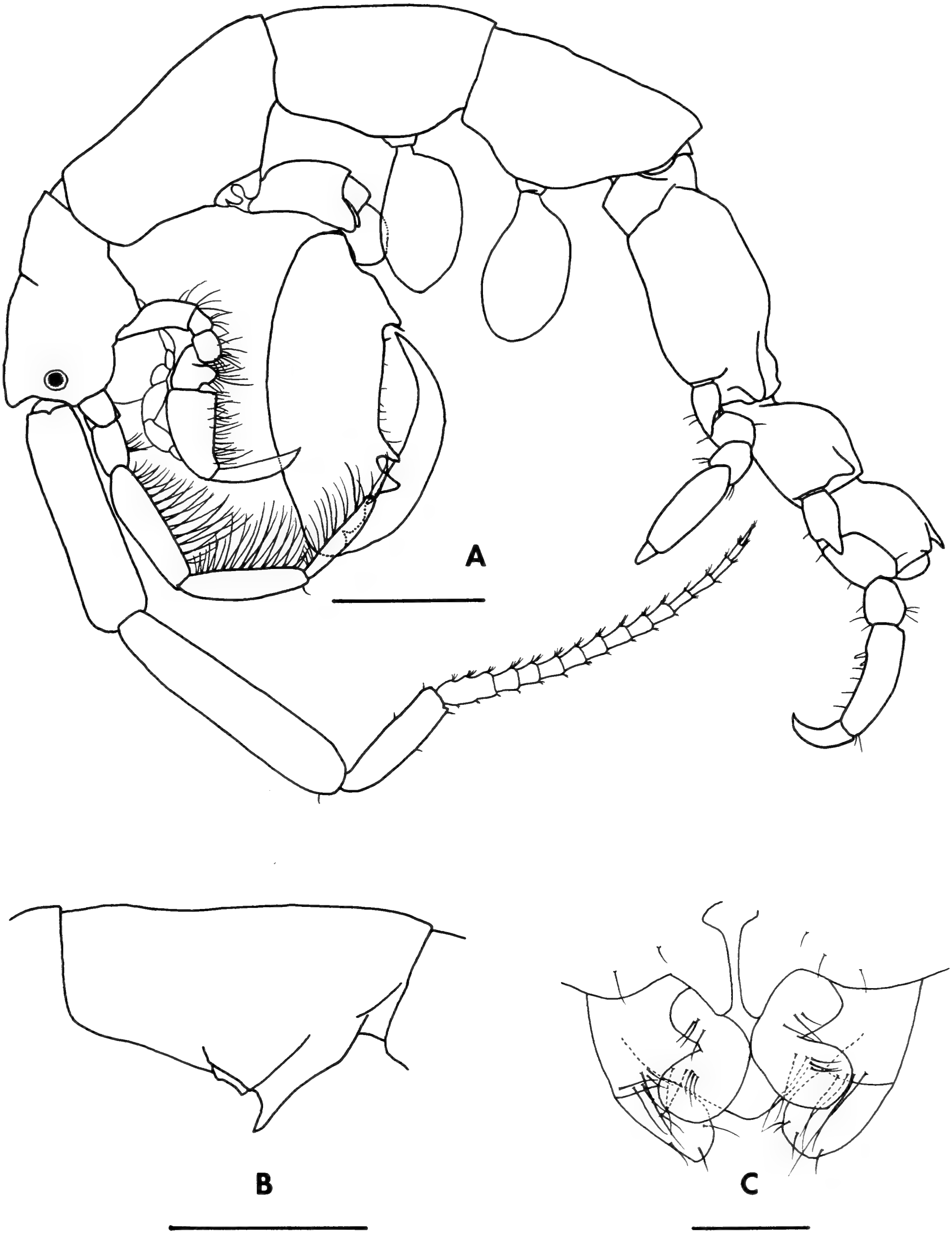

Fig. 1. *Caprella kuroshio,* new species, holotypic male: A, body, lateral view; B, pereonite 2, lateral view; C, abdomen. Scales: A, B = 1.0 mm; C = 0.1 mm.

rows of dense long setae on ventral surfaces; flagellar segment 1 with 2 rows of dense long setae on ventral surface.

Upper lip (Fig. 2A) semicircular, slightly concave on apical margin, densely pubescent. Inner and outer lobes of lower lip (Fig. 2B) well-developed, round, densely pubescent on apicomedial margins; mandibular process developed.

Mandible (Fig. 2C–D) without palp. Left and right sides consisting of 5- and 4-toothed incisor, 5- and 6-toothed lacinia mobilis, and setal row of 3 and 2 plumose setae respectively. Molar process well-developed, with 1 plumose seta; left molar with triangular stout projection; right molar with pubescent molar extension.

Maxilla 1 (Fig. 2E) without inner lobe. Its outer lobe rectangular, with 3 simple and 4 serrate spines on apical margin. Palp 2-segmented. Its distal segment bearing a row of teeth and 6 spines on apical margin, 7 setae on inner margin, 2 rows of setae on ventral surface.

Inner lobe of maxilla 2 (Fig. 2F) shorter than outer lobe, oval, with 2 rows of numerous setae on apicomedial margin. The outer lobe rectangular, with 2 rows of setae on apical margin.

Inner lobe of maxilliped (Fig. 3A) small, with 3 short spines on apical margin, and numerous marginal setae. Outer lobe small, subequal to palpal segment 1 in length, bearing 1 long stout seta on apex, 7 short spines on medial margin, and numerous marginal setae. Palp 4-segmented; segment 1 short; segments 1–2 bearing numerous long setae on medial margins, and segment 3 on apicomedial surface; segment 4 falcate, longer than apical setae on segment 3, with rows of setulae on grasping margin.

Gnathopod 1 (Fig. 3B) robust. Its ischium and merus short, with setae on ventral surfaces. Carpus expanded ventrally, bearing numerous setae. Propodus bearing rows of setae on medial surface. Palm bearing a pair of grasping spines at the proximal corner, its grasping margin straight and minutely serrate, bearing rows of setae. Dactylus falcate, bearing rows of numerous teeth on grasping margin.

Gnathopod 2 (Figs. 1A, 3C) attached to midpoint of pereonite 2. Basis shorter than pereonite 2 in length, bearing laterodistal and mediodistal triangular projections. Ischium bearing lateral triangular projection. Propodus oblong, two times longer than basis. Palmar corner produced, bearing single large grasping spine on apex. Palmar margin slightly concave, bearing a pair of small grasping spines on proximal end, subdistal poison tooth, and distal triangular projection. Dactylus curved and narrowed distally.

Gills (Fig. 1A) present on pereonites 3–4, large, oval.

Pereopods 5–7 (Figs. 4A–C) morphologically similar, but increasing in size posteriorly. Basis bearing triangular dorsal projection at posterior end. Merus inflated dorsally. Propodus longest; palm bearing a pair of grasping spines on proximal corner, and rows of short setae on slightly concave grasping margin. Dactylus bearing minute serration on curved grasping margin.

Abdomen (Fig. 1C) consisting of a pair of appendages, a pair of lateral lobes, and single dorsal lobe. Abdominal appendage 2-segmented; three setae present on both proximal and distal segments; tip of distal segment round. Lateral lobes bearing 6–7 proximal and 4–5 distal setae. Penes large, situated medially.

Description of paratypic female.—Body (Fig. 5A–B) 6.90 mm long. Pereonite 2 subequal to pereonite 3 in length.

Antenna 1 (Fig. 5A) subequal to a half of the body length. Flagellum consisting of 13 segments, subequal to peduncle in length. Antenna 2 (Fig. 5A) longer than peduncle of antenna 1.

Gnathopod 2 (Figs. 5A, C) attached to anterior end of pereonite 2. Propodus oval. Palmar margin slightly convex, bearing subdistal small poison tooth and distal triangular projection. Dactylus slightly curved.

Abdomen (Fig. 5D) consisting of a pair

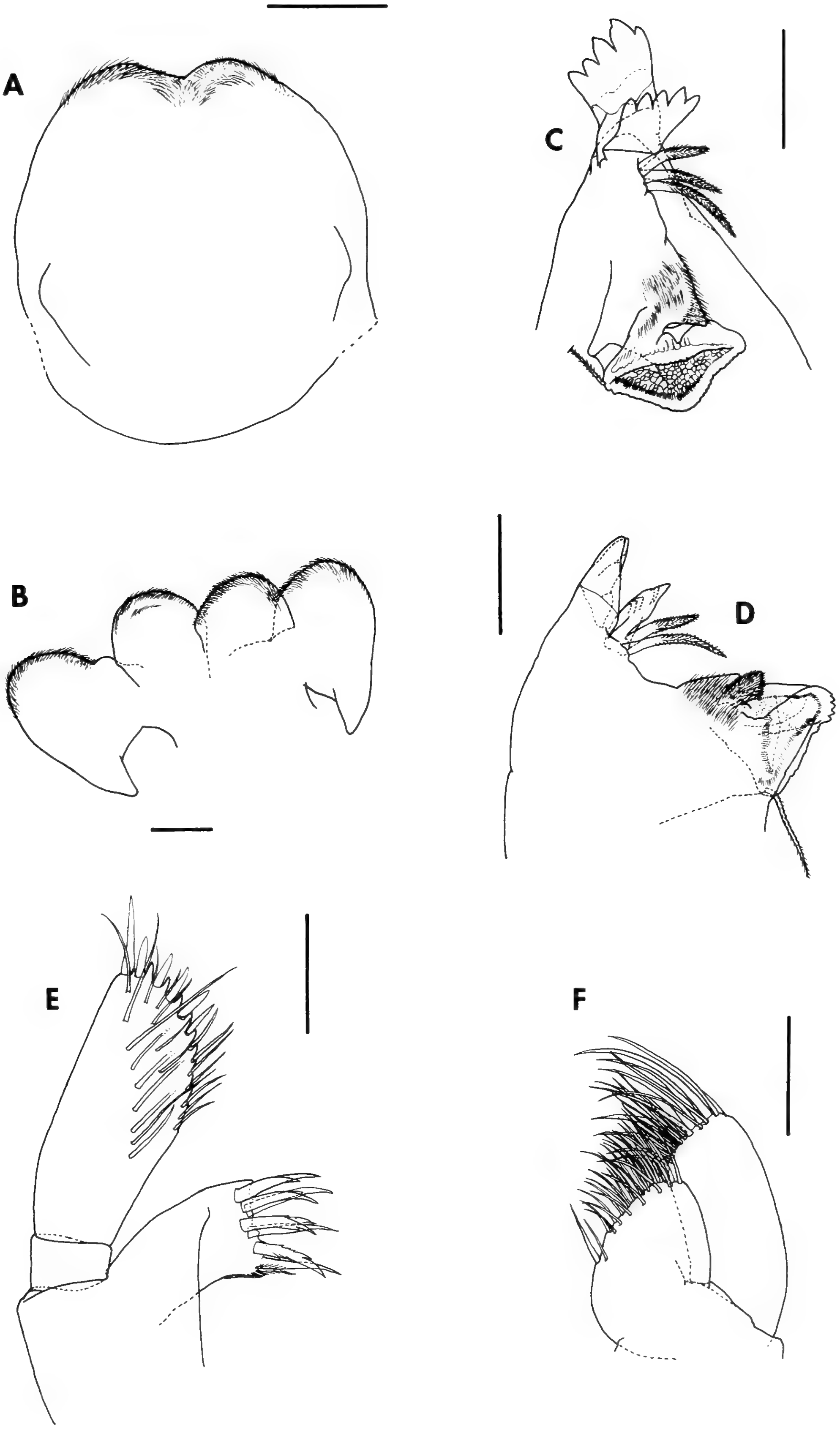

Fig. 2. *Caprella kuroshio,* new species, holotypic male: A, upper lip; B; lower lip; C, left mandible; D, right mandible; E, maxilla 1; F, maxilla 2. Scales: 0.1 mm.

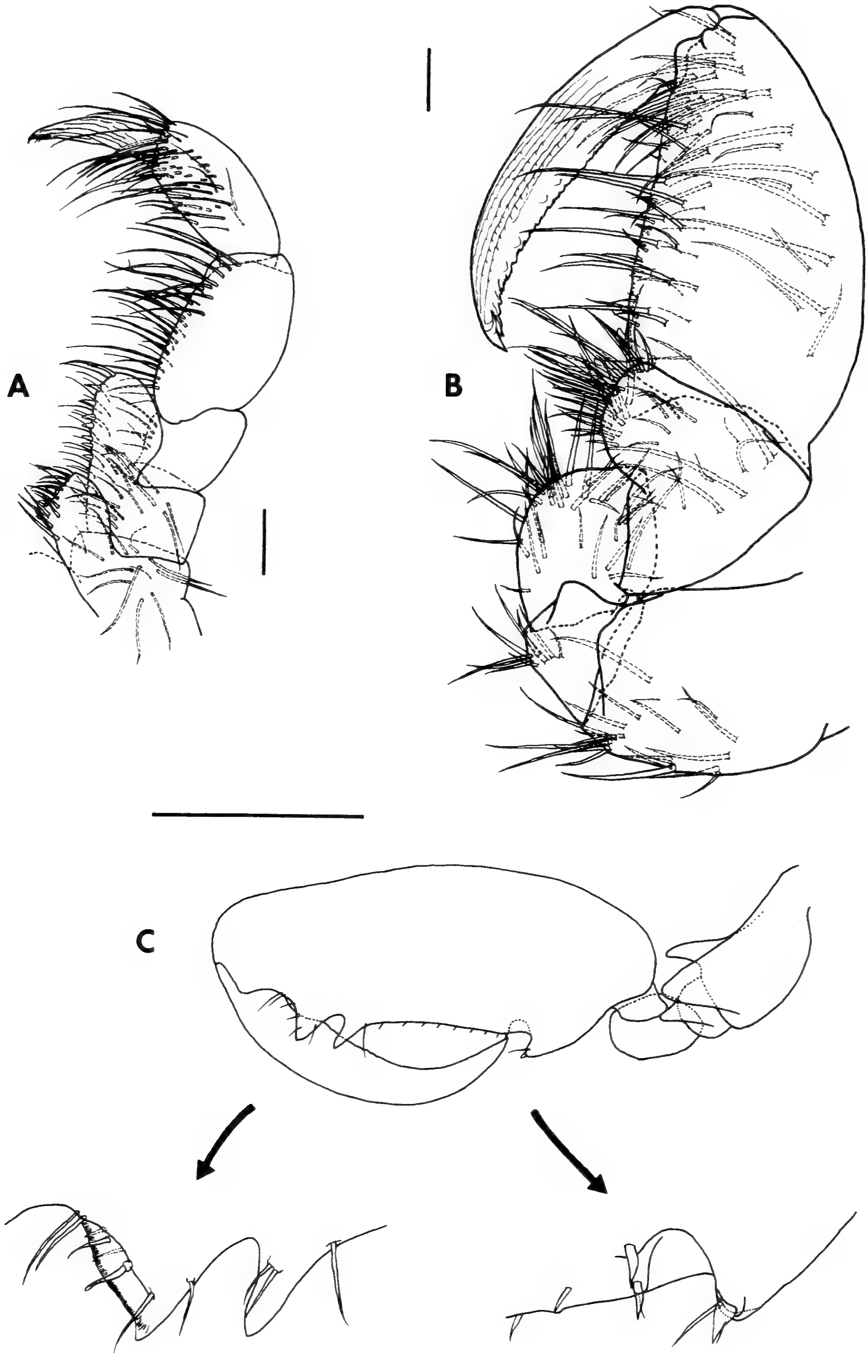

Fig. 3. *Caprella kuroshio,* new species, holotypic male: A, maxilliped; B, gnathopod 1; C, gnathopod 2 with details of palmar projections indicated by arrows. Scales: A, B = 0.1 mm; C = 1.0 mm.

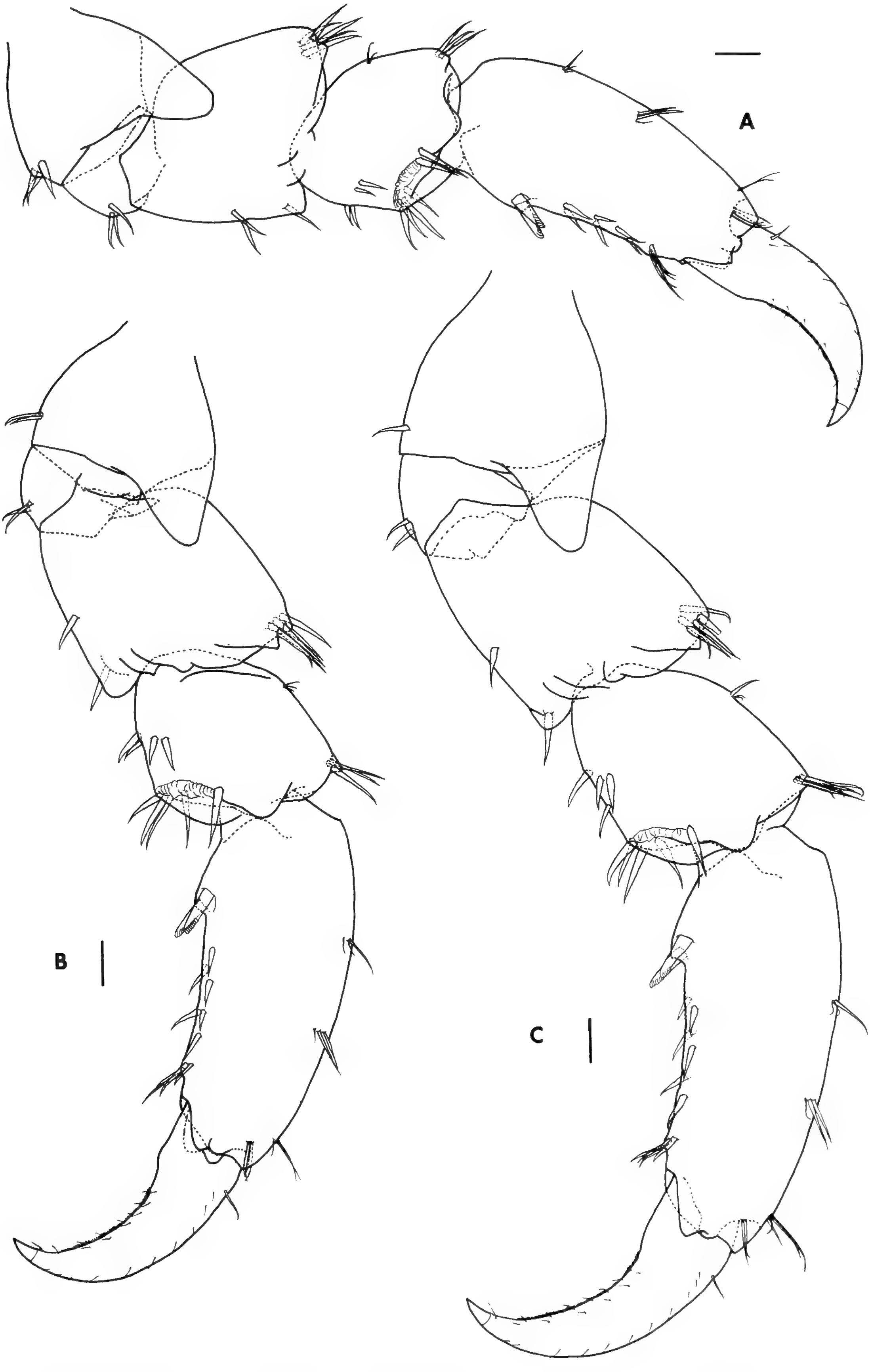

Fig. 4. *Caprella kuroshio,* new species, holotypic male: A, pereopod 5; B, pereopod 6; C, pereopod 7. Scales: 0.1 mm.

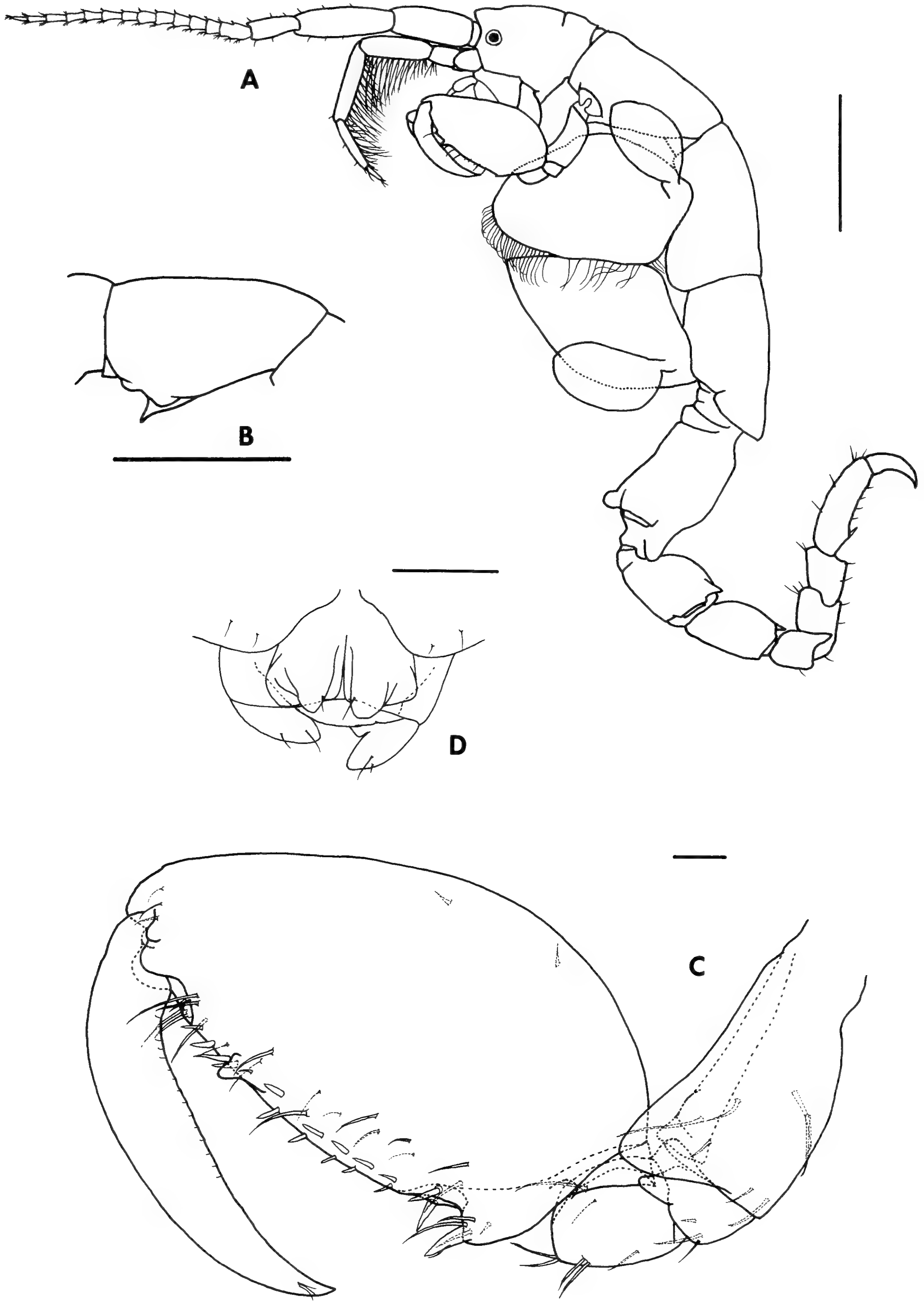

Fig. 5. *Caprella kuroshio,* new species, female: A, body, lateral view; B, pereonite 2, lateral view; C, gnathopod 2; D, abdomen. Scales: A, B = 1.0 mm; C, D = 0.1 mm.

of appendages, a pair of lateral lobes, and single dorsal lobe. Abdominal appendage unsegmented, small, bearing 1 subterminal seta. Lateral lobe with 2 distal setae.

Color in life.—Specimens occurring on the red algae *Gelidium elegans* are scarlet to wine red. A single male collected from the drifting *Sargassum* sp. in Suruga Bay is yellowish.

Etymology.—The specific name is from the Kuroshio current.

Remarks.—*Caprella kuroshio* resembles *Caprella penantis* Leach, 1814 in general appearance. However, the former is distinguishable from the latter by: pereonite 2 with ventral projection; male antenna 1 longer than half the body length; basis of male gnathopod 2 with mediodistal triangular projection; palmar margin of male gnathopod 2 with subdistal poison tooth; female abdomen bearing a pair of appendages.

Caprella kuroshio is also similar to *Caprella cicur* Mayer, 1903, an endemic species to South African waters (Griffiths 1974a, 1974b, 1975, 1976). The species has never been redescribed in detail since Mayer's original description. Here, *C. cicur* is redescribed below using the type material and compared to *C. kuroshio.*

The type series has been deposited in the South African Museum, Cape Town (SAM).

Caprella cicur Mayer, 1903
Figs. 6–10

Caprella cicur Mayer, 1903:75, 97, pl. 4 (figs. 5–7), pl. 8 (figs. 3–5); Griffiths, 1974a:255; Griffiths, 1974b:331; Griffiths, 1975:174; Griffiths, 1976:86, 104.

Material examined.—Syntypes (labeled as "Cotypes"): 1 male, 1 female (SAM 1312), Table Bay, Cape Town, on *Palinurus lalandi,* collected by W. F. Purcell, June 1897.

Description of male.—Body (Fig. 6A) 10.40 mm long. Head with small, acute triangular projection directed straight forward; pereonite 1 longer than head; pereonite 2 longer than pereonite 3, with acute ventral projections between insertions of second gnathopods, and acute lateral projection on insertion of second gnathopod; pereonites 3–4 with ventrolateral small projections on anterior end; pereonite 5 with dorsolateral small projections and lateral blunt knobs on anterior end; pereonite 6 with a pair of dorsal minute projections.

Antenna 1 (Fig. 6A) longer than a half of the body length; flagellum consisting of 14 segments, shorter than peduncle. Antenna 2 (Fig. 6A) shorter than peduncle of antenna 1; peduncular segments 3–5 with 2 rows of dense long setae on ventral surfaces; flagellar segment 1 with 2 rows of dense long setae on ventral surface.

Upper lip (Fig. 7A) semicircular, slightly concave on apical margin, densely pubescent. Inner and outer lobes of lower lip (Fig. 7B) well-developed, round, densely pubescent on apicomedial margins; outer lobe with an apicolateral incomplete fold; mandibular process developed.

Mandible (Figs. 7C–D) without palp. Its left and right sides consisting of 5-toothed incisor, 5-toothed and irregularly-toothed lacinia mobilis, and setal row of 3 and 2 plumose setae respectively. Molar process well-developed, with 1 plumose seta, and triangular stout projection.

Maxilla 1 (Fig. 8A) without inner lobe. Its outer lobe rectangular, with 7 bifid spines on apical margin. Palp 2-segmented. Its distal segment bearing a row of teeth and 8 spines on apical margin, 4 setae on inner margin, rows of setae on ventral surface.

Inner lobe of maxilla 2 (Fig. 8B) shorter than outer lobe, oval, with 2 rows of numerous setae on apicomedial margin. The outer lobe rectangular, with 2 rows of numerous setae on apical margin.

Maxilliped removed.

Gnathopod 1 (Fig. 8C) robust. Its ischium short. Ventral margin of merus produced anteriorly, bearing numerous setae on anteroventral surface. Carpus expanded ventrally, bearing numerous setae. Propo-

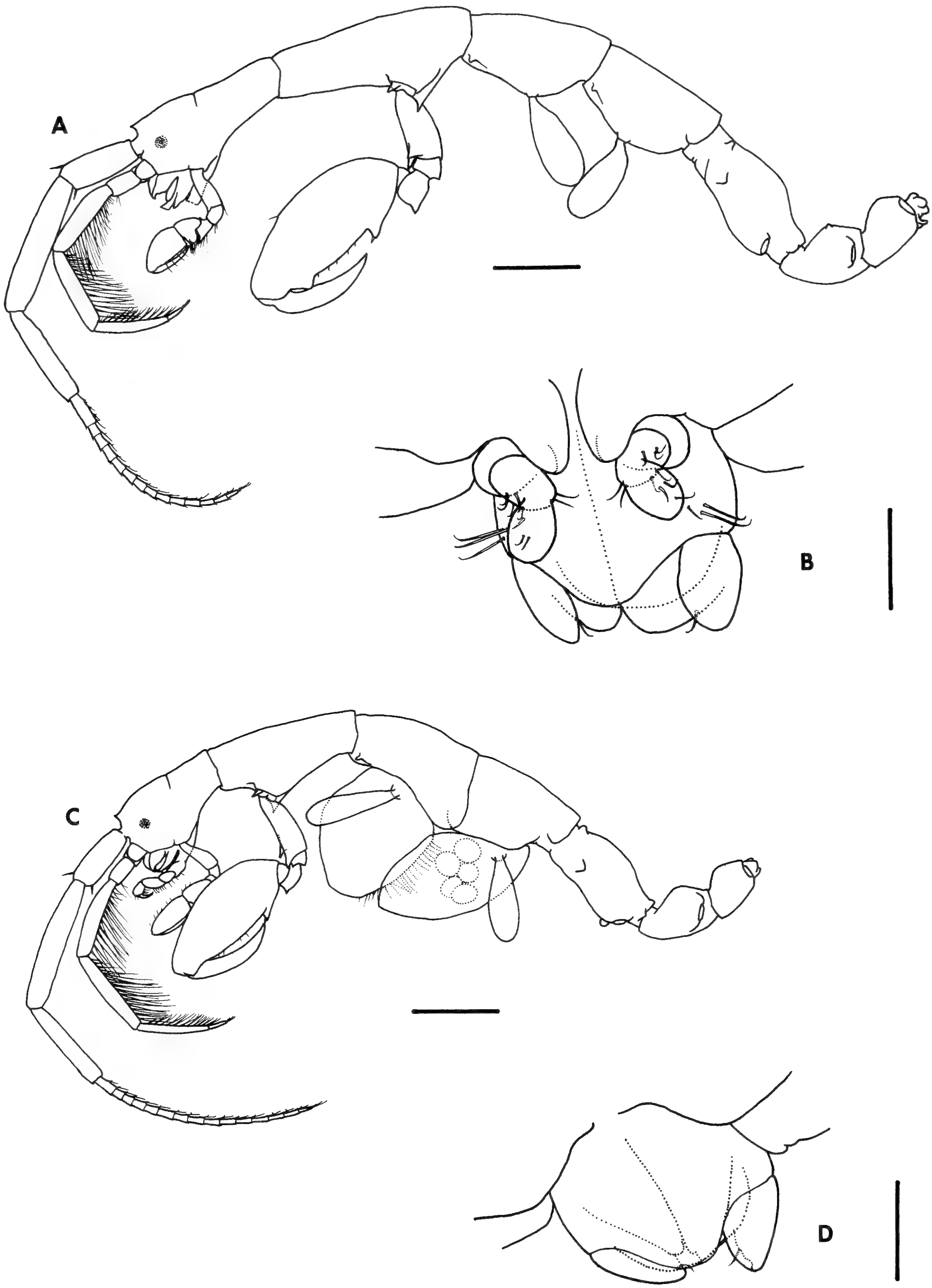

Fig. 6. *Caprella cicur* Mayer, 1903, syntypes: A, male, lateral view; B, male abdomen, ventral view; C, female, lateral view; D, female abdomen, ventral view. Scales: A, C = 1.0 mm; B, D = 0.1 mm.

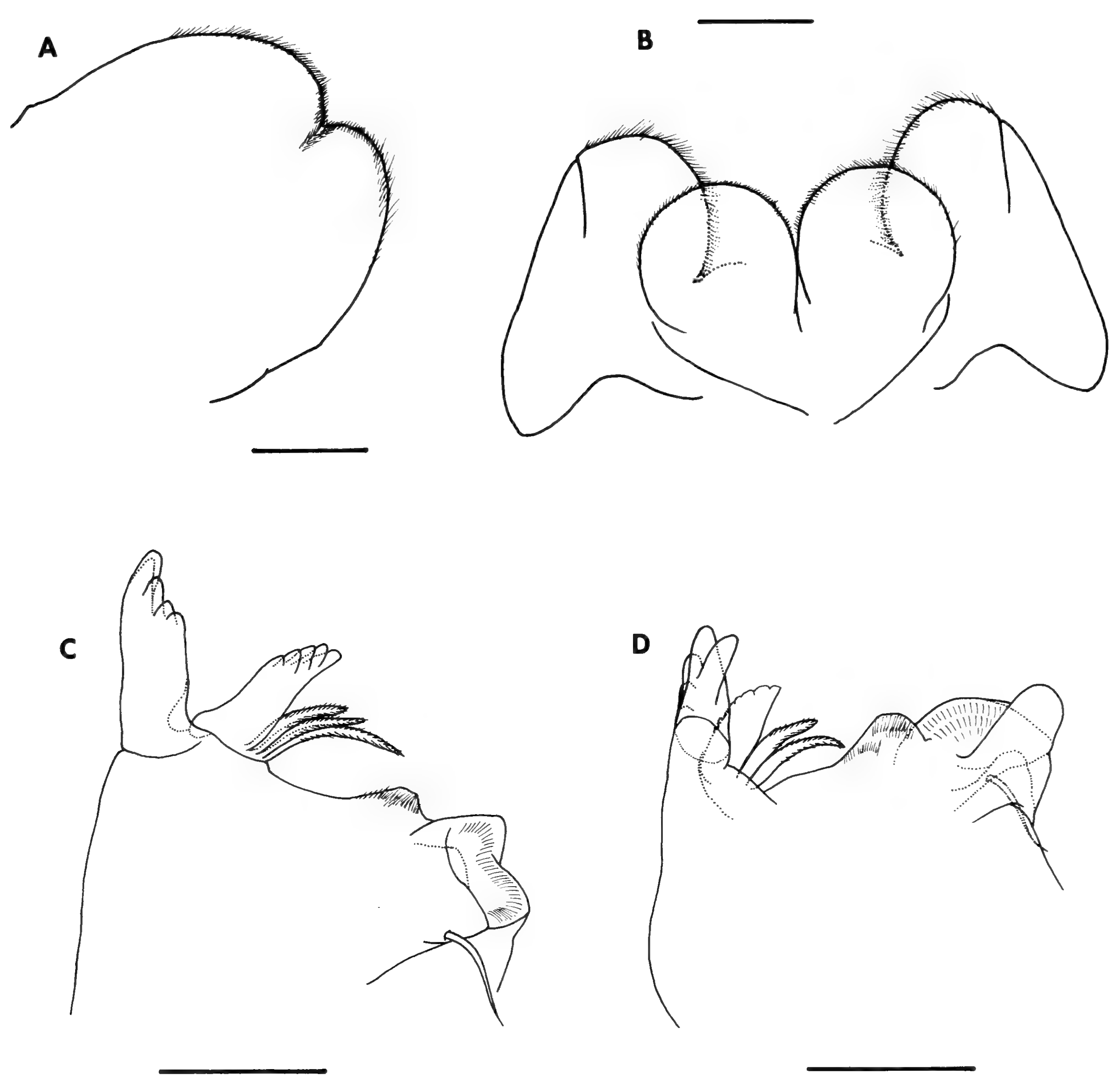

Fig. 7. *Caprella cicur* Mayer, 1903, syntypic male: A, upper lip; B, lower lip; C, left mandible; D, right mandible. Scales: 0.1 mm.

dus bearing rows of setae on medial surface. Palm bearing a pair of grasping spines at the proximal corner, its grasping margin straight, bearing rows of setae. Dactylus falcate.

Gnathopod 2 (Fig. 6A) attached to pereonite 2 posteriorly. Basis shorter than pereonite 2 in length, bearing laterodistal and mediodistal triangular projections. Ischium bearing lateral triangular projection. Merus acutely produced anteroventrally. Propodus oblong, 2.5 times longer than basis. Palmar corner produced, bearing single large grasping spine on apex. Palmar margin without poison tooth, with distal triangular projection. Dactylus curved and narrowed distally.

Gills (Fig. 6A) present on pereonites 3–4, large, elliptical.

Pereopods 5–7 fell off.

Abdomen (Fig. 6B) consisting of a pair of appendages, a pair of lateral lobes, and single dorsal lobe. Abdominal appendage 2-segmented, bearing 10 setae; tip of distal segment round. Lateral lobe bearing 4 proximal and 1 distal setae. Penes large, situated medially.

Description of female.—Body (Fig. 6C)

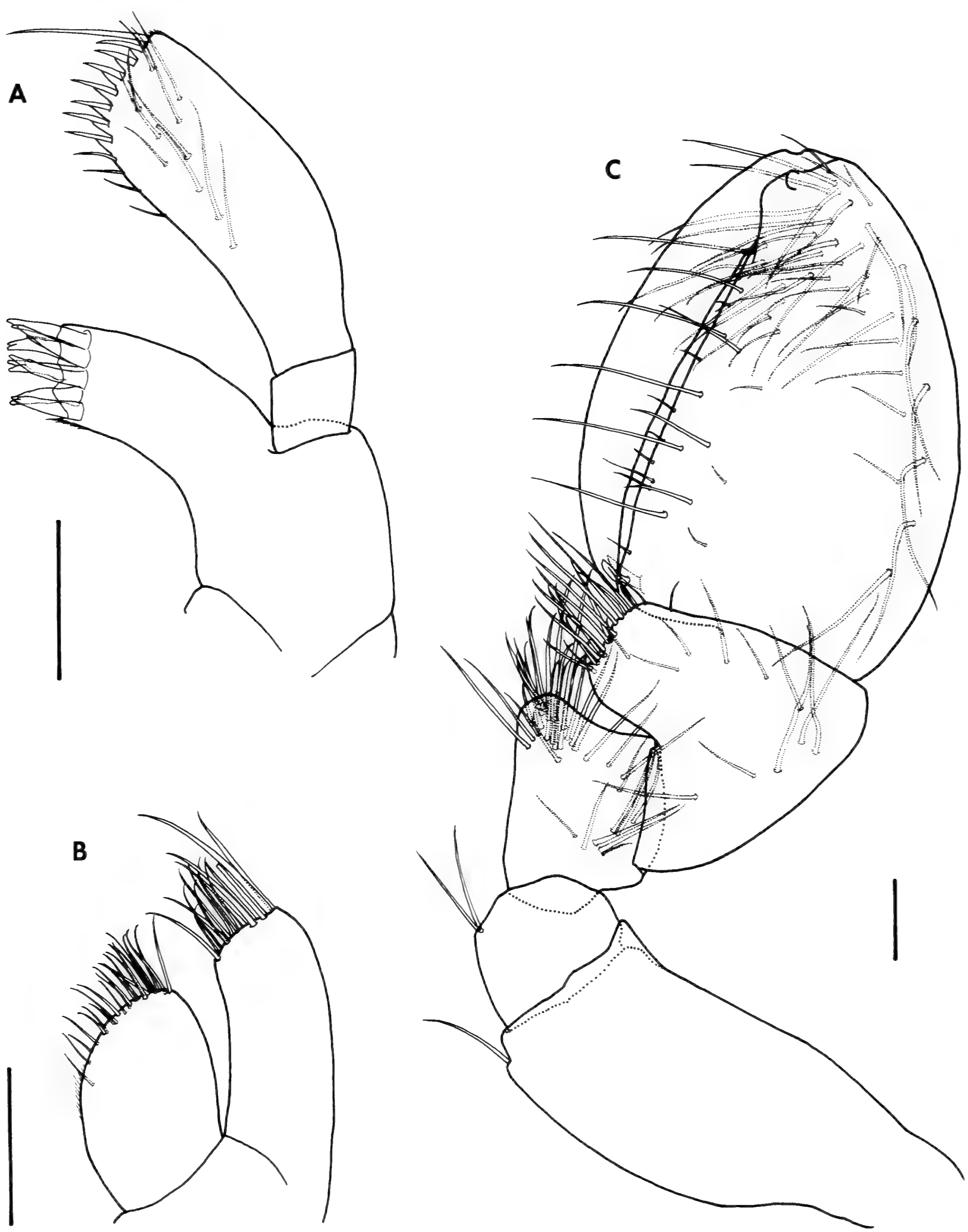

Fig. 8. *Caprella cicur* Mayer, 1903, syntypic male: A, maxilla 1; B, maxilla 2; C, gnathopod 1. Scales: 0.1 mm.

8.40 mm long. Pereonite 1 slightly shorter than head; pereonite 2 slightly longer than pereonite 3; pereonite 4 without ventrolateral small projections on anterior end; pereonite 6 without dorsal projections.

Antenna 1 (Fig. 6C) longer than a half of the body length. Flagellum consisting of 15 segments, slightly shorter than peduncle. Antenna 2 (Fig. 6C) slightly longer than peduncle of antenna 1.

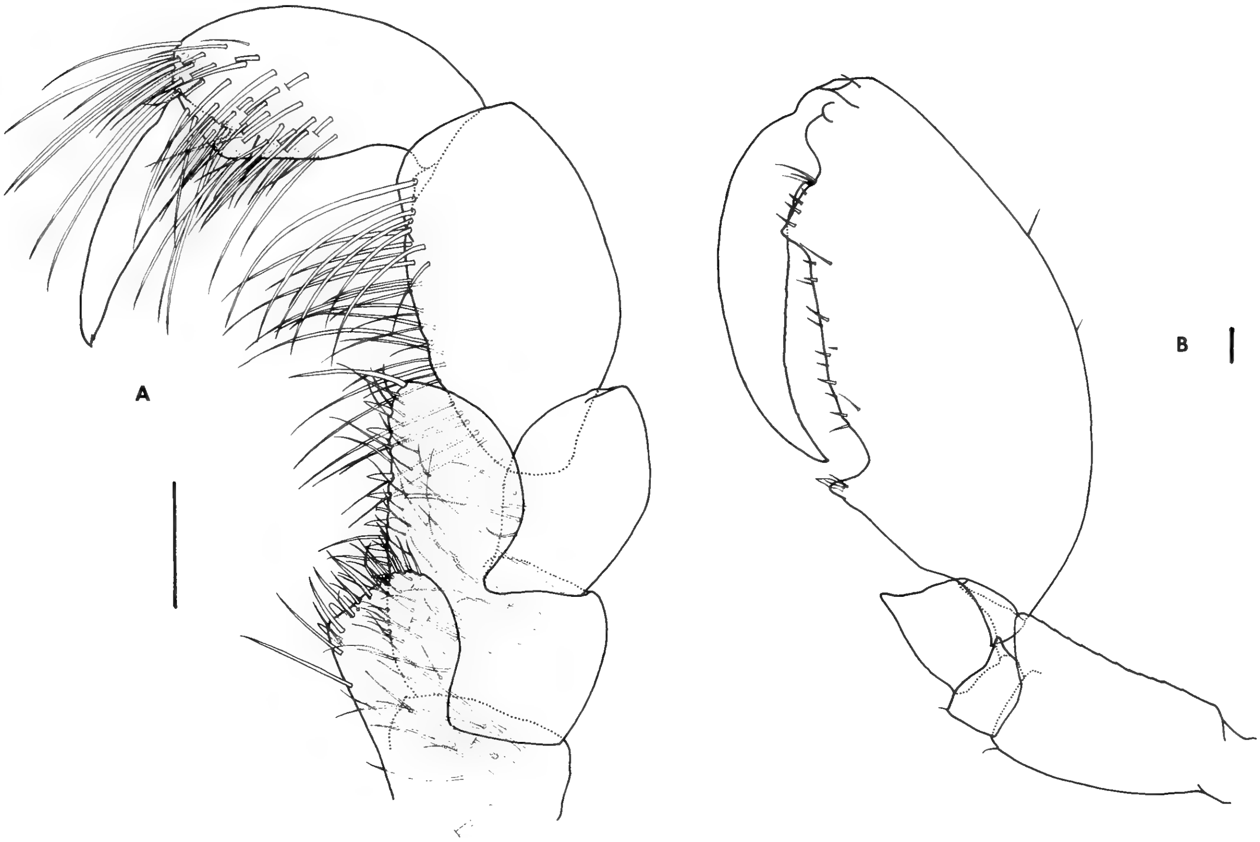

Fig. 9. *Caprella cicur* Mayer, 1903, syntypic female: A, maxilliped; B, gnathopod 2. Scales: 0.1 mm.

Inner lobe of maxilliped (Fig. 9A) small, with 2 short spines on apical margin, and numerous marginal setae. Outer lobe small, subequal to palpal segment 1 in length, bearing 1 long stout seta on apex, 8 short spines on medial margin, and numerous marginal setae. Palp 4-segmented; segment 1 short; segment 2 bearing numerous long setae on medial margin, and segment 3 on apicomedial surface; segment 4 falcate, longer than apical setae on segment 3.

Gnathopod 2 (Figs. 6C, 9B) attached to pereonite 2 anteriorly. Propodus oval. Palmar margin slightly convex. Dactylus slightly curved.

Abdomen (Fig. 6D) consisting of a pair of lateral lobes and single dorsal lobe, without appendages.

Pereopods 5–7 (Fig. 10) morphologically similar. Basis bearing triangular dorsal projection at posterior end. Merus inflated dorsally. Palm of propodus bearing a pair of grasping spines on proximal corner, and rows of short setae on slightly concave grasping margin. (Pereopods 5–7 were detached from the pereonites, and scattered in the vial. Therefore, it is indeterminable to which specimen, and to which pereonite, each pereopod was attached.)

Remarks.—*Caprella kuroshio* is distinguishable from *C. cicur* by: pereonites 1–2 not elongate; pereonites 5–6 without dorsal projections; pereonites 3–5 without lateral projections; insertion of gnathopod 2 without lateral projection; palmar margin of gnathopod 2 with poison tooth; female abdomen bearing a pair of appendages.

Discussion

The most remarkable feature of the new species is the presence of paired abdominal appendages in the female. If the generic diagnosis of Mayer (1903) had been adopted, this species would be assigned to the genus *Metacaprella* Mayer, 1903. However, *Metacaprella* has been considered a questionable genus among the Caprellidea, because it was established only on the basis of the presence of the abdominal appendages in

Fig. 10. *Caprella cicur* Mayer, 1903, pereopods 5–7 of syntypes. Scales: 0.1 mm.

the female (Laubitz 1970). In this section, I assess the taxonomic value of the abdominal appendages based on a survey of the literature to determine whether the genus *Metacaprella* is a valid taxon or not.

History of Metacaprella.—Mayer (1903) suggested the possibility of splitting the genus *Caprella,* and tentatively proposed the genus *Metacaprella* for *Caprella anomala* Mayer, 1903 and *Caprella kennerlyi* Stimpson, 1864, based on the presence of paired abdominal appendages in the female. At that time, however, he hesitated separating the two species from *Caprella.* Subsequently, Dougherty & Steinberg (1953) adopted Mayer's generic distinction. They included the two species to *Metacaprella,* and designated *M. kennerlyi* as the type species of the genus. They also referred *Caprella ferrea* Mayer, 1903 to *Metacaprella* provisionally because of its general resemblance to *M. kennerlyi* and *M. anomala,* even though no females of *C. ferrea* had been found at that time.

In the catalog of the world caprellids, McCain & Steinberg (1970) listed these three species in the genus *Metacaprella.* McCain (1968) and Laubitz (1970) criticized Mayer's generic distinction on the basis of unreliable characters such as the organization of the abdomen. Laubitz (1970) stated, "Thus the separation of *Metacaprella* from *Caprella,* solely on the basis of the female abdomen, is highly unsatisfactory." However, she inconsistently retained the genus *Metacaprella* consisting of *M. anomala* and *M. kennerlyi.* She restored *M. ferrea* to *Caprella,* because there was no sign of the presence of appendages on the female abdomen of the species. Laubitz (1972) transferred *Caprella horrida* G. O. Sars, 1877 to *Metacaprella* based on the presence of a pair of small appendages on the female abdomen. Subsequent authors also have allowed the genus *Metacaprella* to stand in their caprellid faunal studies (Vassilenko 1974, Arimoto 1976, Martin 1977).

Ontogeny of the abdominal appendages.—Sakaguchi (1989) described the postmarsupial development of *Caprella scaura diceros* Mayer, 1890, reared in the laboratory. All the hatchlings (body length 1.25 mm, flagellum of antenna 1 2-segmented, sexes still indistinct) had paired abdominal appendages bearing a single apical seta (Fig. 11A). In males, the appendage was still 1-segmented and small in the specimen with 5-segmented flagellum of antenna 1 (body length 2.62 mm), but became larger and 2-segmented in the older specimens (Figs. 11B–E). In contrast, the appendages of the female had been reduced in the specimen in the early stage (body length 2.66 mm, flagellum of antenna 1 5-segmented), and only their apical seta was left as a vestigial structure (Figs. 11F–H).

Takeuchi (1989) also thoroughly described the postmarsupial development of *Caprella danilevskii* Czerniavski, 1868, *C. okadai* Arimoto, 1930, and *C. generosa* Arimoto, 1977, reared in the laboratory. In these three species, all the early juveniles had paired abdominal appendages bearing single apical setae. The appendages grew larger in males, whereas they were reduced in females, as in *C. scaura diceros.*

The postmarsupial development of *Metacaprella* species have not been investigated, except for Mayer's (1903) illustration of the abdomen of a juvenile of *M. kennerlyi.* The abdomen of the juvenile bears a pair of unsegmented small appendages with single apical setae. It should be noticed that the morphological features of the appendage are almost identical to those of the above-mentioned four *Caprella* species.

Intra-generic morphological variations of abdominal appendages.—Consultation of the literature (above) shows that the intra-generic variations for the morphology of abdominal appendages exist in both *Caprella* and *Metacaprella.*

In *Caprella,* the degree of reduction of the female abdominal appendages varies specifically. In *C. okadai* and *C. cristibrachium* Mayer, 1903, the appendages are completely reduced (Takeuchi 1989, Lee & Lee 1993), whereas in *C. generosa,* a pair of setae is present as a vestigial structure (Takeuchi 1989). Furthermore, the intraspecific morphological variation of the abdomen exists in females of *C. danilevskii.* The female from the Japanese waters has only a pair of vestigial setae on the abdomen (Takeuchi 1989), whereas those from the western North Atlantic and the Mediterranean have a pair of small abdominal appendages (McCain 1968, Krapp-Schickel 1993). In the male, on the other hand, the morphology of the abdominal appendages varies specifically. In *C. simia* Mayer, 1903, they are distinctly 2-segmented (Mori & Yamato 1993), whereas in *C. monoceros* Mayer, 1890 and *C. santosrosai* Sánchez-Moyano, Jiménez-Martín, & García-Gómez, 1995, their segmentation is not distinct (Aoki & Kikuchi 1990, Sánchez-Moyano et al. 1995).

In *Metacaprella,* the degree of development of the female abdominal appendages also varies specifically. The female of *M. anomala* has relatively large, incompletely 2-segmented appendages on the abdomen (Mayer 1903, Laubitz 1970). In females of *M. horrida* and *M. kennerlyi,* the appendages are small and unsegmented (Mayer 1903; Laubitz 1970, 1972). The similar morphology also can be seen in the juvenile of *M. kennerlyi* (Mayer 1903).

Concluding remarks.—It is apparent that the morphology of the abdominal appendage changes ontogenetically in the above-mentioned four *Caprella* species (Sakaguchi 1989, Takeuchi 1989). Furthermore, the intrageneric, and even intraspecific, morphological variations of the abdominal appendage exist in *Caprella* and *Metacaprella* species. These facts emphasize that the external morphology of the abdominal appendage is not an ontogenetically and morphologically stable character enough to di-

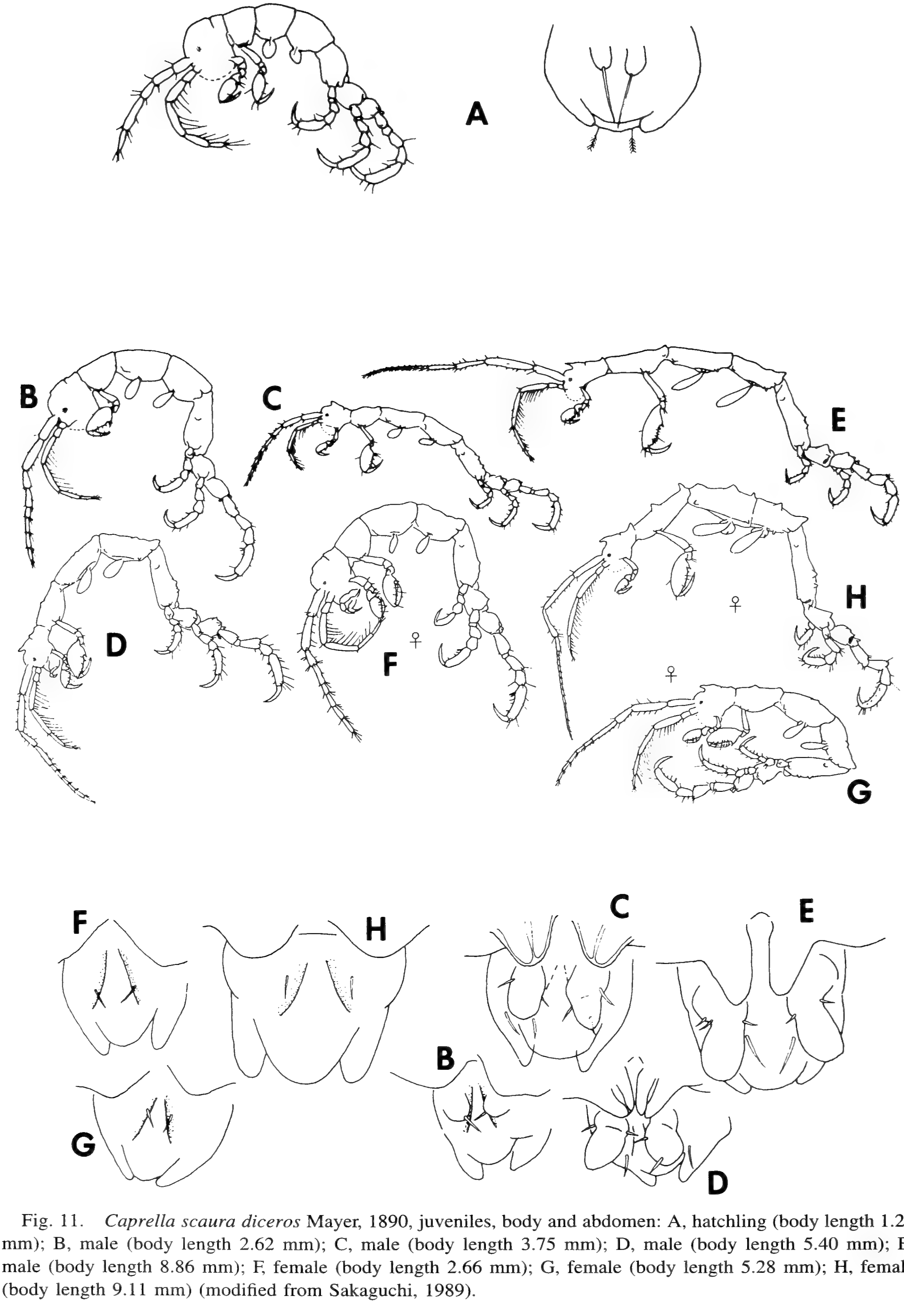

Fig. 11. *Caprella scaura diceros* Mayer, 1890, juveniles, body and abdomen: A, hatchling (body length 1.25 mm); B, male (body length 2.62 mm); C, male (body length 3.75 mm); D, male (body length 5.40 mm); E, male (body length 8.86 mm); F, female (body length 2.66 mm); G, female (body length 5.28 mm); H, female (body length 9.11 mm) (modified from Sakaguchi, 1989).

agnose a genus, and its taxonomic value seems to be relatively low.

In the Caprellidea, the loss and reduction of characters are considered to be apomorphic (Larsen 1997). The ontogenetic information confirms that the reduction of abdominal appendages is an apomorphic character state in the genus *Caprella.* Morphological features of the juvenile abdomens of the four *Caprella* species are almost identical to that of *M. kennerlyi.* Female abdominal appendages are present in early developmental stages of both genera. They are reduced to various degree in later juvenile stages in *Caprella,* while they remain in adults in *Metacaprella.* Because characters appear earlier in the ontogeny are considered to be ancestral and those appear later derived (Eldredge & Cracraft 1980), the presence of the abdominal appendage in the adult female of *Metacaprella* is not an autapomorphy of the genus, but a symplesiomorphy of the species assigned to the genus.

Metacaprella and *Caprella* shares almost all diagnostic characters, and the morphology of female abdominal appendages varies gradually within these two genera, namely, from incompletely 2-segmented (*M. anomala*) through unsegmented (*M. kennerlyi, M. horrida* and Atlantic *C. danilevskii*) or vestigial (*C. generosa* and Japanese *C. danilevskii*) to completely reduced (*C. okadai* and *C. cristibrachium*). No gaps enough to separate *Metacaprella* from *Caprella* could be found. Therefore, the establishment of the genus *Metacaprella* only on the basis of a plesiomorphic character, i.e., abdominal appendage, is considered to be inadequate. Consequently, I decline to adopt the genus *Metacaprella* as a separate taxon, and assign the present new species to the genus *Caprella.*

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Palaemonella hachijo, a new species of shrimp (Crustacea: Decapoda: Palaemonidae) from a submarine cave in southern Japan

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Abstract.—A new species of the pontoniine shrimp genus *Palaemonella* Dana, *P. hachijo,* is described and illustrated on the basis of single male specimen from a submarine cave at Hachijo-jima Island, Izu Islands, southern Japan. It closely resembles *P. dolichodactylus* Bruce, but is readily distinguished by the antennal spine overreaching the distal margin of the antennal basicerite, the posteroventral margin of the fifth abdominal somite armed with an acute tooth, and the ambulatory propodi not segmented.

The genus *Palaemonella* Dana, 1852, is distinguished from other pontoniine genera in having a hepatic spine, a mandibular palp, a strong ventromesial spine on the fourth thoracic sternite, and slender, simple fingers of the first pereiopod (Chace & Bruce 1993, Holthuis 1993, Bruce 1994). Until now, it contained 13 species worldwide (Chace & Bruce 1993).

During a survey of the caridean shrimp fauna of Hachijo-jima Island, the Izu Islands, southern Japan, in the summer of 1998, a specimen of *Palaemonella* was captured in a submarine cave at a depth of 20 m. Although the specimen closely resembled *P. dolichodactylus* Bruce, 1991, known only from the New Caledonian waters at the depths of 44–250 m (Bruce 1991a, 1991b), the specimen differed morphologically from *P. dolichodactylus* and was found to represent a new species. Herein this new species is described and illustrated. The abbreviation CL indicates the postorbital carapace length measured in mm. The specimen is deposited in the Coastal Branch of Natural History Museum and Institute, Chiba (CMNH).

Palaemonella hachijo, new species
(Figs. 1–3)

Material.—Holotype, male, 3.3 mm CL, 33°03.5′N, 139°47.9′E, southern Japan, Izu Islands, Hachijo-jima Island, Occho-gahama, submarine cave, 20 m, 2 Sep 1998, with SCUBA gear, coll. J. Okuno, CMNH-ZC 00017.

Diagnosis.—Small sized pontoniine shrimp with subcylindrical body form. Carapace without supraorbital spine. Rostrum well developed, horizontal, dentate. Antennal spine acute, slightly overreaching dorsodistal margin of antennal basicerite. Posteroventral angle of fifth abdominal somite pointed, armed with acute tooth. Second pereiopod with merus armed with distoventral tooth and carpus lacking strong submarginal tooth. Ambulatory pereiopods long, slender, propodi not segmented.

Description.—Carapace (Fig. 1A) smooth, glabrous; orbit feebly developed, with distinct posterior marginal ridge, without supraorbital spine; antennal spine well developed, acute, slightly overreaching dorsodistal margin of antennal basicerite; hepatic spine acute, situated at lower and posterior levels of antennal spine; epigasteric spine acute; pterygostomian margin rounded.

Rostrum (Fig. 1C) well developed, horizontal and straight, 0.85 times as long as CL, falling short of distal margin of scaphocerite. Dorsal carina with 8 acute teeth, distal tooth subapical, smaller than other

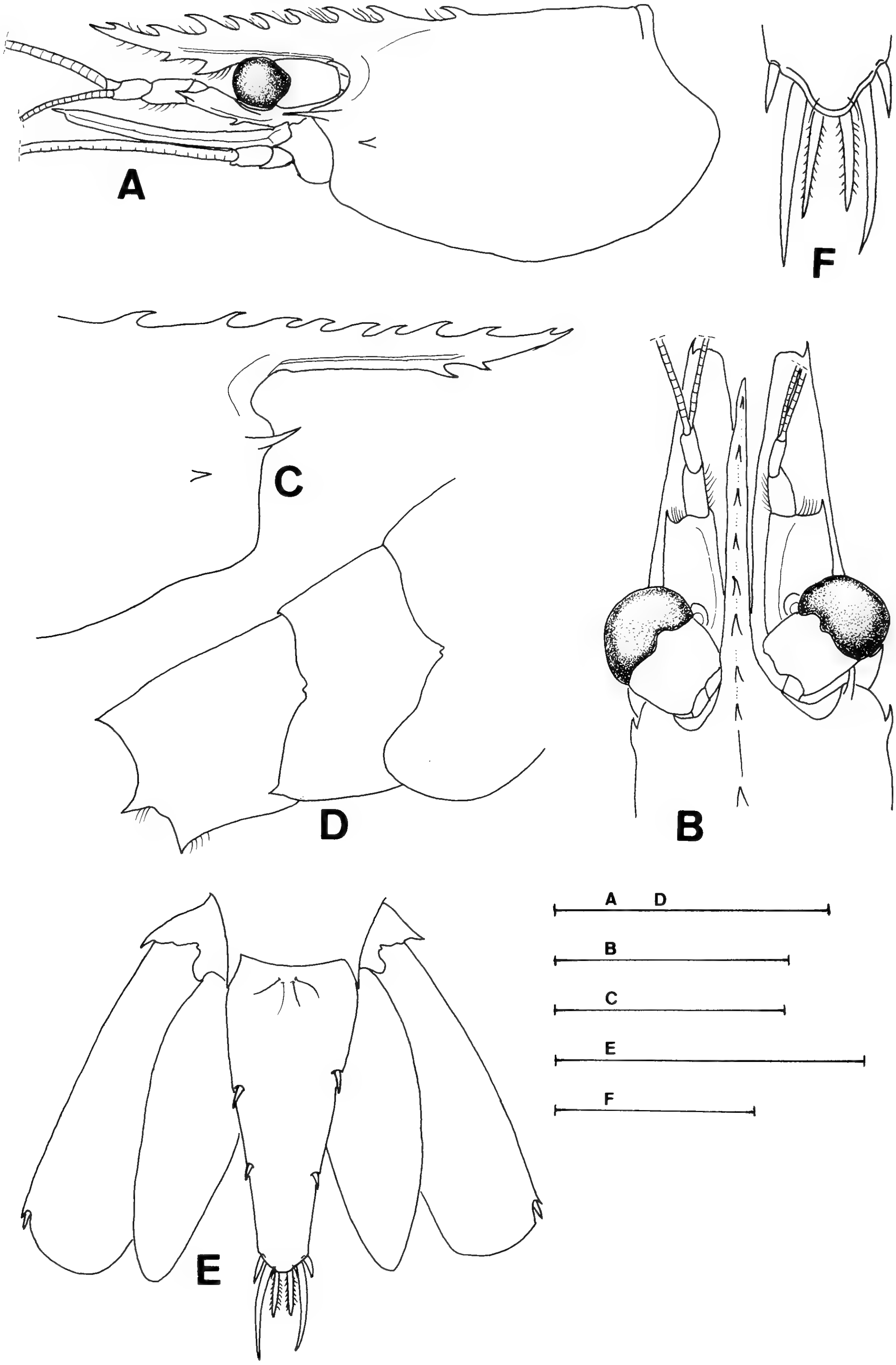

Fig. 1. *Palaemonella hachijo,* new species. Holotype male (CMNH-ZC 00017). A, carapace and left cephalic appendages, lateral view; B, anterior part of carapace with cephalic appendages, dorsal view; C, anterior part of carapace with rostrum, lateral view; D, fourth to sixth abdominal somites, right view; E, telson with uropods, dorsal view; F, posterior margin of telson, dorsal view. Scales: A, 3 mm; B–E, 2 mm; F, 0.5 mm.

posterior teeth, second to eighth teeth equidistant, seventh tooth just above orbit, proximal tooth posterior to postorbital margin, interspaces setose. Ventral carina with 2 acute teeth, situated at distal half of length; lateral carina feebly developed.

Abdominal somites smooth, glabrous; pleura of first to third somites broad, rounded. Posteroventral margin of fourth somite with pleuron produced posteriorly. Fifth somite (Fig. 1D) armed with acute tooth at posteroventral margin of posteriorly produced pleuron. Sixth somite (Fig. 1D) 0.51 times as long as CL, posteroventral margin armed with acute tooth. Telson (Fig. 1E) 0.67 times as long as CL, 2 pairs of acute submarginal dorsal spine; posterior margin (Fig. 1F) rounded, with 3 pairs of spines, intermediate spines longest, lateral and intermediate spines simple, submedian spines with setules.

Eye with large globular cornea, stalk slightly longer than corneal diameter.

Antennular peduncle (Fig. 2A) falling slightly short of rostral apex. Proximal segment with anterolateral margin produced, distal lobe slightly convex, armed sparsely with short setae, with acute distolateral spine overreaching distal lobe, ventromedial margin armed with acute tooth, stylocerite well developed, acute, reaching level of proximal third of the segment, statocyst well developed, rounded; intermediate segment with lateral margin feebly convex, armed densely with short setae, medial margin fringed sparsely with moderately long setae; distal segment non-setose, obliquely articulated with flagella. Upper flagellum (Fig. 2B) biramous, divided at distal third of flagellum length, longer ramus about 4 times as long as shorter ramus, with segments neighboring shorter ramus fringed with simple setae (Fig. 2C).

Antenna (Fig. 2D) with well developed scaphocerite 3.82 times as long as maximum width, with distolateral tooth acute, overreaching distal margin of lamella; carpocerite reaching proximal fifth of scaphocerite; basicerite armed anterolaterally with acute tooth.

Mandible (Fig. 2E) robust, with one-segmented palp with sparse setae; molar process obliquely truncated distally, with blunt teeth; incisor process well developed, with 3 acute distal teeth.

Maxillula (Fig. 2F) with bilobed palp, upper lobe tapering distally, lower lobe slightly curved; upper lacinia slender, with distal margin truncated, armed with 2 rows of acute spines; lower lacinia broken, but probably typical of *Palaemonella.*

Maxilla (2G) with simple palp tapering distally; basal endite developed, deeply bilobed, with numerous short setae distally; coxal endite obsolete; scaphognathite fringed densely with setae.

First maxilliped (Fig. 2H) with simple seta on palp; caridean lobe well developed, with sparse setae, exopod with well developed flagellum; basal endite with medial margin with 3 rows of dense setae, coxal endite with medial margin with numerous short setae; epipod large, triangular, feebly bilobed.

Second maxilliped (Fig. 2I) with oval epipod without podobranch. Dactylar segment laterally with 2 rows of dense setae, distal margin truncated, with dense setae. Propodal segment with broadly rounded distal margin, with dense setae; dorsodistal and ventrodistal margins of carpal segment acute. Distal margin of ischiomeral segment about twice as long as carpal segment. Basal segment with exopodal flagellum well developed.

Third maxilliped (Fig. 2J) with oval epipod. Endopod slender, slightly overreaching midlength of scaphocerite; ultimate segment tapering, with group of short distolateral setae medially, fringed with long setae distally; penultimate segment slightly longer than ultimate segment, lateral and medial margins fringed with setae; ischiomerus widening, with 6 distolateral spinules. Exopod well developed, fringed distally with long setae. Small arthrobranch present.

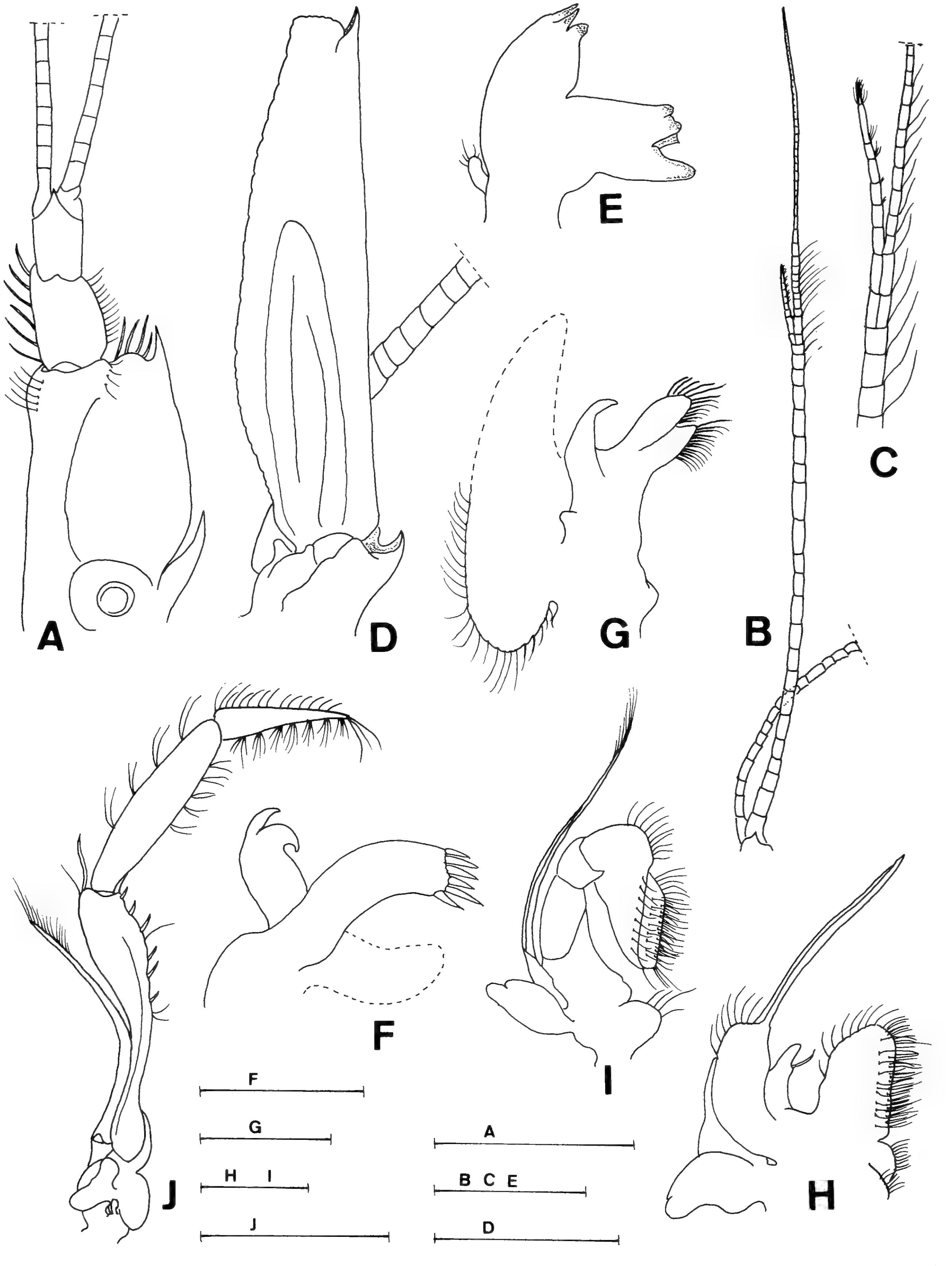

Fig. 2. *Palaemonella hachijo,* new species. Holotype male (CMNH-ZC 00017). A, right antennular peduncle, dorsal aspect; B, same, upper flagellum; C, same, shorter ramus; D, right antenna, dorsal aspect; E, right mandible; F, right maxillula; G, right maxilla; H, right first maxilliped; I, right second maxilliped; J, right third maxilliped. Scales, A, D, J, 1 mm; B, 1.5 mm; C, E–I, 0.5 mm.

Table 1.—Branchial formula of *Palaemonella hachijo,* new species.

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

Branchial formula as in Table 1.

First pereiopod (Fig. 3A) slender, overreaching distal margin of scaphocerite by proximal fourth of carpus. Chela (Fig. 3B) 0.52 times as long as CL, palm with transverse rows of setae proximally; fingers tapering with small hooked tip, with dense setae distally, cutting edges entire. Carpus 0.73 times as long as CL, 1.63 times as long as chela, slightly widening distally, distal margin not denticulate, distoventrally with dense setae.

Second pereiopods (Fig. 3C) long, slender, symmetrical, overreaching distal margin of scaphocerite by distal fourth of meri. Chela 1.70 times as long as CL, 1.26 times as long as carpus, with palm subcylindrical, compressed, entire, flexor margin expanded proximally, slightly shorter than fingers; movable finger (Fig. 3D) with acute hooked tip, distal 2/3 of cutting edge entire, proximal third armed with 2 large blunt teeth; fixed finger (Fig. 3D) with acute hooked tip, distal 3/4 of cutting edge entire, proximal fourth armed with large blunt tooth and quadrate conical projection, marginally serrate, opposite to the teeth on movable finger. Carpus slender, entire, 1.30 times as long as CL, widening distally, without subterminal spine. Merus slender, armed with acute distal tooth on flexor margin, with long setae dorsodistally. Ischium unarmed.

Third pereiopod (Fig. 3E) long, slender, overreaching distal margin of scaphocerite by level of midlength of carpus. Dactylus (Fig. 3F) slightly sinuous, uniunguiculate, midlength to distal third of external margin armed sparsely with long setae. Propodus 4.75 times as long as dactylus, 1.39 times as long as carpus, not segmented, distoventral and dorsodistal angles with long setae, dorsal margin armed with sparse setae. Carpus 0.70 times as long as CL, fringed with sparse setae dorsodistally. Merus 1.05 times as long as CL, 1.48 times as long as carpus, dorsodistal angle fringed with 2 long setae (Fig. 3G). Ischium with sparse setae ventrally.

Fourth thoracic sternite (Fig. 3H) armed with long slender median spine between coxae of first pereiopods. Fifth thoracic sternite (Fig. 3H) armed with pair of acute submedian spines with sinuous lateral borders proximal coxae of second pereiopods. Eighth thoracic sternite (Fig. 3H) armed with stout median process directed anteriorly.

Endopod of first pleopod (Fig. 3I) oblong, fringed with sparse setae distally.

Endopod of second pleopod armed with appendices interna and masculina (Fig. 3J); appendix interna slightly overreaching tip of appendix masculina, with cincinnuli distally; appendix masculina with numerous long setae.

Uropod (Fig. 1E) with protopodite posteroventrally acute; exopod broad, reaching subequal to posterior telson margin, posterior margin feebly rounded, lateral margin straight, with acute distolateral tooth, with strong mobile spine medially; endopod reaching subequal to distal margin of exopod, slightly tapering distally.

Coloration.—Body and appendages transparent. Posterodorsal region of carapace with short, oblique rusty red line. Anterolateral angle of carapace with oblique, feebly undulate rusty red line. Ventral midline and external margin of telson colored with rusty red. Abdominal somites each with transverse rusty red line along posterodorsal margin. Second pereiopod with reddish brown patches at distal margins of merus and carpus, and junction of palm and movable finger.

Etymology.—From locality of capture, Hachijo-jima Island. This island is com-

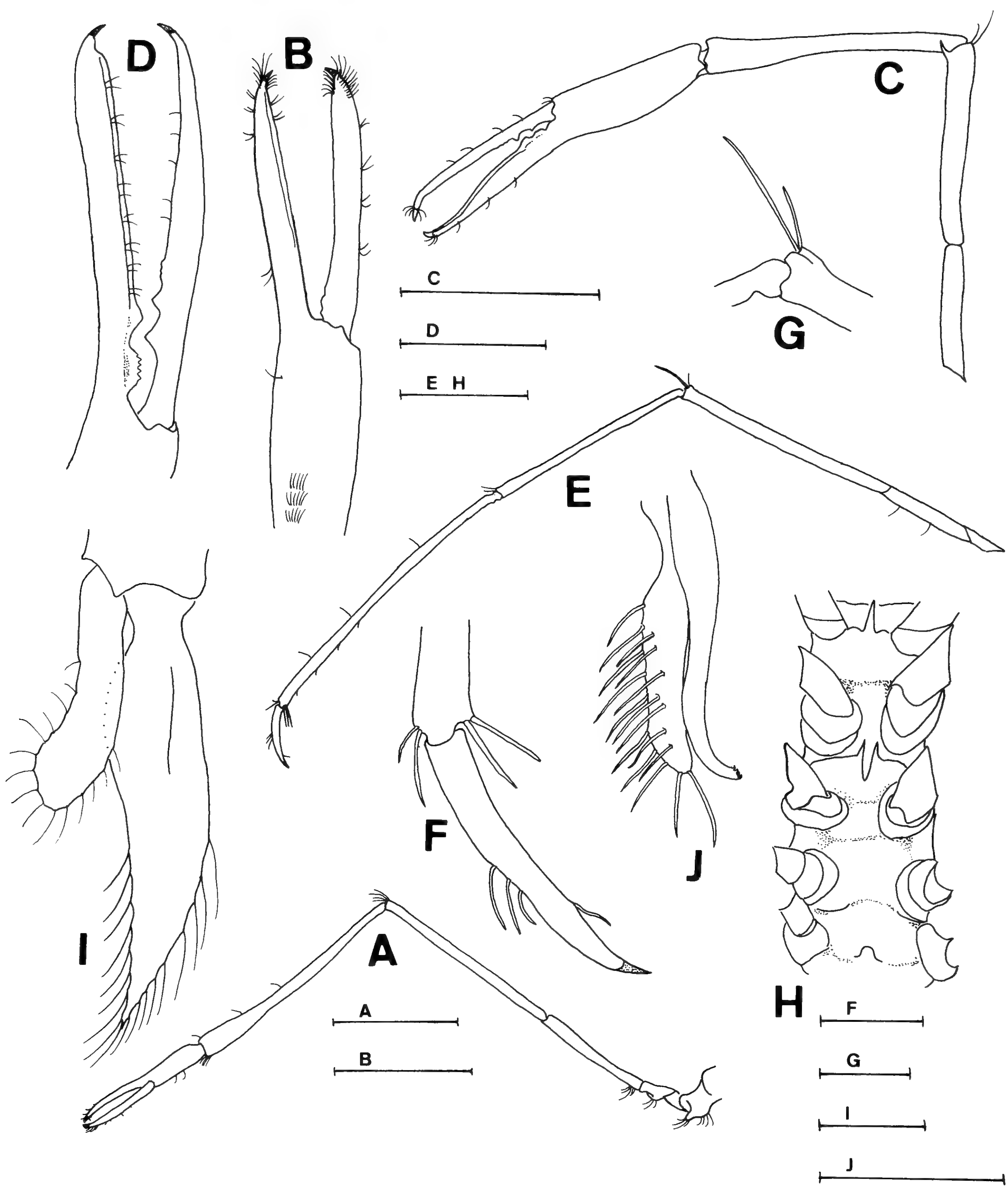

Fig. 3. *Palaemonella hachijo,* new species. Holotype male (CMNH-ZC 00017). A, left first pereiopod; B, same, chela; C, left second pereiopod; D, same, fingers; E, left third pereiopod; F, same, dactylus; G, same, carpomeral articulation; H, thoracic sternites, ventral aspect; I, left first pleopod; J, left second pleopod, appendices interna and masculine. Scales: A, E, 1.5 mm; B, 0.5 mm; C, 3 mm; D, H, 1 mm; F, G, I, J, 0.25 mm.

monly abbreviated to "Hachijo". In this case, the word *hachijo* is used as a noun in apposition.

Distribution.—Known only from the type locality.

Ecological notes.—The collection site of the specimen was in a small crevice in a submarine cave at a depth of 20 m. The crevice was naked, without any sponges or coelenterates, therefore, *P. hachijo* may be considered as a free-living species. This point was about 15 m distance from the cave entrance, and not influenced by incidence of daylight. Several specimens of *Urocaridella* sp. (Palaemonidae) and some *Cinetorhynchus concolor* (Okuno) and *C. erythrostictus* Okuno (Rhynchocinetidae) were also collected.

Remarks.—All ambulatory pereiopods but the left third pereiopod were detached before the specimen was scrutinized. Three unnumbered (probably right fourth and fifth and left fourth) ambulatory pereiopods remained in the bottle. These appendages were similar in form to that of the third pereiopod.

Palaemonella hachijo closely resembles *P. dolichodactylus* sharing the following characters: supraorbital spine absent; merus of second pereiopod armed with distal tooth on flexor margin; carpus of second pereiopod lacking strong submarginal tooth; and ambulatory pereiopods long and slender. The new species differs from *P. dolichodactylus* in the antennal spine overreaching the distal margin of the antennal basicerite, posteroventral angle of the fifth abdominal somite armed with acute tooth posteroventrally, and the ambulatory propodi not segmented. In *P. dolicodactylus,* the antennal spine falls slightly short of the level of the distal margin of the antennal basicerite, and the fifth abdominal somite has the pleuron rounded posteroventrally, and the propodi of ambulatory pereiopods are obscurely segmented (Bruce 1991a, 1991b).

Acknowledgements

I thank Messrs. S. Kato and K. Tanaka of Hachijo-jima Island for their help to capturing the specimen. My thanks go to Dr. Mary K. Wicksten of the Texas A & M University for reading the manuscript, and Mr. John P. Hoover of the Hawaii Medical Library for his help in obtaining literature. This study was supported by a Grant-in-Aid for Encouragement of Young Scientists (No. 10740402).

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A new species of *Macrobrachium* (Crustacea: Decapoda: Palaemonidae), with abbreviated development, from Veracruz, Mexico

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Abstract.—*Macrobrachium tuxtlaense,* a new epigean species of freshwater prawn with abbreviated development from Los Tuxtlas region in the state of Veracruz, Mexico, is described. The new species is most similar to the cave-dwelling *M. acherontium* Holthuis and *M. villalobosi* Hobbs, the two previously known species from Mexico with abbreviated development.

Although abbreviated development is a widespread characteristic among species of Palaemoninae (Pereira & García 1995), which comprises mostly freshwater and estuarine shrimps, only two cave-dwelling species of *Macrobrachium* Bate, 1868 from North America (Mexico and the United States) present this kind of development: *M. villalobosi* Hobbs, 1973 and *M. acherontium* Holthuis, 1977. Until now, within the Palaemoninae from North America, the only epigean species with abbreviated development belonged to *Palaemonetes,* Heller, 1869; and *Cryphiops* (*Bithynops*) Villalobos et al., 1989. In this study we describe a new epigean species of *Macrobrachium* from Los Tuxtlas region, Veracruz, in which females carry few (10–20), large eggs (mean size 2.8 mm by 2.5 mm), and an abbreviated development is present as evidenced by the morphology of the first larval stage (Fig. 1). The presence in the first larval stage of all five pairs of pereiopods, well developed pleopods, and a fan shaped telson, indicate a partially abbreviated development with two larval stages according to Jalihal et al. (1993).

All specimens used are deposited in the Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México (CNCR). Abbreviations used are: cl, carapace length; tl, total length.

Macrobrachium tuxtlaense, new species
Figs. 1–3

Material examined.—Holotype: 1 ♂ cl 10.4 mm, tl 40.5 mm, small stream 1 km S of Coyame (18°26′N, 95°7′W), tributary of lake Catemaco, Municipio de Catemaco, Veracruz, México, Aug 1994, colls. F. Alvarez, M. E. Camacho, J. L. Villalobos, CNCR 13174. Allotype: 1 ♀ cl 8.6 mm, tl 34.3 mm, same locality, date, and collectors as holotype, CNCR 13174. Paratypes: 6 ♂ cl 7.7–10.0 mm, tl 31.5–37.6 mm; 3 ♀ cl 8.5–9.7 mm, tl 33.4–35.3 mm; same locality, date, and collectors as holotype, CNCR 13175. Non-paratypes: 8 ♂ cl 6.4–10.8 mm, tl 26.8–42.2 mm; 12 ♀ cl 6.4–10.8 mm, tl 25.5–40.8 mm, stream 1 km S of Las Margaritas, tributary of lake Catemaco, Municipio de Catemaco, Veracruz, México, Mar 1997, colls. J. C. Molinero, R. Robles, CNCR 17428.

Description.—Small sized shrimp, maximum known size 42.2 mm tl (Fig. 2a). Rostrum reaching beyond distal margin of third segment of antennular peduncle, median rib present along inferior half. Dorsal margin arched, distal third elevated, proxi-

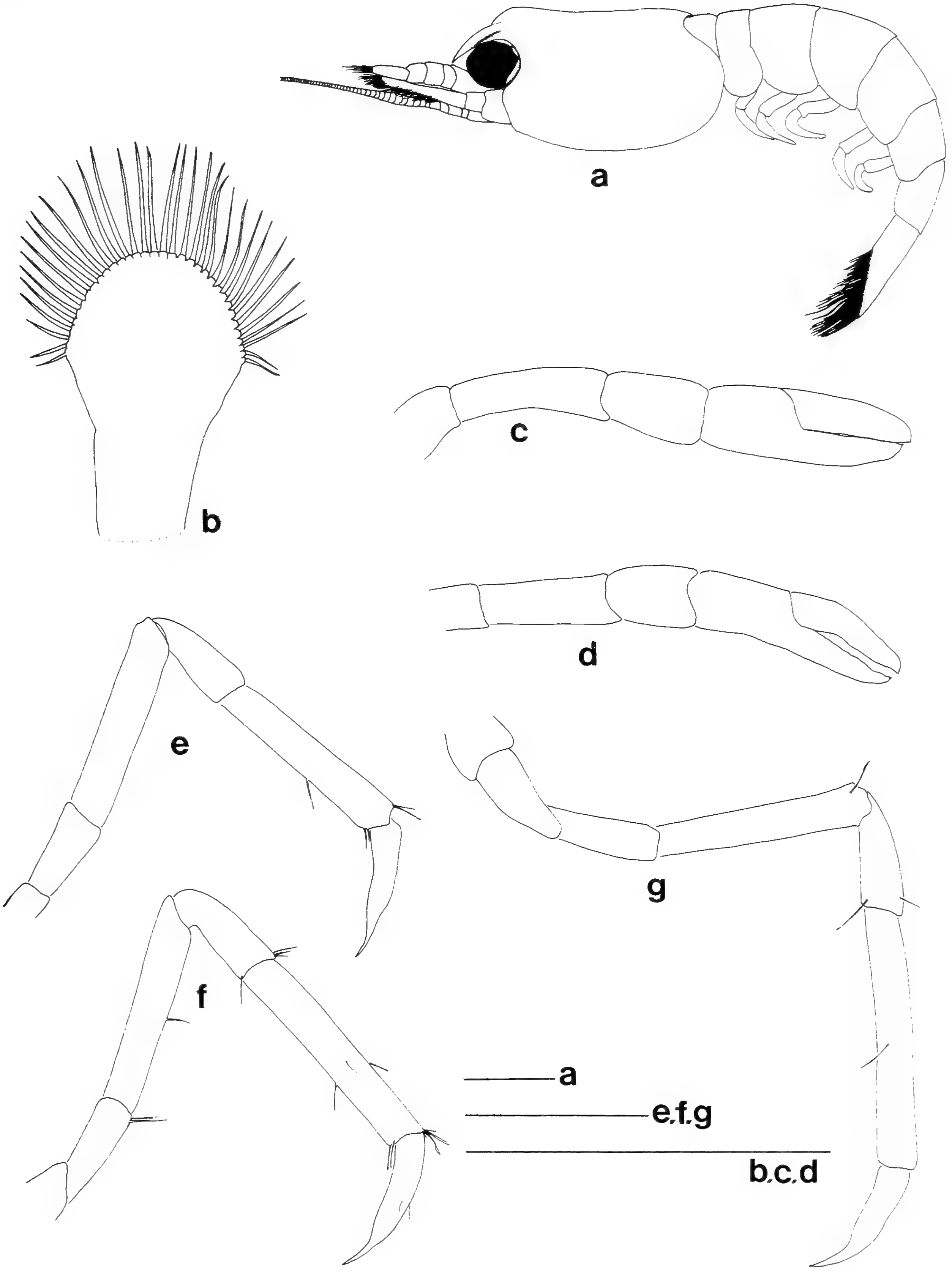

Fig. 1. *Macrobrachium tuxtlaense* new species, first larval stage CNCR 13174b: a, lateral view; b, telson; c, first pereiopod; d, second pereiopod; e, third pereiopod; f, fourth pereiopod; g, fifth pereiopod. Scale bars represent 1 mm.

mal ⅔ oriented downwards; with 9 to 11 short, acute teeth, pointing forward, with setae in between; first 2 teeth located posterior to orbit. Distal ⅔ of ventral margin arched, with 2 teeth, distal one under second and third teeth of dorsal margin and proximal one under third and fourth teeth of dorsal margin.

Carapace smooth, with antennal and hepatic spines. Antennal spine slightly below inferior orbital angle, submarginal; hepatic spine slightly behind and under antennal spine. Inferior orbital angle rounded. Hepatic groove deep, anterior half oriented towards antennal spine.

Abdomen smooth, inferior margin of pleurae of first 3 somites rounded. Posterolateral angle of fourth and fifth somites subacute. Sixth somite 1.7 times as long as fifth; posterior margin with rounded notch flanked by acute angles, and adjacent to articulation of external ramus of uropods.

Telson (Fig. 2e) reaching distal fourth of internal ramus of uropods, narrowing distally; armed with 2 pairs of small, acute dorsal spines on posterior half, first pair at ½ the length of telson, second pair at ¾ the length of telson. Posterior margin subacute, bearing 10–12 thick, plumose setae; distolateral angles armed with 2 articulated spines, internal pair longest reaching beyond tip of telson, external pair ⅓ length of internal pair.

Eyes pigmented, cornea normally developed, globose, wider than ocular peduncle.

Antennules (Fig. 2b) with slender, acute stylocerite, tip reaching beyond half of first peduncular segment. First peduncular segment depressed, concave dorsally to fit eye; lateral margin ending in slender, acute spine; second and third segments subcylindrical.

Antennae with basicerite armed on anterior margin with acute, slender spine. Scaphocerite (Fig. 2c) tapering anteriorly, 2.8 times as long as wide; lateral margin ending distally in short spine, not overreaching distal margin.

Mandibles (Fig. 3a) with 3-segmented palp bearing long setae on tip and articulations; incisor process with 3 conical teeth, molar process with 2 wide, rounded teeth on mesial border.

Maxillules (Fig. 3b) with bilobed palp; distal lobe slender with long, single, subapical seta on anterior margin; proximal lobe rounded, with 1–3 apical setae. Mesial margin of anterior lacinia armed with spiniform teeth, anterior and posterior margins bearing thin setae; posterior lacinia curved with abundant thin setae on distal half.

Maxillae (Fig. 3c) with scaphognathite bordered with plumose setae, anterior lobe narrower and longer than posterior; palp devoid of setae, thick proximally, tapering abruptly on distal half, ending in sharp tip; endite bilobed, divided by deep incision along ¾ of its length, both lobes slender and with terminal tuft of setae.

First maxilliped (Fig. 3d) with 2 endites bearing marginal and submarginal setae, anterior endite twice as long as posterior endite. Exopod slender, 4 times as long as palp, distal third bearing long setae; caridean lobe well formed, fused to base of exopod, bordered with long, plumose setae; palp strong basally, tapering distally; epipodite subtriangular, distal tip rounded.

Second maxilliped (Fig. 3e) subpediform with well developed podobranch; endopodite 4-segmented, distal 2 segments oriented mesially, gnathal border armed with setae and spines; exopodite slender, approximately twice as long as endopodite, tip bearing long, plumose setae.

Third maxilliped (Fig. 3f) pediform, slender, reaching distal margin of second segment of antennular peduncle; with well developed arthrobranch; coxa with rounded, chitinized plate; basis short, bearing articulations with endopodite and exopodite at same level. Endopodite 3-segmented, bearing tufts of setae, becoming denser distally; first segment slender, 1.15 times as long as second segment; third segment shorter than second, ending in rounded tip. Exopodite slender, longer than first segment

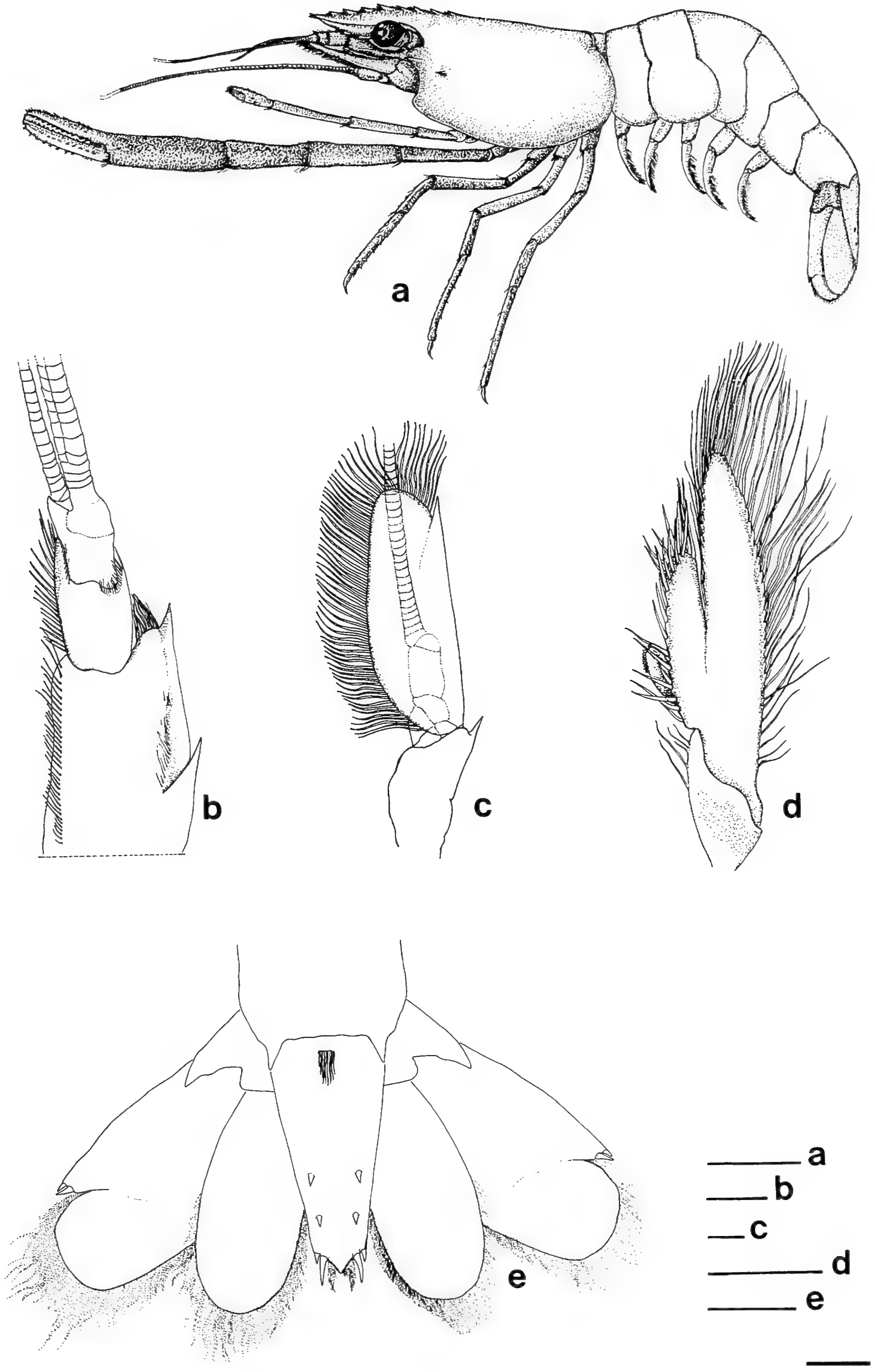

Fig. 2. *Macrobrachium tuxtlaense* new species, male holotype CNCR 13174: a, lateral view; b, distal portion of antennular peduncle; c, distal portion of antennal peduncle; d, appendix masculina on second pleopod; e, telson and uropods, dorsal view. Scales equal 5 mm (a), 1 mm (b–d), and 2 mm (e).

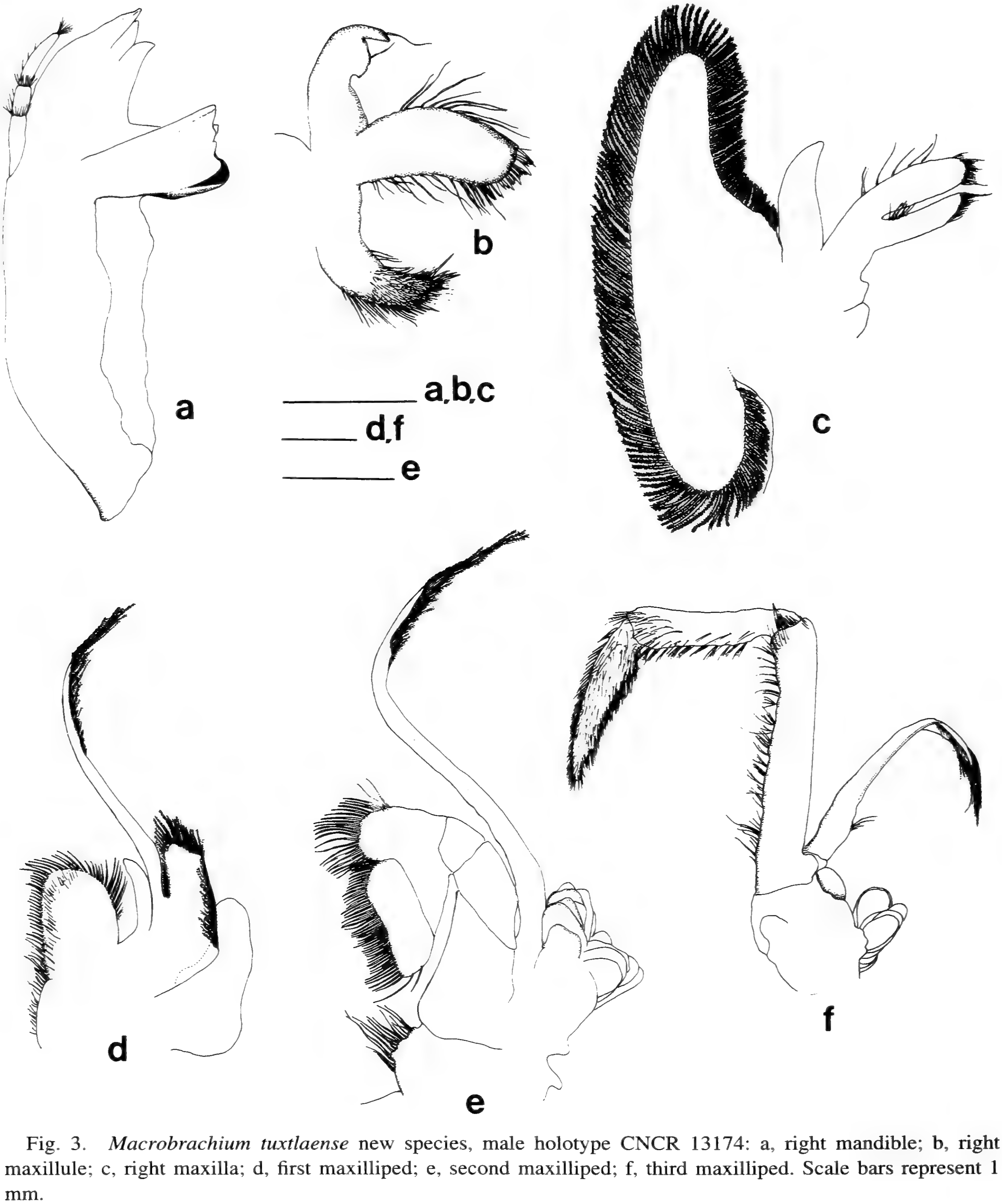

Fig. 3. *Macrobrachium tuxtlaense* new species, male holotype CNCR 13174: a, right mandible; b, right maxillule; c, right maxilla; d, first maxilliped; e, second maxilliped; f, third maxilliped. Scale bars represent 1 mm.

of endopodite, distal third bearing long setae.

First pair of chelipeds slender, shorter than second, distal margin of carpus reaching beyond scaphocerite. Ischium short, 0.65 times as long as merus, 0.57 as long as carpus, subequal in length to chela; ventral margin with tufts of setae on proximal half. Merus shorter than carpus, 1.4 times length of chela, dorsal and ventral margins parallel. Carpus smooth, slender, widening distally, 1.54 times length of chela. Chela wider than distal portion of carpus; palm slightly longer than fingers, with line of setae on proximoventral margin; fingers straight, slightly gaping, with tufts of setae on distal half, tips subacute and corneous, bearing short setae; cutting edge hard, chitinized, devoid of teeth.

Second pair of chelipeds subequal, long, covered with granules and small spines; proximal third of carpus reaching beyond scaphocerite. Ischium moderately compressed, dorsal and ventral margins parallel, of same length as merus and carpus, 0.53 times length of chela. Merus cylindrical, 5 times as long as wide, of same length as carpus, half as long as chela. Carpus becoming slightly wider distally, 3.7 times as long as distal width, 0.52 times length of chela. Chela moderately compressed, dorsal and ventral margins parallel, 6 times as long as high; palm as long as ischium, merus, and carpus, 0.52 times the length of chela, 1.18 times length of movable finger. Fingers slender, covered with scattered setae, tips acute and corneous; cutting margin with conical teeth on proximal half, becoming continuous smooth ridge distally; dactyl with 4 teeth, fixed finger with 5 teeth, distal 2 teeth the largest.

Third to fifth pair of pereiopods slender, increasing in length posteriorly; with scattered short setae, 2 rows of spinules along posterior margin of propodus, tuft of setae on propodus-dactyl articulation, and row of setae along superior border of dactyl; dactyl the shortest segment, ending in sharp tip.

Third pair of pereiopods with distal third of propodus reaching beyond scaphocerite; ischium half length of merus and propodus, subequal in length to carpus, 1.5 times length of dactyl; merus 1.9 times length of carpus, 3.2 times length of dactyl, of same length as propodus; carpus 0.52 times length of propodus, 1.6 times length of dactyl; propodus 3.2 times length of dactyl.

Fourth pair of pereiopods with distal fourth of propodus reaching beyond scaphocerite; ischium half length of merus and propodus, of same length as carpus, 1.6 times length of dactyl; merus 1.63 times length of carpus, 3.4 times length of dactyl, of same length as propodus; carpus 0.6 times length of propodus, twice as long as dactyl; propodus 3.4 times length of dactyl.

Fifth pair of pereiopods with distal margin of propodus reaching beyond scaphocerite; ischium 0.52 times length of merus, 0.75 times length of carpus, 0.41 times length of propodus, 1.57 times length of dactyl; merus 1.47 times length of carpus, 3.1 times length of dactyl, 0.8 times length of propodus; carpus half as long as propodus, twice as long as dactyl; propodus 4 times as long as dactyl.

Pleopods with both rami well developed, except for first pair in both sexes; first pair with reduced endopod, lacking appendix interna. Second pleopod (Fig. 2d) of male with slender appendix masculina, reaching distal third of endopod, mesial border bearing 2 rows of 9 acute setae reaching apex; appendix interna moderately robust, reaching proximal third of appendix masculina.

Uropods (Fig. 2e) with protopodite with external lobe ending in sharp tip. Endopod shorter than exopod, with setae along posterior margin and distal half of lateral margins, posterior margin rounded. Exopod with bare, straight, lateral margin; ending in fixed spine, flanked internally by long, sharp, movable spine; diaeresis incomplete, marked by weak furrow extending through more than half the surface of ramus; internal and posterior margins with setae.

Remarks.—*Macrobrachium tuxtlaense* is probably more closely related to the cave-dwelling *M. acherontium* and *M. villalobosi,* all of which exhibit abbreviated development and are similar morphologically. These three species can be distinguished by the shape of rostrum, length of telson, extent of development of the eyes, and the different proportions of the segments of the first and second pair of pereiopods (Table 1).

Similarly to other species of *Macrobrachium* from the Americas with abbreviated development (e.g., *M. aracamuni* Rodríguez, 1982; *M. cortezi* Rodríguez, 1982; *M. reyesi* Pereira, 1986; *M. pectinatum* Pe-

Table 1.—Comparison of selected characteristics of *Macrobrachium tuxtlaense,* new species, from Los Tuxtlas region, Veracruz, and *M. acherontium* and *M. villalobosi.*

	M. tuxtlaense	*M. acherontium*	*M. villalobosi*
Rostrum	9–11 dorsal teeth/2 ventral teeth, reaching distal margin of scaphocerite	8–11 dorsal teeth/3 ventral teeth, reaching distal margin of scaphocerite	9–11 dorsal teeth/2 ventral teeth, reaching beyond distal margin of scaphocerite
Telson	1.2 times length of 6th abdominal somite	1.2 times length of 6th abdominal somite	1.4 times length of 6th abdominal somite
Eyes	Normally developed	Reduced, globose cornea, narrower than peduncle	Cornea absent
1st pair of pereiopods	Carpus 1.54 times length of chela	Carpus less than twice length of chela	Carpus twice length of chela
2nd pair of pereiopods	Covered with granules and small spines; ischium as long as merus and carpus, 0.53 length of chela	Smooth with scattered setae; ischium 0.93 as long as merus, 0.75 as long as carpus, and 0.63 as long as chela	Smooth with scattered setae; ischium 0.76 as long as merus, 0.5 as long as carpus and chela

reira, 1986; *M. atabapense* Pereira, 1986; *M. dierythrum* Pereira, 1986; *M. rodriguezi* Pereira, 1986; *M. pumilum* Pereira, 1986), *M. tuxtlaense* is a small-sized species with a maximum total length of 42.2 mm. In *M. tuxtlaense,* the egg size (2.8 × 2.5 mm) is the second largest among all *Macrobrachium* species from the Americas, the largest eggs (3.66 × 2.44 mm) being those of *M. ferreirai* Kensley & Walker, 1982 (see Magalhaes & Walker 1988, Pereira & Garcia 1995).

The evolution of abbreviated development in freshwater palaemonid shrimps has been linked to the invasion of nutrient-poor waters where planktotrophic larvae would die in the absence of phyto and zooplankton upon which to feed (Magalhaes & Walker 1988). The distribution pattern of species with abbreviated development coincides with the presence of oligotrophic waters such as small mountain streams or bodies of water inside caves. The three Mexican species of *Macrobrachium* with abbreviated development fit well this pattern, occurring in small streams where species of *Macrobrachium* with planktotrophic larvae do not occur.

Macrobrachium tuxtlaense possibly can be considered an endangered species as it posseses very limited dispersal capabilities and occurs only in two small tributaries of Lake Catemaco, an area that increasingly is being devoted to cattle ranching.

Acknowledgments

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Description of a new spider crab, *Maja gracilipes*, from the South China Sea, with notes on the taxonomic validity of *M. brevispinosis* Dai, 1981 (Crustacea: Decapoda: Brachyura: Majidae)

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Abstract.—A new species of majid crab, *Maja gracilipes,* is described from the South China Sea. It is similar to *M. confragosa* Griffin & Tranter, 1986, described from the Kei Islands, Indonesia, but differs in proportions of the ambulatory legs, structure of the intercalated spine, third maxilliped, male abdomen, and male first pleopod. *Maja brevispinosis* Dai, 1981, is synonymised with *M. compressipes* (Miers, 1879).

Seventeen species of spider crabs of the genus *Maja* Lamarck, 1801, are known, of which 14 occur in the Indo-West Pacific (Griffin & Tranter 1986, Dai 1981). Dai et al. (1986) and Dai & Yang (1991:150) recorded five species from China, *M. japonica* Rathbun, 1932, *M. spinigera* de Haan, 1839, *M. gibba* Alcock, 1895, *M. sakaii* Takeda & Miyake, 1969, and *M. brevispinosis* Dai, 1981. A sixth species also known from China and previously placed in the genus *Leptomithrax, L. compressipes* Miers, 1879, originally described from China, was transferred to *Maja* by Griffin & Tranter (1986).

A new species of *Maja* is here described from the South China Sea. The species is similar to *M. confragosa* Griffin & Tranter, 1986, but can easily be distinguished by the structure of the intercalated spine (between orbital eave and postorbital spine), third maxilliped, ambulatory legs, male abdomen and male first pleopod. The identity of *M. brevispinosis* Dai, 1981, described from southern China, is re-appraised, and the species is here synonymised with *M. compressipes* (Miers, 1879).

The following abbreviations are used: male first pleopod (G1), male second pleopod (G2). The terminology used follows Griffin & Tranter (1986). The leg length is the combined maximum lengths of merus, carpus, propodus and dactylus (measured in a straight line point to point). The type specimen is in the Institute of Oceanology, Chinese Academy of Sciences (IOCAS) in Qingdao, China.

Maja gracilipes, new species
Figs. 1, 2

Material examined.—Holotype, male, carapace width 43.5 mm, carapace length 45.4 mm, rostral length 14.4 mm, IOCAS K33B-34, South China Sea, station 6080, 180 m, on gravel, 21 Apr 1959.

Description of male holotype.—Carapace longitudinally subovate, relatively broad, width subequal to postrostral length; dorsal surface densely covered with numerous granules of various sizes and strength; midline weakly but distinctly elevated, with 6 low spines anteriorly, 2–3 pairs of low, rounded submedian granules posteriorly. Rostrum with 2 long, slender spines, ca. 0.3 times postrostral length; spines gently curving outwards; outer margin with 1–2 small, submedian rounded granules; cleft between base of rostral spines deep.

Orbital eave strongly expanded, anteriorly rounded, posteriorly developed into long, sharp antorbital spine; intercalated spine subtruncate with proximal part much narrower than median part, much shorter than antorbital spine; preorbital spine absent. Eyestalks relatively narrow; cornea large, mostly ventral, ca. half length of entire eye.

Basal antennal segment longitudinally subrectangular; outer lateral spine large, directed obliquely outwards, anterior margin with 3–4 small granules; distal median spine short; anterolateral margin granular but without distinct spine or larger granule; median surface with 2–3 large rounded granules. Suborbital lobe separated from basal antennal segment by distinct fissure. Pterygostomial region relatively smooth; margin with 5 large rounded granules. Epistome smooth, unarmed.

Postorbital tooth reaching slightly but distinctly further anteriorly than antorbital spine, basally broad, partially excavated, narrow and acutely triangular distally, tooth directed anteriorly and obliquely outwards; basal part with several small granules. Hepatic spine much shorter, ca. 0.3 times length of postorbital tooth; base and area posterior to it covered with numerous large rounded granules.

Branchial region with 4 low but distinct spines (or large sharp granules), 3 clearly marginal and 1 submarginal in position; dorsal surface with 1 large, rounded granule which is smaller than marginal ones, adjacent to median cardiac spine. Mesogastric region with 4 low, large, rounded median granules, not spiniform; urogastric region with 1 low, large median granule. Cardiac region with 1 median and 1 anterior low, large, rounded median granules; posterior surface with 2 sharper granules. Anterior surface of intestinal region with 2 large submedian granules; posterior surface with 2 small sharp spines.

Merus of third maxilliped with posteromedian margin raised, not distinctly granulated, anteroexternal angle rounded, subauriculiform; inner posterolateral angle triangular, strongly produced. Ischium with broad, shallow oblique median depression; margins of depression with low rounded granules. Exopod relatively broad, medially with low longitudinal ridge, not distinctly granular.

Chelipeds elongate, subequal, ca. subequal postrostral carapace length. Chelae not swollen, surfaces smooth; fingers 0.7–0.8 times length of palm; cutting edges unarmed, not pigmented. Carpus relatively short, dorsal surface with distinct sulcus; dorsal margin with very low crest, more prominent on proximal part, crest with 2 low sharp teeth. Merus with one very low submedian granule on dorsal margin, otherwise smooth. Basis-ischium smooth, unarmed.

Surfaces of ambulatory legs smooth, first leg ca. subequal in length to postrostral carapace length; second to fourth legs 1.6, 1.5–1.6, 1.4 and 1.1–1.2 times postrostral carapace length respectively. Merus of first leg slender, ca. 7.5 times longer than high; dorsal margin with low, rounded distal tooth, otherwise unarmed, inner surfaces with scattered long stiff setae. Carpus on all legs with median sulcus, inner surface (especially of first leg) with numerous long, stiff setae; propodus laterally flattened, slender. Second to fourth legs with merus ca. 7.5, 7.0, 5.8 times longer than high respectively; dorsal margin of merus smooth, without distinct distal tooth; inner surfaces of merus and carpus with scattered long, stiff setae. Dactylus of all legs gently curved, unarmed, ventral margin with numerous short, stiff setae.

Thoracic sternites 1 and 2 fused, demarcated by granular ridge; sternites 2–4 completely fused, without trace of sutures, surface smooth, lateral margins cristate; surfaces of sternites 5–8 covered with numerous small granules. Telson semicircular; segments 4–6 longitudinally rectangular, lateral margins of each segment gently concave; segment 3 trapezoidal, anterolateral margin gently concave, posterolateral mar-

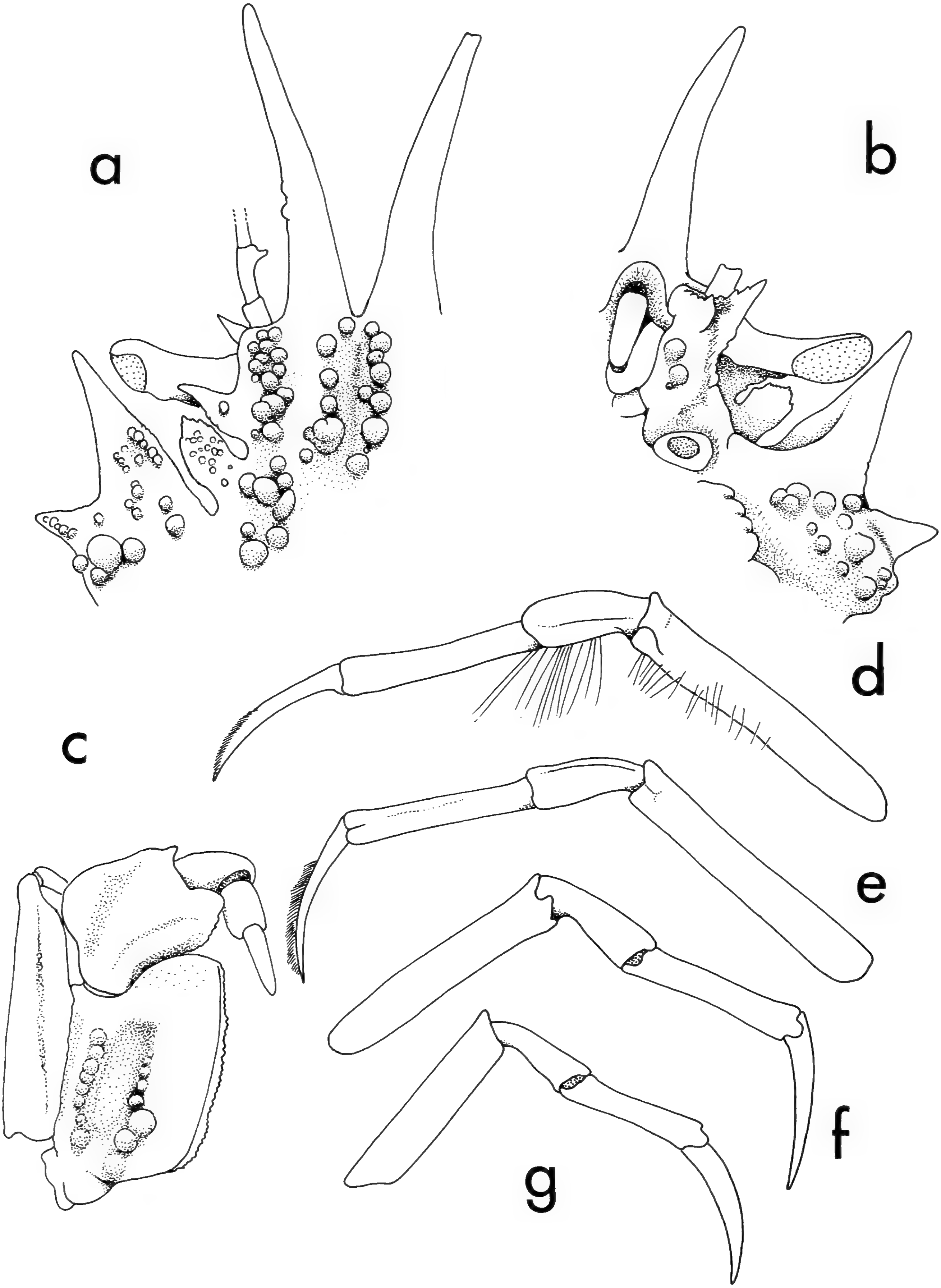

Fig. 1. *Maja gracilipes,* new species. Holotype male, carapace width 43.5 mm, IOCAS K33B-34. a, left frontal part of carapace (dorsal view); b, left frontal part of carapace (ventral view); c, right third maxilliped; d, left first ambulatory leg; e, left second ambulatory leg; f, right third ambulatory leg; g, right fourth ambulatory leg.

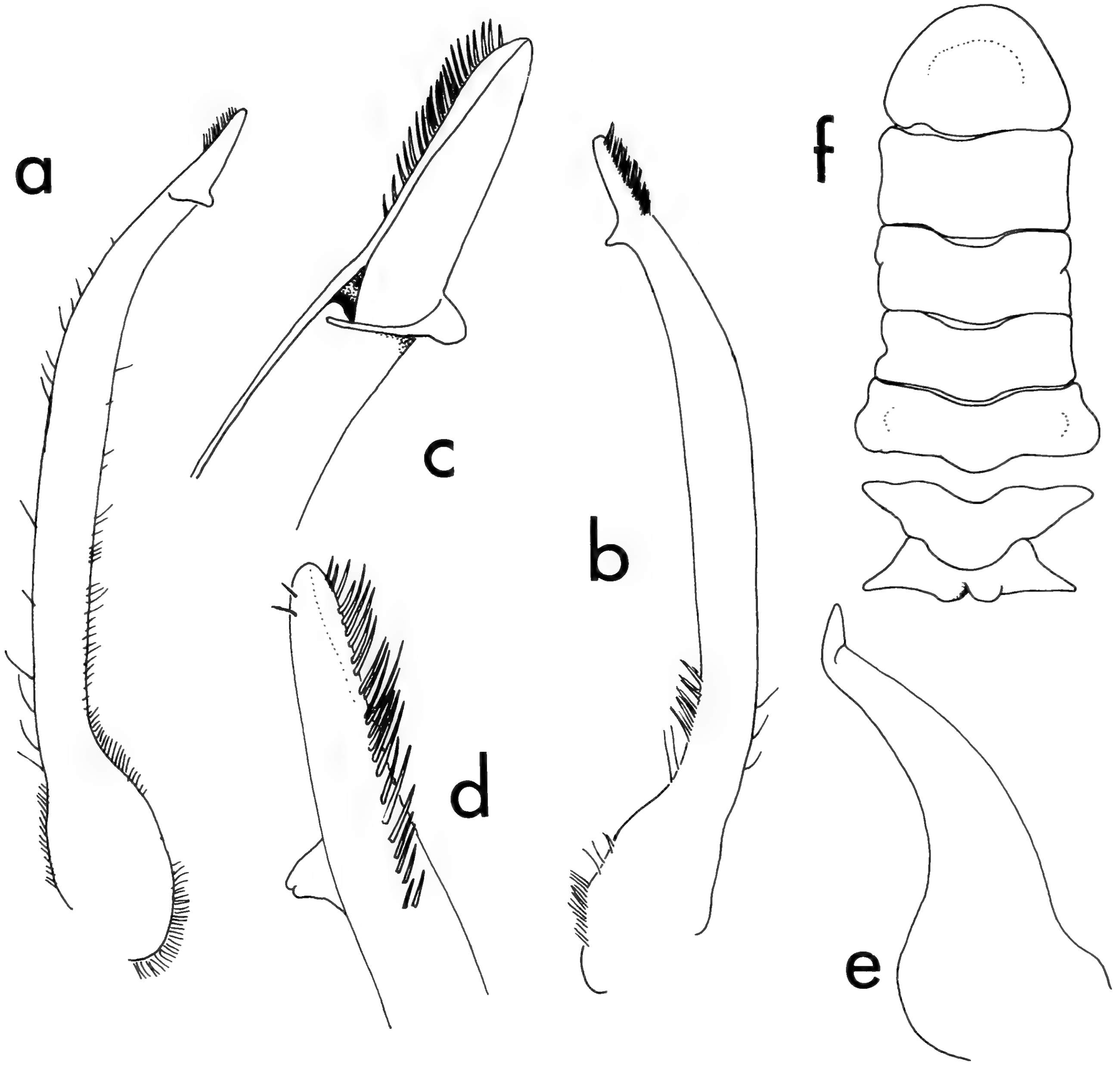

Fig. 2. *Maja gracilipes,* new species. Holotype male, carapace width 43.5 mm, IOCAS K33B-34. a, b, left G1; c, d, distal part of G1; e, left G2; f, abdomen (schematic outline only).

gin rounded; surfaces with scattered granules.

G1 relatively long; basal part dilated; median part almost straight from ventral view but gently curving when viewed in situ; distal part with one perpendicular tooth-like projection, dorsal margin with numerous stiff setae. Male second pleopod very short.

Etymology.—The name is derived from the Latin *gracilis* (for slender) and *pes* (for leg), alluding to the relatively long ambulatory legs of the species. Used as a noun in apposition.

Remarks.—*Maja gracilipes,* new species, is closest to *M. confragosa,* especially with regards to the general carapace morphology, presence of a large spine on the lateral margin of the basal antennal segment, and general structure of the G1 (Griffin & Tranter 1996:210). *Maja gracilipes* can easily be separated from *M. confragosa* by the presence of a subtruncate intercalated tooth with the median part broader than the proximal part (Fig. 1a) (against acutely triangular with the median part distinctly narrower than the proximal part); anteroexternal angle of the third maxilliped ischium is angular (Fig. 1c) (against rounded); proportionately longer ambulatory meri and propodi (Figs. 1d–g); relatively broader male abdomen, notably segment 3 (Fig. 2f); and the distal part of the G1 (beyond the lateral subdistal projection) is proportionately longer (Figs. 2a–d) (cf. Griffin & Tranter 1986: 214, 215, Figs. 72a–c, 73a, pl. 16).

Maja confragosa was originally described by Griffin & Tranter (1986) from only one male (carapace length 39.0 mm) from the Kei Islands in Indonesia, and considering its slender chelipeds, appears to be a subadult specimen. Its G1, however, is fully developed. The male specimen of *M. gracilipes* is somewhat larger (carapace length 45.4 mm) and the chelipeds are already relatively enlarged. The differences observed between the male specimens, especially in the proportions of the legs, cannot be accounted for by size-associated variation.

On another matter, *M. brevispinosis* Dai, 1981, bears a striking resemblance to *M. compressipes* (Miers, 1879) in its carapace features, short ambulatory legs and possession of an ambulatory carpus which is very broad and triangular in shape. Interestingly, *M. compressipes* is known only from the holotype female from Canton (= Guangdong), China, while *M. brevispinosis* was described from two males and a female from the same area. From the descriptions and figures of the holotype female of *M. compressipes* (cf. Griffin & Tranter 1986: 211, pl. 16) and types of *M. brevispinosis* (see Dai 1981:37, figs. 1:6–10; Dai & Yang 1991:151, pl. 18(2), figs. 77(1–4)), we can find no reason to separate the two species. As such, *Maja brevispinosis* Dai, 1981, is here synonymised with *M. compressipes* (Miers, 1879).

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On the identities of two Pacific species of deep-water porter crabs, *Hypsophrys longirostris* Chen, 1986, and *Homologenus donghaiensis* Chen, 1986 (Crustacea: Decapoda: Brachyura: Homolidae)

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Abstract.—The identities of two species of poorly known deep-water homolid crabs, *Hypsophrys longirostris* Chen (presently in the genus *Lamoha*) and *Homologenus donghaiensis* Chen from the East and South China Seas are clarified. The publication validating these taxa is not well circulated, and both names have been missed by most carcinologists. *Hypsophrys futuna* Guinot & Richer de Forges, described from the Wallis and Futuna Islands in the central Pacific, is shown to be a junior synonym of *Lamoha longirostris*.

Chen (1986) published a short abstract in Chinese on the deep-water homolids from the East China Sea in the proceedings of a meeting of the Chinese Crustacean Society. The text of this short abstract listed five species: *Homola orientalis* Henderson, 1888, *Paromola macrochira* Sakai, 1961, *Paromolopsis boasi* Wood-Mason & Alcock, 1891, and two new species, *Hypsophrys longirostris* and *Homologenus donghaiensis*. The two new species were treated separately, with their key characters highlighted, albeit very briefly by Chen (1986). Although no specimens were mentioned or sizes indicated in Chen (1986), her two names are nevertheless valid under the International Code of Zoological Nomenclature (1985). Chen had treated the abstract only as a provisional document in the proceedings of a local meeting and did not regard it as a scientific publication or the names as having any validity. She had originally intended to formally describe both species in a full paper later on, but for various reasons, this was never done. The proceedings of the meeting was not easily available outside China and as such, has been missed by most carcinologists.

Since Chen's (1986) publication, many species of homolids have been described from the Pacific in the important revision by Guinot & Richer de Forges (1995). Unfortunately, Guinot & Richer de Forges (1995) were not aware of Chen's (1986) abstract. In any case, full descriptions and figures of the two species in question were not provided by Chen (1986), and it would not have been possible to ascertain the actual identities of *Hypsophrys longirostris* and *Homologenus donghaiensis* just from her brief text.

The present paper clarifies the outstanding taxonomic problems with Chen's (1986) two taxa, *Hypsophrys longirostris* and *Homologenus donghaiensis*. Both species are redescribed based on Chen's (1986) original material, figures provided and types designated. Measurements indicated are of the carapace length (tip of rostrum of posterior carapace margin) and width (maximum, between tips of lateral-most spines) respectively. The terminology used follows Guinot & Richer de Forges (1995). The abbreviations P1–5 refer to the pereiopods (P1, cheliped; P2–5, first to fourth ambulatory legs respectively). Specimens examined are deposited in the Institute of Oceanology, Chinese Academy of Sciences, Qingdao (IOCAS); Taiwan Museum, Taipei (TMCD); Muséum national d'Histoire naturelle, Paris (MNHN); and Zoological Reference Collection of the Raffles Museum, National University of Singapore (ZRC).

Systematic Account

Family Homolidae

Genus *Lamoha* Ng, 1988a

Type species.—*Hypsophrys superciliosa* Wood-Mason, *in* Wood-Mason & Alcock, 1891.

Remarks.—The better known generic name *Hypsophrys* Wood-Mason & Alcock, 1891, was found by Ng (1998a) to be preoccupied by *Hypsophrys* Agassiz, 1859, a genus of American freshwater fish, and Wood-Mason & Alcock's name was replaced by *Lamoha* Ng, 1998a. Nine species of *Lamoha* are now recognized from the Indo-Pacific and Atlantic (Guinot & Richer de Forges 1995; Ng 1998a, 1998b).

Lamoha longirostris (Chen, 1986)

Figs. 1, 2

Hypsophrus longirostris Chen, 1986:227 (misspelling of *Hypsophrys*).

Hypsophrys futuna Guinot & Richer de Forges, 1995:456, figs. 61l, 66a, g.

Material examined.—Lectotype male (22.7 by 18.2 mm) (IOCAS KY8B-73), East China Sea, 28°45′N, 127°30′E, 900 m, on soft mud, coll. 3 Jan 1981.

Paralectotypes.—1 male (23.5 by 19.0 mm) (ZRC 1999.007), same data as lectotype. 1 male (21.2 by 18.0 mm), 1 ovigerous female (22.0 by 18.5 mm) (IOCAS K69B-30), South China Sea, 19°00′N, 113°30′E, 1100 m, on soft mud, 13 Jul 1959.

Others.—2 males (18.3 by 14.8 mm, 14.6 by 11.7 mm), 1 female (23.7 by 17.6 mm), paratypes of *Hypsophrys futuna* Guinot & Richer de Forges, 1995: MUSORSTOM 7, station CP 623, Wallis and Futuna Islands, 12°5′S, 178°11.5′W, 1300 m, 28 May 1992 (MNHN B-24696). 1 male (24.7 by 19.0 mm) (TMCD), 1 male (26.3 by 20.5 mm) (ZRC 1999.410), Tungsha Islands, South China Sea, 1265 m, 25 Apr 1996, coll. P.-H. Ho.

Description.—Carapace longitudinally subrectangular, regions clearly defined (Fig. 1a). Entire carapace and pereiopod surfaces with scattered stiff, simple setae which do not obscure margins or surface, those on lateral surfaces longer, those on dorsal surface very short. Rostrum well developed, simple, slightly bent downwards, dorso-median part furrowed; lateral margins gently converging to rounded tip (Fig. 1a, b, f, g). Pseudorostral spines absent (Fig. 1a, f). Supraorbital margin sinuous, without spine but with low subdentiform median lobe (Fig. 1a, f). Basal part of eyestalk dilated, outer surface finely granular (Fig. 1a, f). Anterolateral margin with 1 short but distinct, slightly curved lateral spine. Posterolateral margin weakly convex, finely granulated (Fig. 1a). Posterior margin of carapace weakly concave (Fig. 1a). Protogastric and epigastric regions with scattered low granules. Mesogastric and metagastric regions unarmed. Branchial regions covered with scattered coarse granules (Fig. 1a). Antennal spine strong, anteriorly directed. Subhepatic region with 1 large, anteriorly directed inner spine and 1 small, often small outer spine or granule; subventral surface with small, sharp spiniform or very low granule (Fig. 1b, g). Posterior part of pterygostomial region covered with small granules (Fig. 1a, b, g). Gastro-cervical groove deep, contiguous medially, meeting below distinct gastric pits. Branchio-cardiac groove deep. Linea homolica distinct, sinuous (Fig. 1a). Basal antennal article unarmed. Antennular peduncle subglobular, unarmed. Proepistome with low, subtruncate lamelliform tooth, otherwise unarmed (Fig. 1b, g). Merus of third maxilliped unarmed, almost smooth; ischium subrectangular; palp when appressed against ischium reaching to proximal margin of ischium;

exopod slender, reaching to 1/3 length of outer margin of merus, with long flagellum (Fig. 1b).

P1 (chelipeds) subequal, elongate, relatively slender (Fig. 1c). Basis-ischium 3-faceted; inner surface distinctly granular, other surfaces almost smooth; inner ventral margin with 4 distinct spines and 1 small distal spinule; outer ventral margin with 2 spines; dorsal margin with 2 spines (Fig. 1c). Merus with all margins distinctly spiniform; inner surface granular; outer and ventral surfaces almost smooth. Surfaces of carpus spiniform, with 2 large spines on inner distal angle (Fig. 1c). Outer and inner surfaces of palm with numerous spines and spinules; inner surface with 1 distinct longitudinal row of strong spines (Fig. 1c). Fingers elongate, distal part gently curving inwards, anterodorsal margin of dactylus flattened; cutting edge of dactylus with 1 distinct subproximal, obliquely directed tooth which fits anterior to distinct proximal tooth on cutting edge of pollex, rest of cutting edges of both fingers blade-like (Fig. 1c, h). Inner and outer surfaces of base of pollex of both chelae with large ovate pigmented spot each (Fig. 1c, h).

P2 and P3 longest. Coxa of P2–P5 unarmed. Dorso-distal margin of basis-ischium of P2–P5 with 2 small spines bracketing merus. Dorsal margin of M2–4 with 14 or 15 distinct spines, distal 0.14–0.17 of segment usually unarmed; proximal part of ventral margin with 2 rows of spines which converge into 1 uneven row of spines along distal part; anterior surface granular; posterior surface almost smooth. Distal edge of propodus with 2 stiff, movable setae bracketing proximal edge of dactylus. Ventral margin of dactylus with row of stiff but movable setae. P5 very slender; when merus articulated forwards, distal end reaching to base of anterolateral spine; all segments unarmed; hooked dactylus and distal part of propodus forming distinct subchelate structure (Fig. 1d).

Male and female abdomens covering entire thoracic sternum; female abdomen slightly broader than male abdomen (Fig. 1e); surfaces of all segments and telson almost smooth; telson subtriangular, lateral margins sinuous, with distal part weakly concave, and proximal part convex (Fig. 1e, i).

Male first pleopod stout, relatively straight; distal part dilated into distinct flap (Figs. 1j, 2a, b). Male second pleopod stout, short, distally cupped (Fig. 1k).

Remarks.—Lamoha longirostris was described by Chen (1986) as *Hypsophrys longirostris* without designating types or indicating the number of specimens available. The original syntype series consisted of three males and a female. One of the male specimens from the East China Sea is here designated as the lectotype. *Lamoha futuna,* as *Hypsophrys futuna,* was described by Guinot & Richer de Forges (1995) from three males and two females collected from the Wallis and Futuna Islands in the central Pacific.

Although all the known male specimens of *L. futuna* are relatively small, the largest male specimen being the holotype measuring 18.0 by 15.0 mm; and the present male specimens of *L. longirostris* from the East and South China Seas are all much larger than the holotype male of *L. futuna,* we could discern no major differences between the two taxa. As such, we here regard *Lamoha futuna* (Guinot & Richer de Forges, 1995) as a junior subjective synonym of *Lamoha longirostris* (Chen, 1986).

In describing their species, Guinot & Richer de Forges (1995:444) recognized two main groups of *Hypsophrys,* but felt that *H. superciliosa* Wood-Mason & Alcock, 1891, and *H. futuna* (= *L. longirostris*) had intermediate characters which excluded them from either group. *Lamoha superciliosa* and *L. longirostris* are distinguished from all other *Lamoha* species in having the merus of the last ambulatory leg completely unarmed and the rostrum being simple (i.e., not bifurcated at the tip) (Fig. 1a, f). Guinot & Richer de Forges (1995: 458) used three main characters to separate

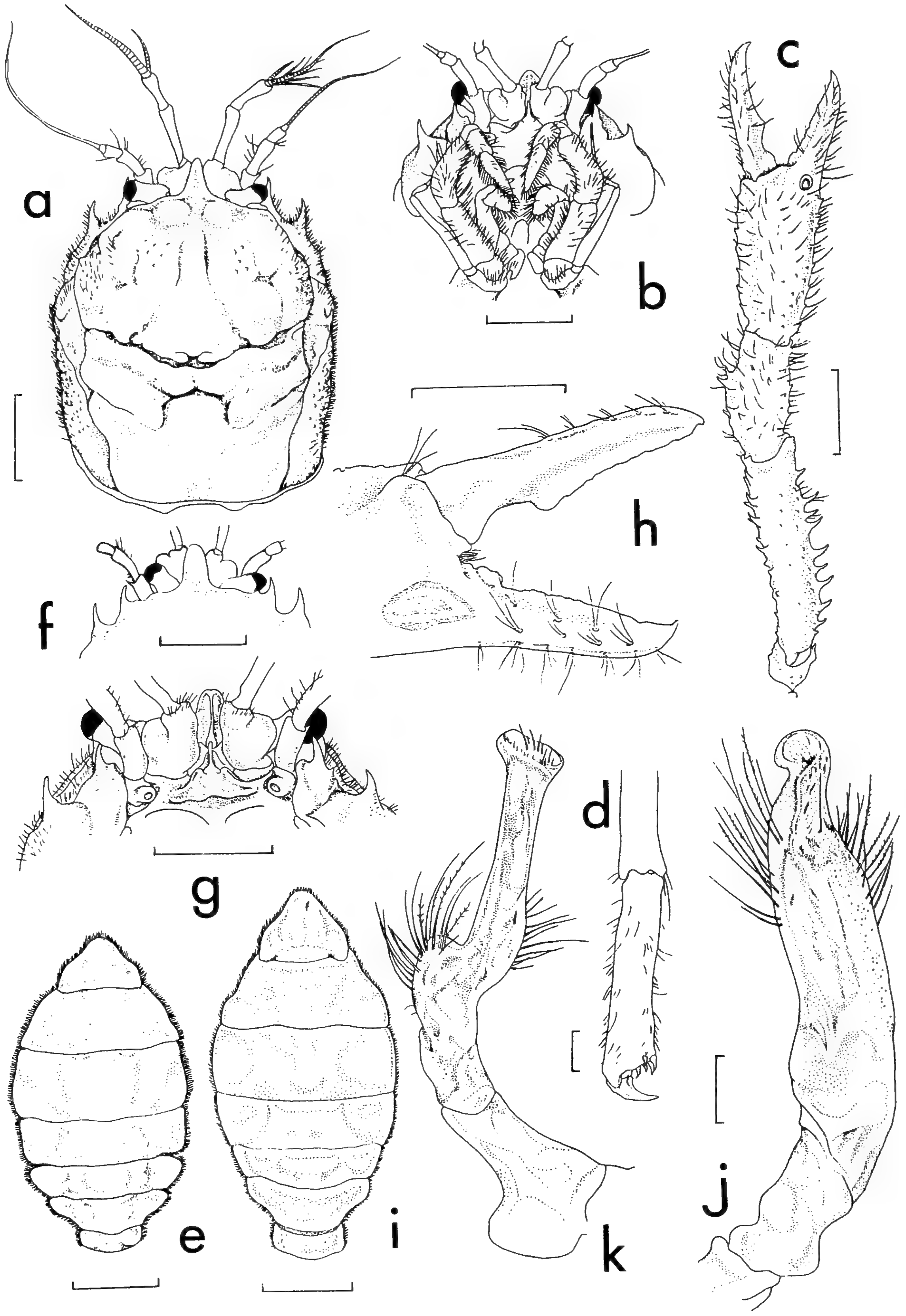

Fig. 1. *Lamoha longirostris* (Chen, 1986). a–e, paralectotype female (22.0 by 18.5 mm) (IOCAS K69B-30); f–k, paralectotype male (21.2 by 18.0 mm) (IOCAS K69B-30). a, carapace (dorsal view); b, buccal cavity showing third maxillipeds; c, right cheliped (outer view); d, subchelate dactylus and propodus of P5; e, abdomen; f, frontal region of carapace; g, epistome, orbit, antennae and antennules; h, distal end of left chela (inner view); i, abdomen; j, left male first pleopod (ventral view); k, left male second pleopod (dorsal view). Scales equal 5.0 mm (a, b, e, g–i), 1.0 mm (c, d, f), 0.5 mm (j, k).

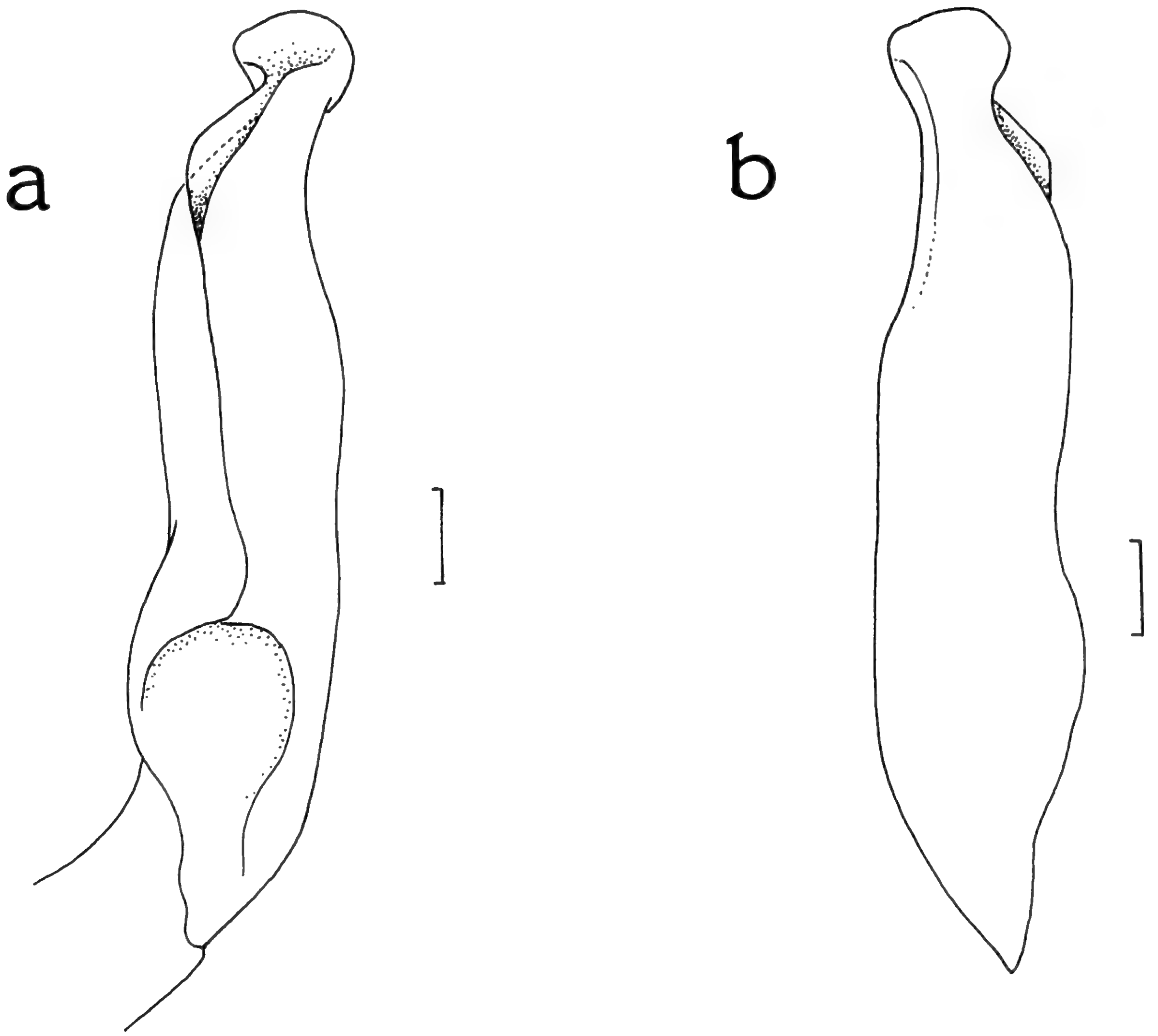

Fig. 2. *Lamoha longirostris* (Chen, 1986). Male (18.3 by 14.8 mm), paratype of *Hypsophrys futuna* Guinot & Richer de Forges, 1995 (MNHN B-24696). Left male first pleopod (setae not drawn). a, ventral view; b, dorsal view. Scales equal 0.5 mm.

L. longirostris from *L. superciliosa:* subhepatic region with one spine (Fig. 1a, b, f, g) (two spines in *L. superciliosa*), protogastric region smooth (Fig. 1a) (with some short spinules in *L. superciliosa*), and absence of a spine on the supraorbital margin (Fig. 1a, f) (present in *L. superciliosa*). These characters are evident on all the specimens examined.

The two pigmented spots at the base of the pollex on the inner and outer surfaces of each chela are large and distinctive (Fig. 1c, h) in *Lamoha longirostris.* In the freshly preserved specimens (in 70% ethanol) from the Tungsha Islands, they are dark blue in the center and bluish along the edges. The spots in the types of *L. longirostris* and Tungsha specimens are much larger than those figured by Guinot & Richer de Forges (1995:fig. 66g) and on the types of *L. futuna* examined, but this is probably associated with size. As noted above, the South and East Chinese Seas specimens specimens are larger than the holotype male of *L. futuna* available to Guinot & Richer de Forges (1995).

The type specimens of *L. longirostris* from the East and South China Seas vary in several features, none of which are regarded as significant. The lateral margins of the rostrum are subparallel in the paralectotype male (ZRC 1999.007) from the East China Sea but gently converging distally in the lectotype male (IOCAS KY8B-73). The pteryogostomial region has a small sharp granule on each side in the lectotype but in a paralectotype male (ZRC 1999.007), the right granule is spiniform while the left one is only granular. The right inner subhepatic spine of a paralectotype male (ZRC 1999.007) is bifurcated distally but all the other subhepatic spines in the other specimens are simple.

The known distribution of *L. longirostris* is disjunct, being known only from the East and South China Seas, as well as over 7500 km to the east in the Wallis and Futuna Islands. There are no other records. This, however, may be due to inadequate sampling, especially considering the depths in which this species occurs. The type specimens of *L. longirostris* were collected by trawls from a depth of about 900–1100 m. Guinot & Richer de Forges (1995:200) obtained their specimens of *H. futuna* (= *Lamoha futuna*) from 1300 m. None of the specimens were recorded carrying any object although members of this genus are known to carry sea anemones (Guinot et al. 1995).

Genus *Homologenus* A. Milne-Edwards, *in* Henderson, 1888

Type species.—*Homolopsis rostratus* A. Milne-Edwards, 1880.

Remarks.—Nine species of *Homologenus* are currently known, of which one occurs in the Indian Ocean and six are present in the Pacific (Guinot & Richer de Forges 1995). *Homologenus donghaiensis* Chen, 1986, is the seventh species known from the Pacific.

Homologenus donghaiensis Chen, 1986
Fig. 3

Homologenus donghaiensis Chen, 1986: 227.

Material examined.—Holotype male (11.0 by 10.3 mm), East China Sea, 900 m, on soft mud, 3 Aug 1981 (IOCAS KY8B-71).

Description of holotype male.—Carapace longitudinally subrectangular, regions well defined (Fig. 3a). Entire dorsal carapace surface with numerous small granules and scattered short, stiff setae which do not obscure surface (Fig. 3a). Rostrum well developed, 3-pronged; accessory spines long, directed obliquely upwards; median projection very long, reaching well beyond accessory spines, directed gently downwards. Pseudorostral spines very strong, directed laterally, reaching well beyond eyes (Fig. 3a). Supraorbital margin sinuous, granulated, inner part with very small slender spine. Basal part of eyestalk not distinctly dilated (Fig. 3a). Anterolateral margin with well developed, obliquely directed long spine; surfaces of spine finely granular. Posterolateral margin gently convex, finely granulated, some granules sharp. Posterior margin of carapace distinctly concave (Fig. 3a). Protogastric and epigastric regions with scattered low granules, those on epigastric region especially sharp. Mesogastric region with distinct, long sharp spine. Branchial regions covered with numerous small granules. Subhepatic region with 1 large, obliquely directed spine; ventral surface with oblique ridge armed with 4 or 5 small spines (Fig. 3a). Antennal spine long, directed obliquely, longer than subhepatic spine. Pterygostomial and sub-branchial regions covered with small granules. Gastrocervical groove shallow but discernible (Fig. 3a). Branchio-cardiac groove very broad, shallow, hardly discernible. Linea homolica sinuous (Fig. 3a). Basal antennal article unarmed; peduncle with opening for gland directed inwards. Antennular peduncle subglobular, with 3 spinules. Proepistome with low, subtruncate lamelliform tooth. Anterior edge of buccal cavity with 2 small spines. Outer surfaces of third maxilliped covered with granules; merus elongate, unarmed; ischium subrectangular, granules on outer margin larger; inner margin of palp with several spinules; exopod slender, reaching to mid-point of outer margin of merus, with long flagellum (Fig. 3f).

P1 (chelipeds) subequal, elongate, slender; surfaces covered with numerous short,

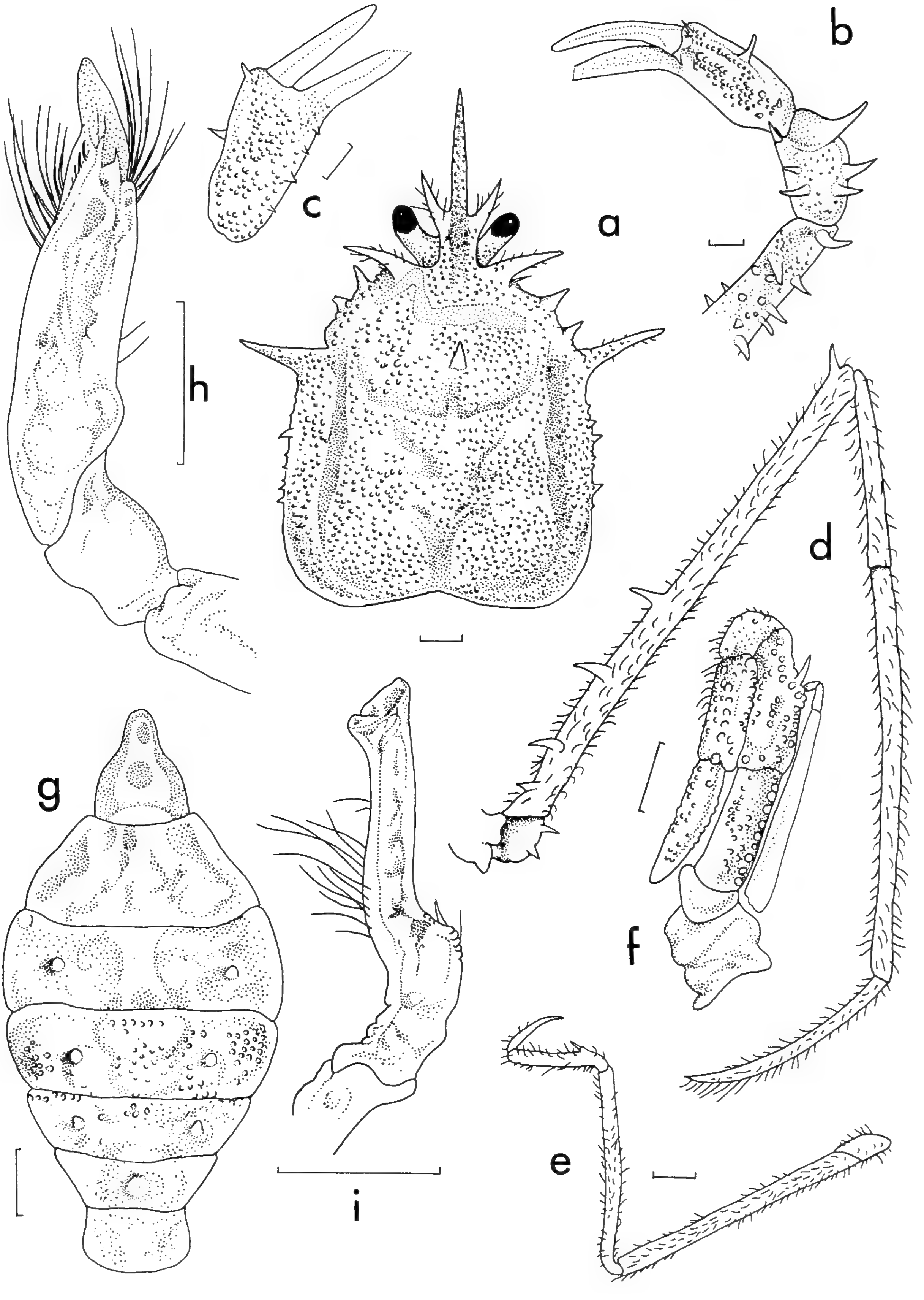

Fig. 3. *Homologenus donghaiensis* Chen, 1986. Holotype male (11.0 by 10.3 mm) (IOCAS KY8B-71). a, carapace (dorsal view); b, right cheliped (outer view); c, right chela (outer view); d, right P2; e, right P5; f, left third maxilliped; g, abdomen; h, left male first pleopod (ventral view); i, left male second pleopod (dorsal view). Scales equal 1.0 mm.

hooked setae which do not obscure margins (Fig. 3b). Coxa with inner distal margin distinctly expanded, armed with 2 small spines. Basis-ischium with 3 spines on ventral surface; 1 spine on dorsal surface. Inner margin of merus with 5 or 6 sharp spines; outer margin with 5 spines; inner surface granular or with scattered spines. Outer surface of carpus with 2 distinct median spines and 1 long subdistal spine; inner surface with 3 evenly spaced spines; ventral surface with 1 distal spine (Fig. 3b). Outer and inner surfaces of palm with numerous granules; with 4 short spines on subventral surface; dorsal margin with 1 small distal spine and 1 longer submedian spine. Fingers elongate, cutting edges of both fingers blade-like (Fig. 3b, c).

Surfaces of P2–P5 covered with numerous short, hooked setae which do not obscure margins (Fig. 3d, e). P2 and P3 longest. Ventral surface of basis-ischium of P2 and P3 with 2 small spines (Fig. 3d). Dorsal margin of merus of P2–4 with 4 strong, posteriorly directed spines along proximal half, distal half mostly unarmed except for small subdistal spine and longer distal spine; proximalmost part of ventral margin with 2 spines with small subdistal spine (Fig. 3d, e). Basis-ischium with small spine. Carpus unarmed (Fig. d, e). P5 slender, when articulated forwards, distal edge of merus reaching to gastric spine; merus and carpus unarmed; propodus with a strong knob on proximoventral margin which is tipped with large, slightly movable seta; curved dactylus and propodus forming subchelate structure (Fig. 3e).

Abdomen covering entire thoracic sternum; surface of segment 1 weakly granular; segment 2 with large, sharp median granule; surfaces of segments 3–4 with large, sharp granule on side of each segment, rest of surface with scattered low granules; segment 5 with 2 groups of submedian granules; surfaces of segment 6 and telson almost smooth; telson subtriangular, lateral margins sinuous, distal part concave and proximal part convex (Fig. 3g).

Male first pleopod stout, distal part conical, gently curved (fig. 3h). Male second pleopod stout, short, distally cupped (Fig. 3i).

Remarks.—Homologenus donghaiensis belongs to a group of species which have a long rostrum, a strong gastric spine and the dorsal margin of the ambulatory merus with a pronounced distal spine (Guinot & Richer de Forges 1995:470). Two species are currently known from this group, *H. malayensis* Ihle, 1912, and *H. levii* Guinot & Richer de Forges, 1995.

With regards to its unarmed ambulatory meri and long P5, *H. donghaiensis* is morphologically most similar to *H. malayensis* from Sulawesi, Ceram, Kei Islands, Philippines and possibly Japan (Ihle 1912, 1913; Guinot & Richer de Forges 1995; Nagai 1994). *Homologenus donghaiensis,* however, differs markedly from *H. malayensis* in having proportionately much longer first to third ambulatory meri (Fig. 3d) (maximum length of P4 merus is ca. 33 times maximum width in *H. donghaiensis*; 22 times in *H. malayensis,* cf. Ihle 1913:pl. 2, figs. 13–15). In addition, the P5 of *H. donghaiensis* (Fig. 3e) is proportionately longer, with the merus, when articulated above the carapace, reaching to the base of the gastric spine (vs. reaching to below the anterolateral spine in *H. malayensis,* cf. Ihle 1913:pl. 2, figs. 13–15); and the distal part of the male first pleopod is relatively stouter (Fig. 3h) (vs. more slender in *H. malayensis,* cf. Ihle 1913:fig. 31). The specimen figured by Nagai (1994:50, pl. 1, fig. 3) from Kii Peninsula in Japan appears to be closer to *H. malayensis* sensu stricto with regards to its relatively shorter legs, although it should be re-examined.

The holotype specimen of *H. donghaiensis* was trawled from some 900 m. The related *H. malayensis* has been recorded from a depth range of 769–1190 m (Guinot & Richer de Forges 1995).

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Neocallichirus raymanningi, a new species of ghost shrimp from the northeastern coast of Venezuela (Crustacea: Decapoda: Callianassidae)

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Abstract.—A new species of ghost shrimp, *Neocallichirus raymanningi*, is described based on specimens collected in subtidal habitats in the Gulf of Cariaco, northeastern Venezuela. This new species is most similar to *N. rathbunae* (Schmitt), but differs from it primarily in having a broadly rounded rostrum, and in the case of males, unique armature of merus and dactylus on the major cheliped. A checklist of all known species in the world currently assigned to the genus *Neocallichirus* Sakai is included.

Recent studies of thalassinideans from the northeastern coast of Venezuela have shown the existence of at least 18 species of these ecologically important infaunal crustaceans commonly called ghost shrimps. Several species had not been recorded previously from this coast or were found to be undescribed (Blanco Rambla & Liñero Arana 1994, Blanco Rambla et al. 1995, Blanco Rambla (unpublished data)). During a recent faunistic survey of the Gulf of Cariaco, specimens were obtained of yet another undescribed species as here described.

The genus *Neocallichirus* Sakai, 1988 was originally proposed for nine Indo-West Pacific and two Atlantic species. Manning & Felder (1991) later assigned to this genus four more western Atlantic species. Subsequently, Manning & Lemaitre (1994) re-assigned four western Atlantic species previously in *Neocallichirus* to the genus *Sergio* Manning & Lemaitre, 1994. With the description of the new species, there are now 18 species recognized worldwide in *Neocallichirus*. In addition to the new species, five other *Neocallichirus* species occur in the western Atlantic: *N. rathbunae* (Schmitt, 1935), *N. grandimana* (Gibbes, 1850), *N. nickellae* Manning, 1993, *N. lemaitrei* Manning 1993, and *N. cacahuate* Felder & Manning 1995. Species of this genus are characterized primarily by: carapace with well defined oval, lacking rostral carina or cardiac protuberance; corneae dorsal, subterminal, disk-shaped; antennular peduncles no longer or stouter than antennal peduncles; third maxillipeds lacking exopod, with ischium-merus subpediform, and merus not projecting beyond articulation with carpus; major cheliped lacking meral hook; in both sexes, first pleopod uniramous, and second pleopod biramous; second pleopod with appendix interna well developed in females, with appendix interna reduced or short and slender in males; and endopod of third to fifth pleopods with stubby, embedded appendix internae (Sakai 1988, Manning & Felder 1991).

Specimens of the new species were captured with yabby pumps at three localities in northeastern Venezuela on the southern and northern coasts of the Gulf of Cariaco (approximately at 10°30′N, 64°00′W). The Gulf has about 170 km of shoreline, and includes diverse habitats.

Measurements (mm) were made with an ocular micrometer. Carapace length (cl) was measured along the middorsal line of the carapace from the anterior margin of rostrum to the posterior margin of the carapace. Total length (tl) was measured from the tip of the rostrum to posterior margin of the telson. Specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and Laboratorio de Carcinología, Instituto Oceanográfico de Venezuela, Universidad de Oriente (IOV).

Family Callianassidae Dana, 1852
Subfamily Callichirinae Manning & Felder, 1991
Neocallichirus Sakai, 1988
Neocallichirus raymanningi, new species
Figs. 1–4

Holotype.—Playa Cristal, south coast of Gulf of Cariaco, Sucre State, Venezuela, 10°27′07,0″N, 63°57′01,7″W, sandy substrate, 0.5 m, 5 Aug 1997, coll. J. P. Blanco Rambla, M. Gómez, & A. De La Rosa: 1 ♂ cl 23.1 mm, tl 76.1 mm, USNM 276147.

Paratypes.—Same locality data as holotype: 1 ♀ (dry, damaged) cl 20.6 mm, tl 69 mm, USNM 276150.—Las Maritas, north coast of Gulf of Cariaco, Sucre State, Venezuela, 10°33′05.2″N, 63°50′45.5″W, subtidal sand-mud substrate, 4 Feb 1997, colls. J. P. Blanco Rambla, M. Gómez, & A. De La Rosa: 1 ♀ cl 23.1 mm, tl 80.1 mm, USNM 276148.—La Peña, south coast of Gulf of Cariaco, Sucre State, Venezuela, 10°28′08.5″N, 63°42′26.4″W, mud-sand substrate, 0.5 m, 26 Jun 1997, coll. J. P. Blanco Rambla, M. Gómez & A. De La Rosa: 1 ♀ cl 21.9 mm, tl 79.0 mm, USNM 276149; 1 ♀ cl 19.1 mm, tl 70.6 mm, IOV 1976.

Diagnosis.—Front of carapace with rostrum broadly rounded, each lateral projection armed with terminal spine slightly exceeding rostrum. Inferior portion of lateral wall of carapace with 3 small sharp or blunt spines: 1 on hepatic boss, and 2 just posterior to hepatic boss. Major cheliped merus armed with row of strong bifid teeth on inferior margin proximally; prehensile margin of dactylus with large proximal subrectangular tooth separated from distal margin by deep quadrate cleft. Male second pleopod with distinct, slender appendix interna bearing short stiff setae terminally.

Description.—Mature male and females of relatively large size, ranging in known specimens from cl 19.1 to 23.1 mm, and tl from 69.0 to 80.1 mm.

Frontal margin of carapace (Fig. 1a, b) consisting of broadly rounded rostrum, and subtriangular lateral projections to each side; rostrum with short marginal setae; lateral projections each with terminal spine slightly exceeding rostrum and reaching to about midline of basal segment of antennal peduncle. Carapace lacking rostral carina, with distinct linea thalassinica; dorsal oval with distinct tubercle on each side of anterior half, oval distinctly marked posteriorly by deep transverse cardiac furrow, latter extending anteroventrally to either side above linea thalassinica as shallow groove marking posterior half of dorsal oval. Frontal margin of carapace continued ventrolaterally beyond intersection with linea thalassinica as thickened oblique ridge ending anteriorly to prominent hepatic boss, latter surmounted with small sharp or blunt tubercle followed posteriorly by 2 small sharp or blunt spines. Subantennular region of epistome bearing dense tuft of long setae.

Eyestalks (Fig. 1a, b) subtriangular, with flattened and moderately pigmented corneae occupying less than half width of stalk. Length of exposed eyestalk in dorsal view about 1.5 times basal width; tips lobate to obtusely angular, reaching distal end of basal segment of antennular peduncle; mesial margins of eyestalks closely appressed proximally, diverging terminally.

Antennular peduncle shorter and heavier than antennal peduncle; terminal article about 1.8 times length of penultimate, reaching to about proximal third of terminal antennal article; penultimate and terminal articles with ventromesial and ventrolateral rows of long setae; rami of flagellum sub-

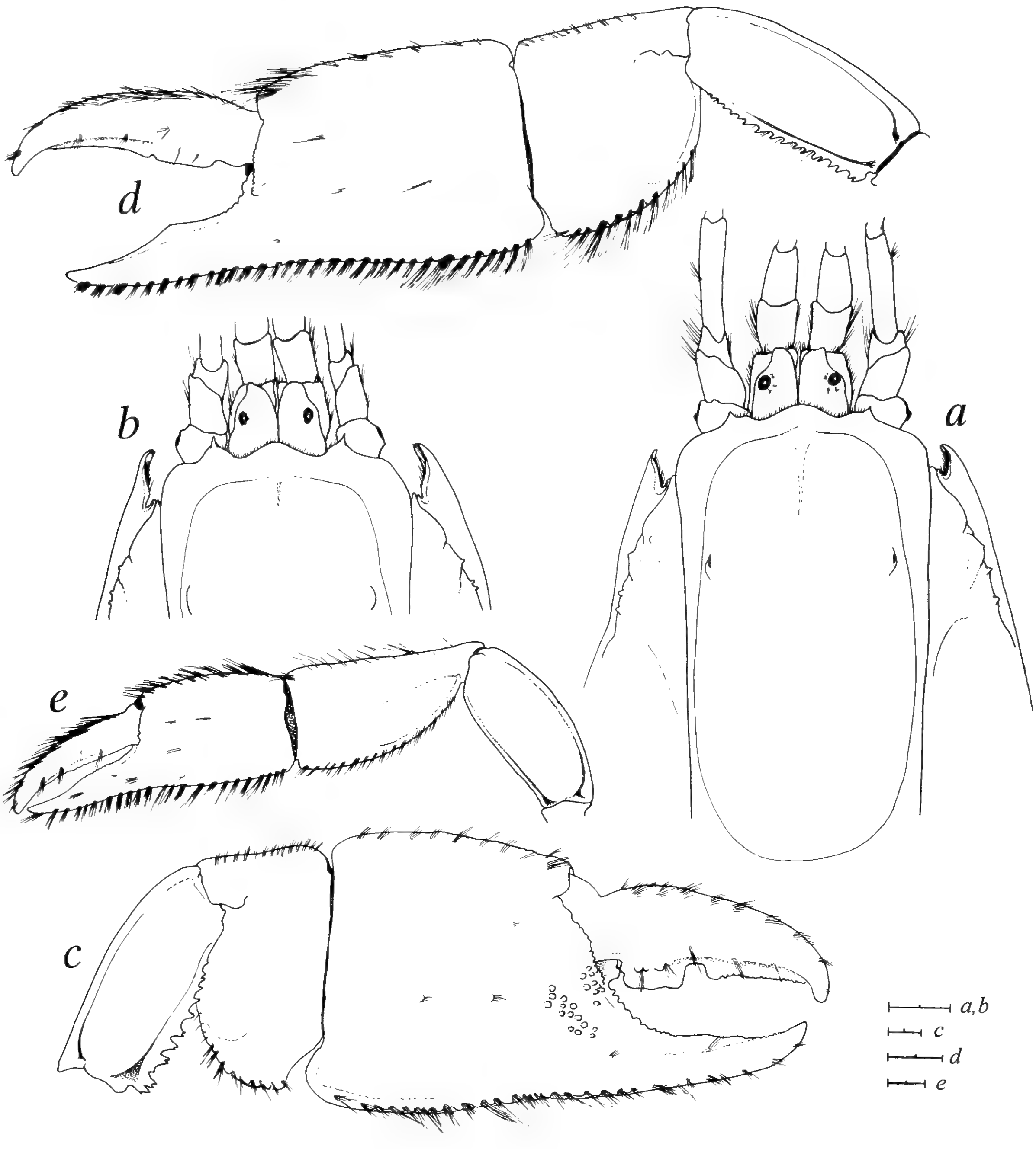

Fig. 1. *Neocallichirus raymanningi,* new species, Gulf of Cariaco, Venezuela. a, c, e, Male holotype (cl 23.1 mm), USNM 276147; b, d, Female paratype (23.1 mm), USNM 276148. a, Anterior carapace, eyestalks and peduncles of cephalic appendages, dorsal view; b, Anterior carapace, eyestalks and portion of peduncles of cephalic appendages, dorsal view; c, Male major cheliped, internal surface; d, Female major cheliped, internal surface; e, Minor cheliped, internal surface. Scales equal 2 mm.

equal in length, dorsal ramus with sparse setae, ventral ramus with dense long setae.

Antennal peduncle with terminal article slightly shorter than penultimate; basal article with slightly produced excretory pore; second article with distinct oblique ventral suture, distolaterally with tuft of setae; third article narrower than second; fourth article longest, slightly narrower than third, and with tuft of long setae distolaterally.

Mandible (Fig. 2a) with large, 3-segmented palp; third article of palp elongated, rounded distally, and with short, weakly hooked setae on extensor surface; second article of palp with long setae distally; first article as long as wide, without setae. Incisor process with cutting margin consisting of well defined blunt corneous teeth on proximal half, and long, low tooth on distal half; internal surface with lip giving rise to molar process with about 5 blunt teeth; paragnath (Fig. 2b) scaliform, with small sclerotized projection on upper distal half, set against and below molar process. First maxilla (Fig. 2c) with endopodal palp long, narrow, and with terminal article deflected proximally at articulation; proximal endite with dense fine setation on most of lower mesial margin, terminal lobe with long, distally bifurcate setae; distal endite elongate, narrow proximally, mesial margin with short bristles often bifurcated distally; exopod obsolete, marked by low truncate lobe with setae. Second maxilla (Fig. 2d) with endopod terminally flexed, rounded distally; proximal and distal endites each longitudinally subdivided and densely setose terminally, setae on second endite consisting of dense bristles; proximal endite with arcuate setose crest across internal surface; exopod forming large, broad, scaphognathite. First maxilliped (Fig. 2e) with proximal endite narrowly produced, marginally setose; distal endite robust, subrectanglar, external surface with median longitudinal row of long setae directed mesially; exopod ovoid, marginally setose, with marked notch on mesial margin, and short arcuate row of setae on external surface; epipod large, posterior lobe broad, anterior end narrowing terminally. Second maxilliped (Fig. 2f) with long, narrow endopod; endopodal merus more than 4 times as long as broad, flexor margin with dense fringe of long setae; carpus short; propodus about half as long as merus, slightly arcuate, widening distally; dactylus elongate, about half as long as propodus, with terminal brush of short stiff setae; exopod narrow, slightly arcuate, overreaching end of endopodal carpus, and fringed with long setae; epipod small. Third maxilliped (Fig. 2g) without exopod; endopod with long setation on mesial margin; terminal 3 articles also with long setation on extensor margins; length of merus-ischium more than 2.5 times its width; ischium subrectangular, distinctly longer than broad, proximomesial margin rounded, internal surface with well defined crista dentata consisting of curved row of sharp spines, distalmost spines closely set, median spines distinctly larger and wide apart; merus subtriangular, broader than long; carpus subtriangular, with setose lobe on flexor margin, internal surface with dense semicircular field of fine setae; propodus subrectangular, height more that 1.3 its length, internal surface with median subcircular field of fine dense setae, anterior margin setose and ending distally as lobe; dactylus narrow, slightly arcuate, longer than propodus, with small brush of stiff bristles; lacking epipod.

Branchial formula includes exopods and epipods as described for first to third maxillipeds. Other branchiae consisting of 1 rudimentary arthrobranch on second maxilliped, pair of arthrobranchs on third maxilliped, and pair of arthrobranchs on each of first to fourth pereopods.

First pereopods forming markedly dissimilar chelipeds. Major cheliped of male (Fig. 1c) heavy, strongly calcified; ischium with row of well spaced sharp or blunt spines on inferior margin; merus about 2.3 times as long as high, superior margin slightly arcuate distally, inferior margin keel-like and armed with row of strong teeth decreasing in size distally, teeth bifid proximally and simple distally; carpus short, about 1.9 times higher than long, superior margin keel-like and with tufts of short setae on inner side, posterior and proximal part of inferior margins crenulate with tufts of setae on inner side, evenly curved and forming blunt angle with distal part of inferior margin; chela about 1.8 times as long as high (greatest height on palm proximally); palm about 1.1 times as high as long (length measured on superior margin), outer surface smooth, glabrous except for scattered tufts of short setae, inner surface with scattered tufts of setae and cluster of low tubercles medially near base of fixed finger, superior margin broadly arcuate and with tufts of setae on inner side, inferior margin keel-like and turned inwards, crenulate and with tufts of long setae

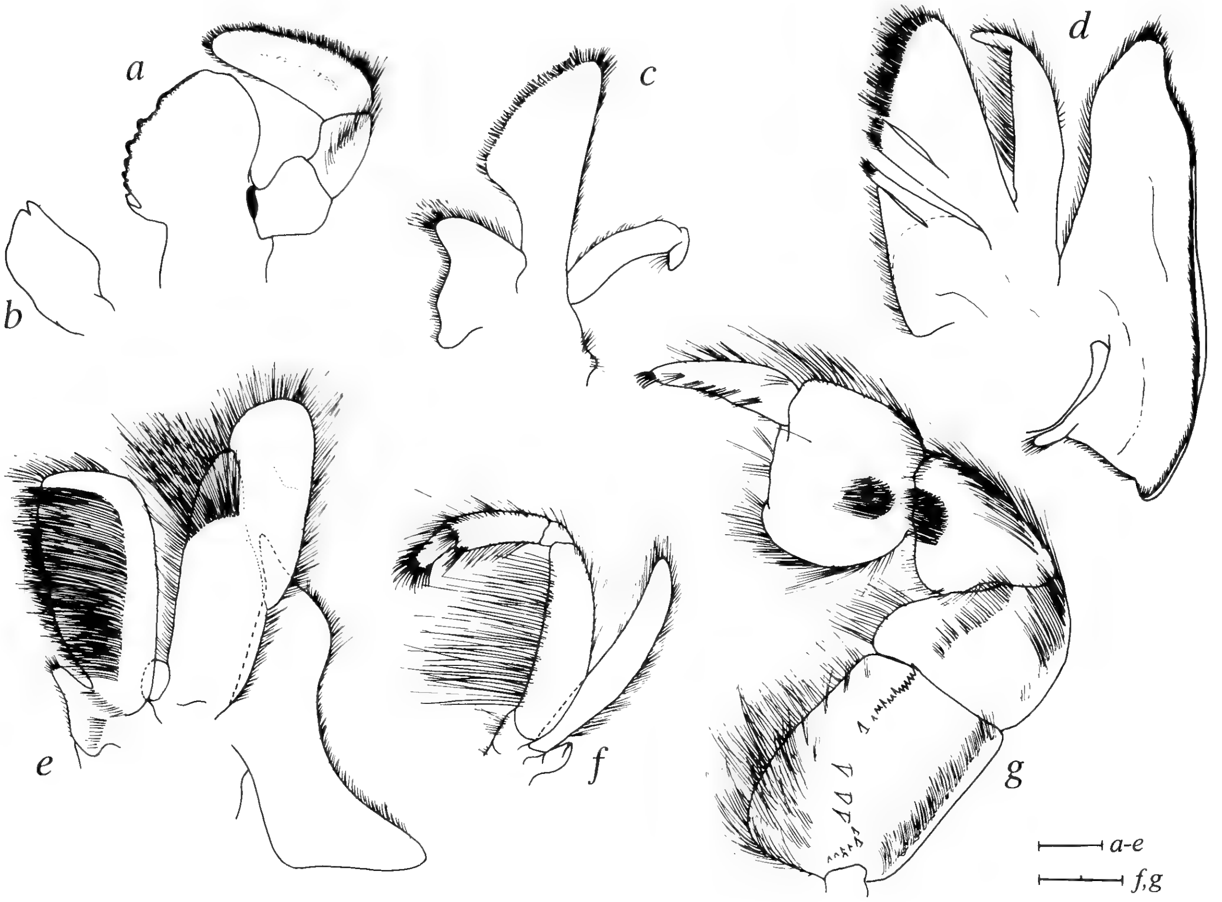

Fig. 2. *Neocallichirus raymanningi,* new species, male holotype (cl 23.1 mm), Gulf of Cariaco, Venezuela, USNM 276147, left mouthparts: a, Mandible, external surface; b, Paragnath, external surface; c, First maxilla, external surface; d, Second maxilla, external surface; e, First maxilliped, external surface; f, Second maxilliped, external surface; g, Third maxilliped, internal surface. Scales equal 1 mm (a–e), and 2 mm (f, g).

on inner side; fixed finger with tip curved upward, inferior margin with tufts of setae on inner side, prehensile margin with small rounded teeth proximally, and small or inconspicuous rounded teeth distally; dactylus slightly longer than palm, outer and inner surfaces with tufts of long setae in proximity to opposable margin, superior margin arcuate and with tufts of setae on inner and outer sides, tip curved downward, prehensile margin with large subrectangular tooth proximally and separated by deep subquadrate cleft from low rounded tooth, followed distally with row of small rounded teeth. Major cheliped of female (Fig. 1d) not as heavy and massive as in male; differing from that of male as follows: merus slightly more slender, about 2.4 times as long as high; teeth on inferior margin of merus simple; carpus about as long as high; chela more slender, about 2.3 times as long as high, palm about 1.2 times as long as high (length measured on superior margin); fixed finger with prehensile margin forming a broadly triangular tooth at midline; opposable margin of dactylus with proximal tooth broader and lower.

Minor cheliped (Fig. 1e) similar between sexes, well calcified much less massive and more slender than in male; outer and inner surfaces of segments glabrous except for scattered tufts of short setae on chela. Ischium with inferior margin unarmed. Merus about 2.3 times as long as high, inferior margin slightly sinuous. Carpus about twice as long as high, slightly longer than merus, superior and inferior margins unarmed, with row of tufts of setae on interior side. Chela about 2.7 times as long as high. Palm about 1.3 times as long as high (length measured on superior margin), superior margin with row of tufts of setae; palm and fixed finger with inferior margin slightly concave at base of fixed finger, with row of tufts of setae. Fixed finger shorter than dactylus, tip curved upward; prehensile margin minutely denticulate. Dactylus slightly longer than palm, tip curved downward; superior margin with tufts of setae; opposable margin minutely denticulate on proximal half.

Second pereopod (Fig. 3a) chelate. Ischium with sparse long setae on inferior margin. Merus with longitudinal row of well-spaced tufts of short setae on outer surface; flexor margin with dense row of long setae over most of margin, setae diminishing in length distally. Carpus with long setae on superior and inferior margins; outer surface with scattered setae in addition to row of tufts of short setae parallel to distal margin; inner surface with well spaced tufts of setae. Chela with fingers straight prehensile and opposable margins of fingers corneous, micropectinate proximally and smooth distally; outer and inner surfaces of palm and fingers with well spaced tufts of setae.

Third pereopod (Fig. 3b) with merus about 2.8 times as long as high. Carpus widening distally, twice as long as high, with patches of long setae terminally. Propodus with inferior margin produced into large lobe directed proximally; outer surface with numerous tufts of short setae except on longitudinal median portion; inner surface with scattered tufts of short setae; superior margin with tufts of long setae; inferior margin with dense tufts of long setae. Dactylus tear-shaped, terminating in corneous tip hooked toward external side; outer surface densely covered with long setae; inner surface with scattered setae.

Fourth pereopod (Fig. 3c) subchelate. Ischium about 2.6 times as long as high. Merus longer and heavier than carpus, about 4 times as long as high. Carpus slender, nearly 6 times as long as high, slightly widening distally. Propodus about 3.5 times as long as high; inferodistal corner produced into short, blunt fixed finger; outer surface densely covered with long microserrate setae except on longitudinal median portion; inner surface with scattered setae. Dactylus about twice as long as high, terminating in short corneous tip hooked toward external side; outer surface densely setose.

Fifth pereopod (Fig. 3d) minutely chelate. Merus and carpus with scattered setae. Propodus with dense patch of dense setae on distal half, upper limit of patch oblique. Fixed finger and dactylus with opposable surfaces spooned; prehensile lip of fixed finger corneous, minutely pectinate. Dactylus curving inward, densely setose on outer surface.

Abdominal somites smooth, glabrous dorsally except for short setae near posterior margin. Third to fifth somites laterally with semicircular tuft of dense short setae laterally. Sixth somite with 3 dorsal pairs of setae or tufts of setae (1 pair anteriorly, 1 pair medially, and 1 pair of longer setae on posterior margin), and short fine marginal setation; with short posterior mid-dorsal sulcus reaching posterior margin.

First pleopod of male and female uniramous, 2-segmented; in male (Fig. 4a), distal segment spatulate, shorter than proximal, subdivided into 2 lobes by weak longitudinal furrow, anterior lobe terminally rounded and setose, posterior lobe terminally acute and setose with tip directed anteriorly; in female (Fig. 4d), both articles narrow and elongate, proximal article curved outward and setose distally, terminal article marginally setose on distal half and with distinct setose shoulder at midlength. Second pleopod of male and female biramous; in male (Fig. 4b), exopod setose distally, slender and curved inward, endopod with distal lobe demarcated by weak transverse suture and longer than poorly demarcated appendix masculina, appendix interna (Fig. 4c) short and slender, with 3 short stiff setae distally; in female (Fig. 4e), exopod with marginal setae distally, endopod with well developed appendix interna (Fig. 4f) about 0.5 as long as distal lobe of endopod and with short hooked setae distally. Third to fifth pairs of pleopods forming large,

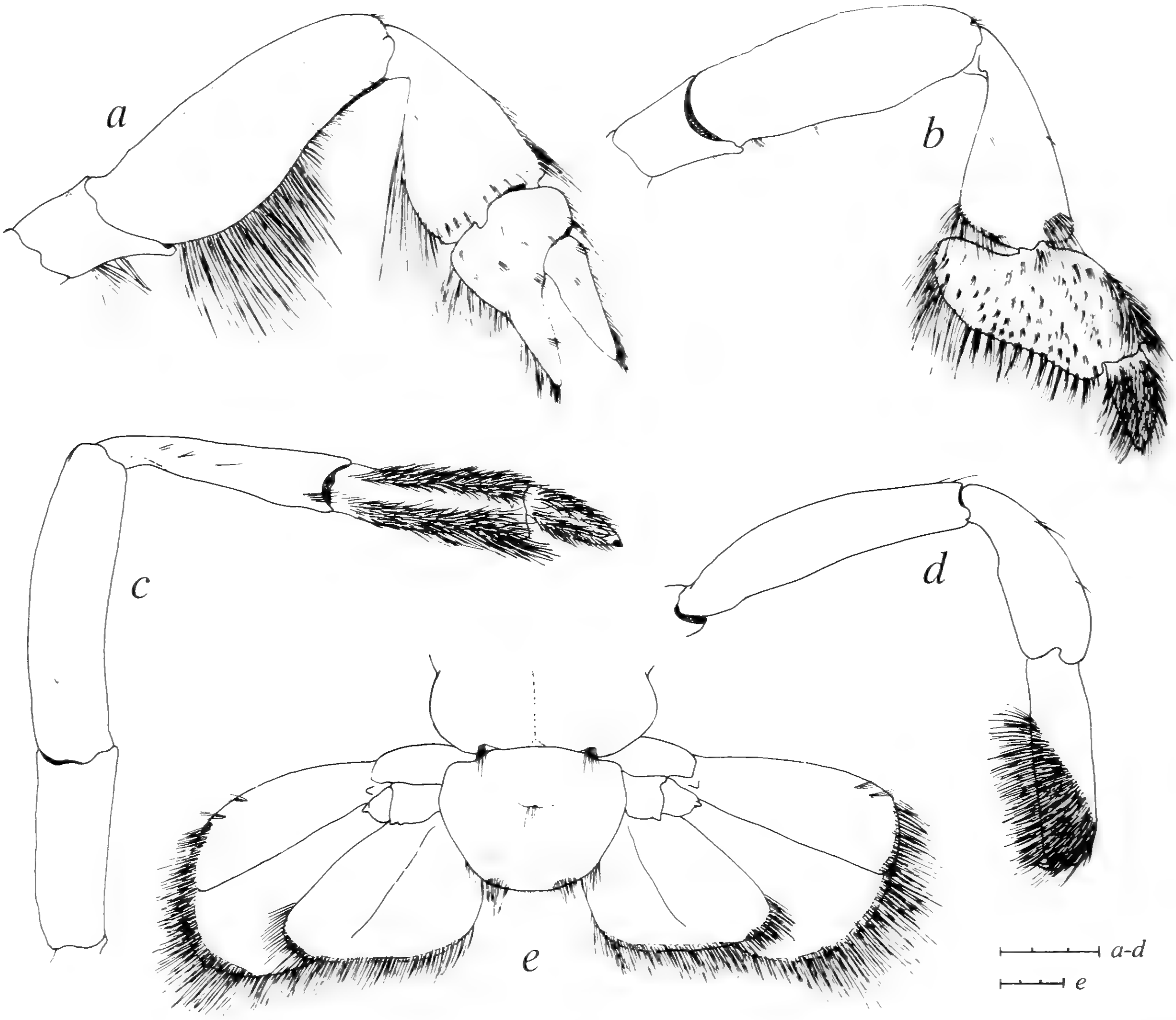

Fig. 3. *Neocallichirus raymanningi,* new species, male holotype (cl 23.1 mm), Gulf of Cariaco, Venezuela, USNM 276147: a, Right second pereopod, external surface; b, Right third pereopod, external surface; c, Right fourth pereopod, external surface; d, Right fifth pereopod, external surface; e, Telson and uropods, dorsal view. Scales equal 3 mm.

posteriorly cupped fans when coupled at mesial margins of endopods; endopod of each (Fig. 4g, h) subtriangular, short, with stubby appendix interna embedded into mesial margin of endopod.

Telson (Fig. 3e) about 1.3 times as broad as long, broadest at lateral lobes on anterior half; posterior margin broadly rounded or weakly sinuous, setose; posterolateral corners rounded, each bearing tuft of long setae; dorsal surface anteromedially elevated and with tuft of setae medially. Uropod with posterolaterally directed rounded lobe of protopod overreaching anterior margin of endopod; endopod broader than long, subrectangular, posterior margin truncate, nearly straight dorsal surface with longitudinal carina and broad tuft of long setae on posterolateral corner; exopod with anterodorsal plate with dense spiniform setae distally, posterior plate marginally with dense, long spiniform setae grading posteriorly into thinner setae.

Known range and habitat.—Known only from the northern and southern shores of the Gulf of Cariaco, Venezuela. The specimens were found in shallow subtidal habitats at about 0.5 m in depth, on sand or sand-mud substrates. Salinity and temperature ranged from 34 to 35 ppt, and 23.6° to 25°C, respectively.

Etymology.—The specific name is given in honor of our colleague and friend, Raymond B. Manning, in recognition of his

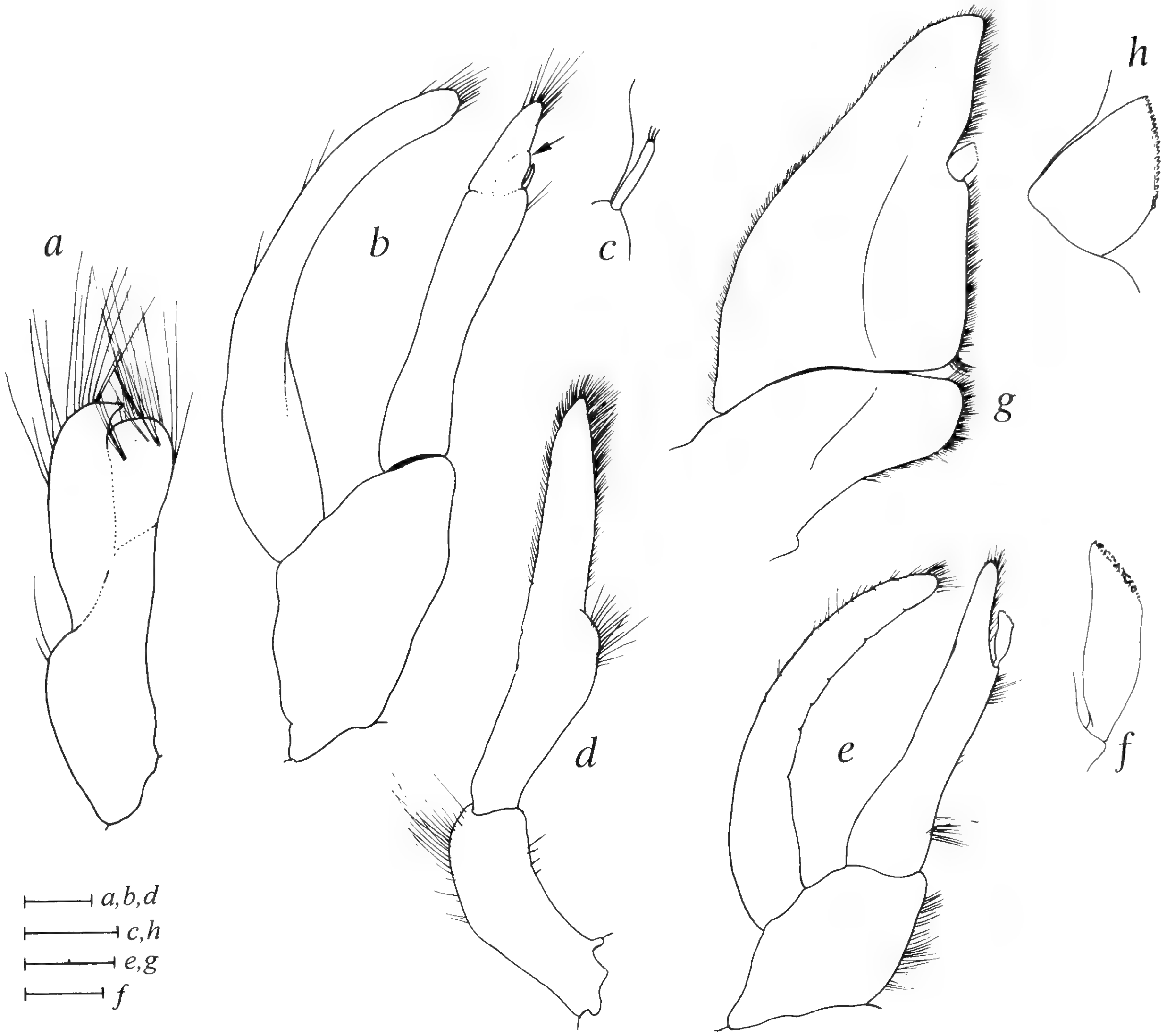

Fig. 4. *Neocallichirus raymanningi,* new species, Gulf of Cariaco, Venezuela. a–c, g, h, Male holotype (cl 23.1 mm), USNM 276147; d–f, Female paratype (23.1 mm), USNM 276148. a, Male left first pleopod, posterior surface; b, Male left second pleopod, posterior surface (arrow indicates appendix masculina); c, Appendix interna of same; d, Female first right pleopod, posterior surface; e, Female second right pleopod, posterior surface; f, Appendix interna of same; g, Third pleopod, posterior surface; h, Appendix interna of same, posterior surface. Scales equal 1 mm (a, b, d, c, h), 2 mm (e, g) and 0.5 mm (f).

contributions to the systematics of the Callianassidae. Over the years he has helped and encouraged us to collect and study these poorly known crustaceans.

Remarks.—Among the western Atlantic species of *Neocallichirus, N. raymanningi,* new species, is most similar to *N. rathbunae* (Schmitt, 1935). The two can be separated easily by differences in the frontal margin of the carapace and, in the case of males, the major cheliped. In the new species the rostrum is broadly rounded and unarmed, whereas in *N. rathbunae* the rostrum is subtriangular and has a terminal spine. The major cheliped of the only known male of the new species has a row of irregular, bifid teeth on the inferior margin of the merus; the prehensile margin of the dactylus has a large proximal subrectangular tooth, which is separated from the distal part of the margin by a deep subquadrate cleft. In contrast, the major cheliped in males of *N. rathbunae* have simple spines on the inferior margin of the merus; the prehensile margin of the dactylus has a large, low subrectangular tooth proximally, which is separated from the rest of the margin by a shallow rounded (U-shaped) cleft.

The second pleopod of the male in *Neocallichirus raymanningi,* new species, and *N. rathbunae,* is distinct from that of other western Atlantic congeners in having a well developed, slender appendix interna with short stiff setae terminally (Fig. 4b). In other western Atlantic congeners the appendix interna is obsolete or at most a vestige is present in the form of a small patch of short microsetae.

The following is a checklist of all *Neocallichirus* species currently known from the world, and their general distribution:

N. cacahuate Felder & Manning, 1995: western Atlantic (Florida, U.S.A.).
N. caechabitator Sakai, 1988: western Pacific (Australia).
N. darwinensis Sakai, 1988: western Pacific (Australia).
N. denticulatus Ngoc-Ho, 1994: western Pacific (Australia).
N. grandimana (Gibbes, 1850): western Atlantic (Bermuda; Caribbean Sea; Brazil), and eastern Pacific (Panama to Ecuador).
N. horneri Sakai, 1988: western Pacific (Australia).
N. indica De Man, 1905: Indo-West Pacific (Mauritius; Java Sea; Japan).
N. lemaitrei Manning, 1993: western Atlantic (Colombia).
N. limosa (Poore, 1975): western Pacific (Australia).
N. manningi Kazmi & Kazmi, 1992: Indian Ocean (Arabian Sea, Pakistan).
N. moluccensis (De Man, 1905): western Pacific (Indonesia).
N. natalensis (Barnard, 1947): western Indian Ocean (Natal, South Africa).
N. nickellae Manning, 1993: western Atlantic (Tobago).
N. pachydactyla (A. Milne-Edwards, 1870): eastern Atlantic (Cape Verde Islands; Senegal; Ghana).
N. rathbunae (Schmitt, 1935): western Atlantic (Florida, U.S.A.; Bahamas; U.S. Virgin Islands; Jamaica).
N. raymanningi, new species: western Atlantic (Venezuela).
N. sassandrensis (Le Loeuff & Intès, 1974): eastern Atlantic (Ivory Coast).
N. taiaro Ngoc-Ho, 1995: South Pacific (French Polynesia).

Acknowledgments

We thank R. B. Manning (USNM), for his helpful advice and valuable suggestions; and A. De La Rosa and M. Gómez (IOV), for their assistance during field work. This study was possible thanks to support provided to one of us (JPBR) through grant CI-5-1803-0767/96-97 from Consejo de Investigación, Universidad de Oriente, Venezuela (CIUDO). Travel to the National Museum of Natural History, Smithsonian Institution, Washington, D.C., was possible thanks to funds provided by CIUDO, and Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICIT), Caracas, Venezuela.

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Cucumaria flamma, a new species of sea cucumber from the central eastern Pacific (Echinodermata: Holothuroidea)

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Abstract.—*Cucumaria flamma,* n. sp. from the central eastern Pacific is of medium size with mouth and anus terminal, directed upward; a conspicuous deep antero-posterior groove in the dorsal skin extending from near base of tentacles to anus. Ventral skin ossicles are knobbed buttons and smooth perforated plates, dorsal skin ossicles are smooth perforated plates and smooth buttons. Distributed from Mazatlán, Sinaloa, México to Isla de la Plata, Ecuador from 4 to 12 m on rocky substrata.

Resumen.—*Cucumaria flamma,* n. sp. del Pacífico este central, es una especie de talla mediana, con boca y ano en posición terminal, dirigidos hacia arriba, con un surco antero-posterior en la superficie dorsal, que se extiende desde cerca de la base de los tentáculos hasta el ano. Los osículos de la pared ventral del cuerpo son botones abollonados y placas lisas perforadas, los de la pared dorsal son placas lisas perforadas y botones lisos. Distribuido desde Mazatlán, Sinaloa, México hasta Isla de la Plata, Ecuador, de los 4 a los 12 m de profundidad, sobre substratos rocosos.

Of the two hundred and forty seven species currently named in the family Cucumariidae, the genus *Cucumaria* (Subfamily Cucumariinae), embraces one hundred and sixty four. As far as we know, three of these species occur in the central eastern Pacific: *Cucumaria crax* Deichmann, 1941, *C. pseudocurata* Deichmann, 1938 and *C. salma* Yingst, 1972. Lambert (1998a) removed *C. curata* Cowles, 1907 from the genus based on morphology and DNA evidence. The systematic status of certain groups within the family remains somewhat confused, but the works of Panning (1949–1971), Pawson & Fell (1965), Pawson (1970, 1982) and Lambert (1998a, 1998b) are steadily eliminating the confusion. The purpose of this paper is to describe a new species of *Cucumaria* from the eastern Pacific coast.

Material and Methods

Live specimens were relaxed with chloral hydrate and fixed with 70% ethyl alcohol. Ossicles were extracted from pieces of skin (4 mm square) from mid-dorsal and mid-ventral body wall, tentacles and introvert. The skin was dissolved with fresh household bleach in centrifuge tubes. After centrifugation at 2750 rpm for 10 minutes, bleach was pipetted off and the ossicles were flooded and centrifuged three times with ethyl alcohol. After drying, the ossicles were observed by scanning electron microscopy.

Results

Order Dendrochirotida Grube, 1840
Family Cucumariidae Ludwig, 1894

Diagnosis.—Body wall essentially soft, ossicles small and inconspicuous. Calcareous ring simple, lacking posterior processes. Usually 10–20 tentacles are present; tube feet most commonly restricted to the radii, where they may be scattered or arranged in regular rows. In several species some feet may also be scattered in dorsal interradii (after Pawson 1982).

Remarks.—The family was emended by Pawson & Fell (1965).

Subfamily Cucumariinae Panning, 1949

Diagnosis.—Ten tentacles. Calcareous ring simple, low, without forked tails, or at most medium high, with short undivided forked-tails, the radials and inter radials undivided. In the skin, only plates, no cups, no tables, no table-like constructions (after Panning 1949).

Genus *Cucumaria* de Blainville, 1834

Diagnosis.—Ten tentacles, of equal size, or the ventral ones smaller. Feet large, soft, in 5 bands, in some forms also scattered in the interradii, particularly dorsally. Calcareous ring low, simple. Ossicles plates or buttons, knobbed or smooth, often reduced. Feet with simple end plates or none at all; walls of feet supported by rods, often 3 armed, or plates. Introvert and tentacles with perforated plates and rods. Ossicles show tendency to become reduced in many forms (after Deichmann 1941). Type species: *Cucumaria frondosa* Gunnerus, 1770.

Remarks.—The diagnosis embraces only the members of the genus *Cucumaria* sensu stricto. The genus contains about 165 described and attributed species, of which about 43 are currently recognized. The genus was emended by Panning (1949).

Cucumaria flamma, new species
Figs. 1–5

Pattalus mollis Nepote, 1998: 50–52, fig. 16. Non: *Pattalus mollis* Selenka, 1868.

Diagnosis.—Body curved, mouth and anus terminal, directed upward. Medium size form, reaching a length of approximately 150 mm; skin soft, smooth; feet soft, large, retractile, particularly abundant in ventral region, not arranged in bands, also present in interambulacra. A conspicuous antero-posterior deep groove in dorsal skin extends from near base of tentacles to anus. Ten large dendritic tentacles with broad base, soft, richly branched, bushy; often deep orange, speckled with black. Calcareous ring simple, low and stout with short anterior projections, lacking posterior processes. Radial and interradial pieces almost same size. Ventral skin ossicles four to six-holed knobbed buttons (110–150 μm) and less abundant smooth perforated plates (200 μm). Dorsal skin ossicles smooth perforated plates and smooth buttons with two central holes bigger than rest. Introvert with star-shaped (~340 μm) or elongated perforated plates (200 μm). Tentacle ossicles in two forms: abundant large, perforated, robust rods, tree-branched, curved or elongated, and scarce oval perforated plates, with scalloped margins.

Material examined.—Thirty specimens from 9 localities on the Mexican Pacific Coast: four in Sinaloa, one in Nayarit, one in Colima and three in Guerrero, and two localities in Central America: one in Panama and one in Ecuador (Fig. 5). Number of specimens in parentheses after the catalogue number; depth in meters (m). The abbreviations used in this paper are: United States National Museum (USNM), California Academy of Sciences (CASIZ), Royal British Columbia Museum (RBCM), Natural History Museum of Los Angeles County (LACM), Instituto de Ciencias del Mar y Limnología, Colección Nacional de Equinodermos, Universidad Nacional Autónoma de México (ICML-UNAM).

Holotype.—USNM E48072 (1), collected by F. A. Solís-Marín & R. Ramírez-Murillo, 18 Jun 1993, length 142 mm (measured along the outside of the curved body), female.

Type locality.—Mexican Pacific coast, La Pedregosa Beach, Zihuatanejo, Guerre-

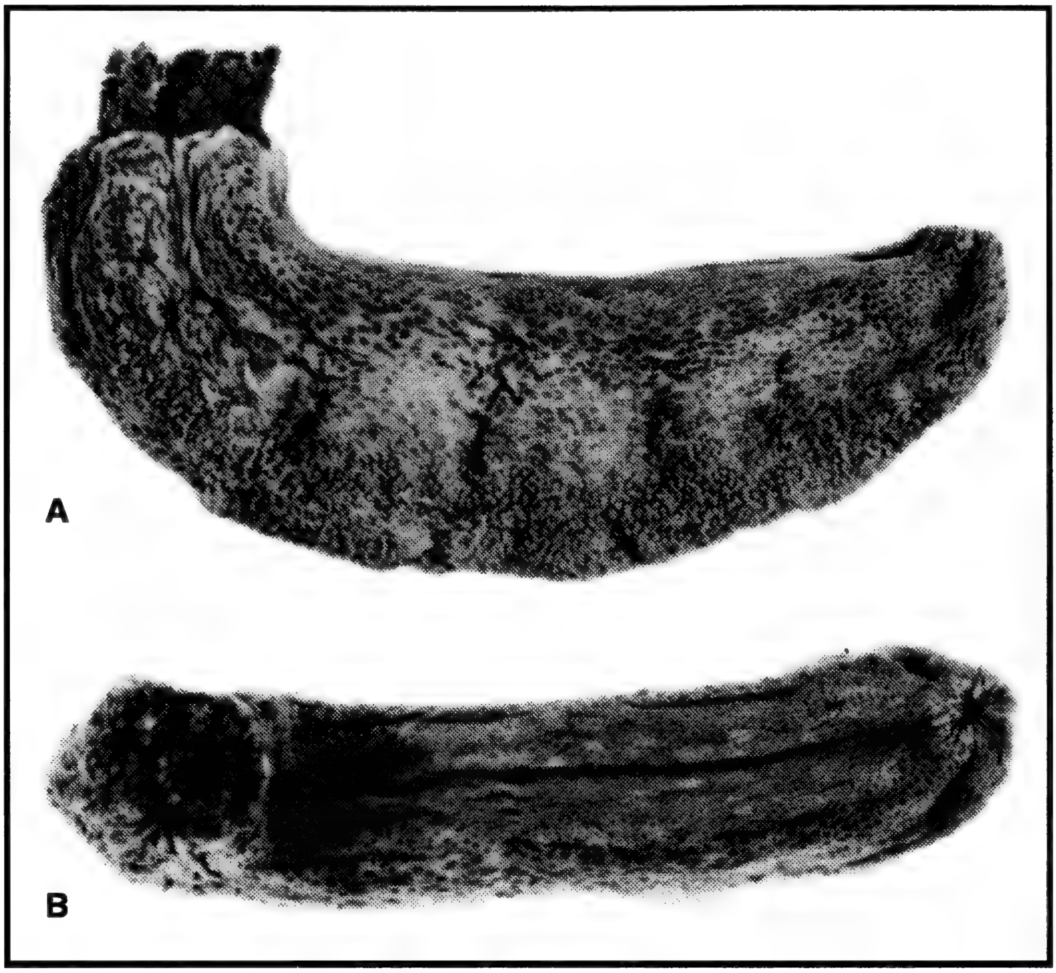

Fig. 1. Paratype of *Cucumaria flamma* collected by scuba from 6 m, Playa La Pedregosa, Zihuatanejo, Guerrero, Mexico, (17°37′06″N, 101°31′52″W), length 140 mm, ICML-UNAM 5.8.0. Female. 1A, left lateral view. 1B, dorsal view. Note conspicuous dorsal groove.

ro, Mexico, (17°37′06″N, 101°31′52″W), 6 m, rocky substrate.

Paratypes.—USNM E48073 (1), collected by F. A. Solís-Marín & R. Ramírez-Murillo, 18 Jun 1993, La Pedregosa Beach, Zihuatanejo, Guerrero, Mexico, (17°37′06″N, 101°31′52″W), 6 m, rocky substrate, specimen length 141 mm. ICML-UNAM 5.8.0 (2), collected by F. A. Solís-Marín & R. Ramírez-Murillo, 18 Jun 1993, Playa La Pedregosa, Zihuatanejo, Guerrero, Mexico, (17°37′06″N, 101°31′52″W), 6 m, rocky substrate, specimens length from 130 to 151 mm. ICML-UNAM 5.8.1 (1), collected by Elaine M., Playa La Peruana, Morro Púlpito, Colima, Mexico, 6 m, 10 Jan 1995, length 62 mm. ICML-UNAM 5.8.2 (1), Collected by J. M. Salcedo, 22 Nov 1981, Morro del Tigre, Bahía de Zihuatanejo, Guerrero, Mexico, (17°38′04″N, 101°33′07″W), 5 m, rocky substrate, specimen length 90 mm. ICML-UNAM 5.8.3 (6), Collected by Facultad de Ciencias, UNAM, 5 Sep 1965, Playa Las Gatas, Zihuatanejo, Guerrero, Mexico, (17°38′10″N, 101°33′0″W), 4 m, rocky substrate, specimens length from 55 to 132 mm. ICML-UNAM 5.8.4 (1), Collected by Caso, M. E., 17 Jun 1980, Isla Cardones, Bahía de Mazatlán, Sinaloa, Mexico, (23°11′09″N, 106°24′24″W), 8 m, rocky substrate, specimen length 85 mm. ICML-UNAM 5.8.5 (2), Collected by O. López, 19 Mar 1992, Isla Venados, Bahía de Mazatlán, Sinaloa, Mexico, (23°15′39″N, 106°28′38″W), 12 m, rocky substrate, specimens length from 99 to 130 mm. ICML-UNAM 5.8.6 (3), Collected by O. López, 22 Mar 1992, Off Isla Cardones, Bahía de

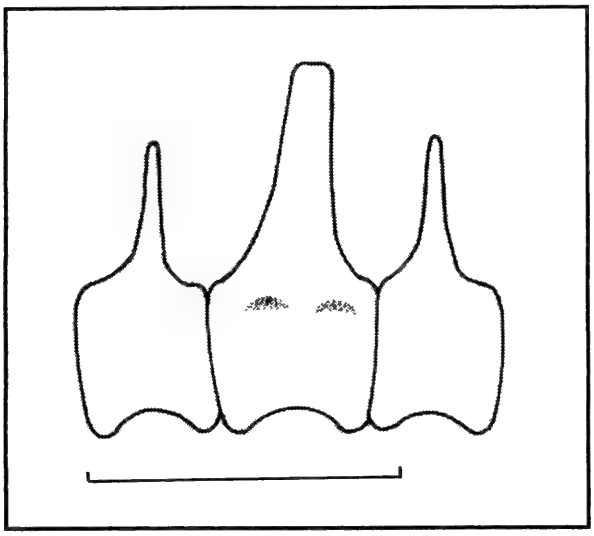

Fig. 2. Calcareous ring of *Cucumaria flamma*; scale bar 6 mm. From paratype (USNM E48073), one radial and two interradials pieces.

Mazatlán, Sinaloa, Mexico, (23°11′04″N, 106°24′23″W), 10 m, rocky substrate, specimens length from 80 to 125 mm. ICML-UNAM 5.8.7 (1), Collected by O. López, 25 Jan 1992, Isla Chivos, Bahía de Mazatlán, Sinaloa, Mexico, (23°13′46″N, 106°27′53″W), 8 m, rocky substrate, specimen length 85 mm. ICML-UNAM 5.8.8 (1), Collected by M. E. Caso, 25 Jan 1983, Isla Cardones, Bahía de Mazatlán, Sinaloa, Mexico, (23°11′03″N, 106°24′10″W), 8 m, rocky substrate, specimen length 102 mm. ICML-UNAM 5.8.9 (1), Collected by M. E. Caso, 24 Jan 1983, Isla Pájaros, Bahía de Mazatlán, Sinaloa, Mexico, (23°15′00″N, 106°28′52″W), 10 m, rocky substrate, specimen length 90 mm. ICML-UNAM 5.8.10 (2), Collected by M. E. Caso, 20 Jan 1983, Isla Venados, Bahía de Mazatlán, Sinaloa, Mexico, (23°15′39″N, 106°28′38″W), 4 m, rocky substrate, one specimen length 72 mm, the other specimen was partially destroyed. ICML-UNAM 5.8.11 (1), Collected by A. C., Nepote, 20 May 1996, Islas Marietas (Isla Larga), Bahía de Banderas, Nayarit, Mexico (20°41′98″N, 105°34′72″W), 4 m, rocky substrate, specimen length 120 mm. ICML-UNAM 5.8.12 (1), Collected by F. A. Solís-Marín, 21 Mar 1996, Islas Marietas (Isla Redonda), Bahía de Banderas, Nayarit, Mexico (20°42′04″N, 105°33′53″W), 10 m, rocky substrate, specimen length 132 mm. USNM E47607 (1), Collected by Emlet, R., 14 Nov 1983, North Pacific Ocean, Panama, Taboguilla Island, depth unknown, subtidal rock holes, specimen length 139 mm. USNM E47750 (1), Collected by F. Rivera, May 1998, Isla de La Plata, Ecuador, (1°16′N, 81°06′W), 5 m, rocky substrate and coral debris, specimen length 104 mm (female). CASIZ 102949 (1), Collected by O. López, 22 Mar 1982, Off Isla Cardones, Bahía de Mazatlán, Sinaloa, Mexico, (23°11′04″N, 106°24′23″W), 10 m, subtidal rock holes, specimen length 100 mm. RBCM 999-00015-001 (1), Collected by Facultad de Ciencias, UNAM, 5 Sep 1965, Playa Las Gatas, Zihuatanejo, Guerrero, Mexico, (17°38′10″N, 101°33′0″W), 4 m, rocky substrate, specimens length 80 mm. LACM 92-193.1 (1), Collected by O. López, 19 Mar 1992, Isla Venados, Bahía de Mazatlán, Sinaloa, Mexico, (23°15′39″N, 106°28′38″W), 12 m, rocky substrate, specimens length 99 mm.

Description.—Total length 55–151 mm (measured along the greater curvature of the body); mean length 101 mm. Holotype 141 mm long. Body curved, mouth and anus terminal, directed upward; anterior region wider than posterior. Deep groove in dorsal region, runs from near base of tentacles to anus (Fig. 1a, b). Skin soft, smooth. Podia slender, soft, large, retractile, widely dispersed and particularly larger and abundant in ventral region, not arranged in bands; also present in interambulacra. Specimens typically deep red, tentacles deep orange with black tips in life and reddish brown in alcohol. Ten tentacles almost equal. Madreporite in dorsal mesentery about one-half of distance from anterior end of calcareous ring. Circular, bilobate madreporite with a long narrow stone canal. Two polian vesicles on ventral side of ring. From left and right sides of cloaca arise two respiratory trees; each splits into a dorsal and ventral branch; in left side tree, ventral

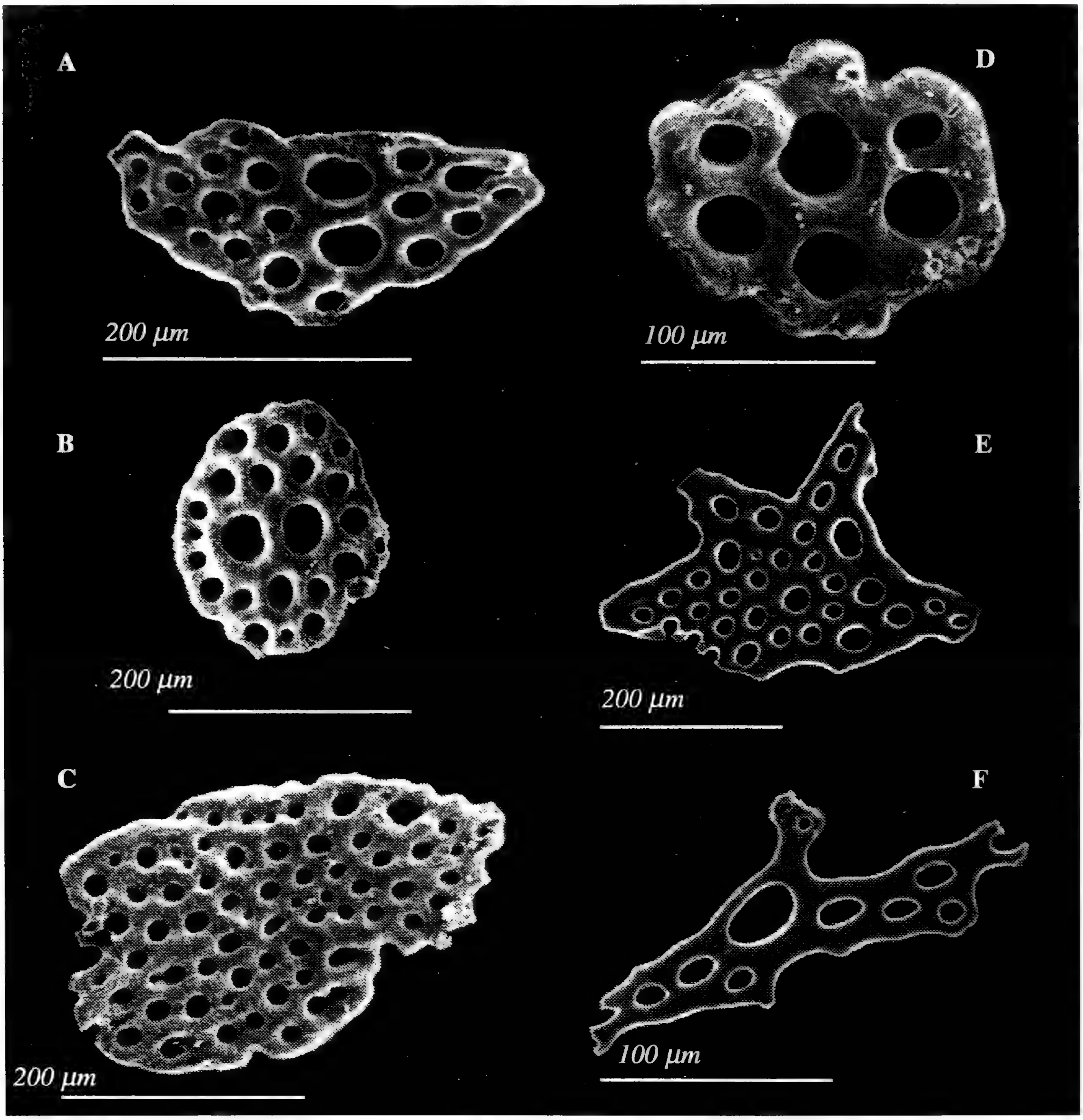

Fig. 3. Ossicles of *Cucumaria flamma.* (a–d) dorsal skin ossicles, smooth perforated plates and smooth buttons with two central holes; (e–f) Introvert with star-shaped and elongated perforated plates. All from holotype (USNM E48072).

branch runs full length of body, the dorsal branch three-quarters of length, in right tree, ventral branch runs the full length of body but the dorsal branch runs to middle of body because of presence of gonad mass (in mature specimens). Respiratory trees usually light brown or yellowish, each with a main trunk. Cloaca occupies approximately one-tenth of length of the body. Gonads arranged in two tufts of unbranched tubules, attached by a mesentery to right-mid dorsal side of the body.

Thin retractor muscles join to body wall at a point level with anterior end of calcareous ring. Plates of calcareous ring almost of same size, with anterior projections, radials longer than interradials; anterior projection of interradials narrower than radials (Fig. 2).

Dorsal skin ossicles smooth perforated

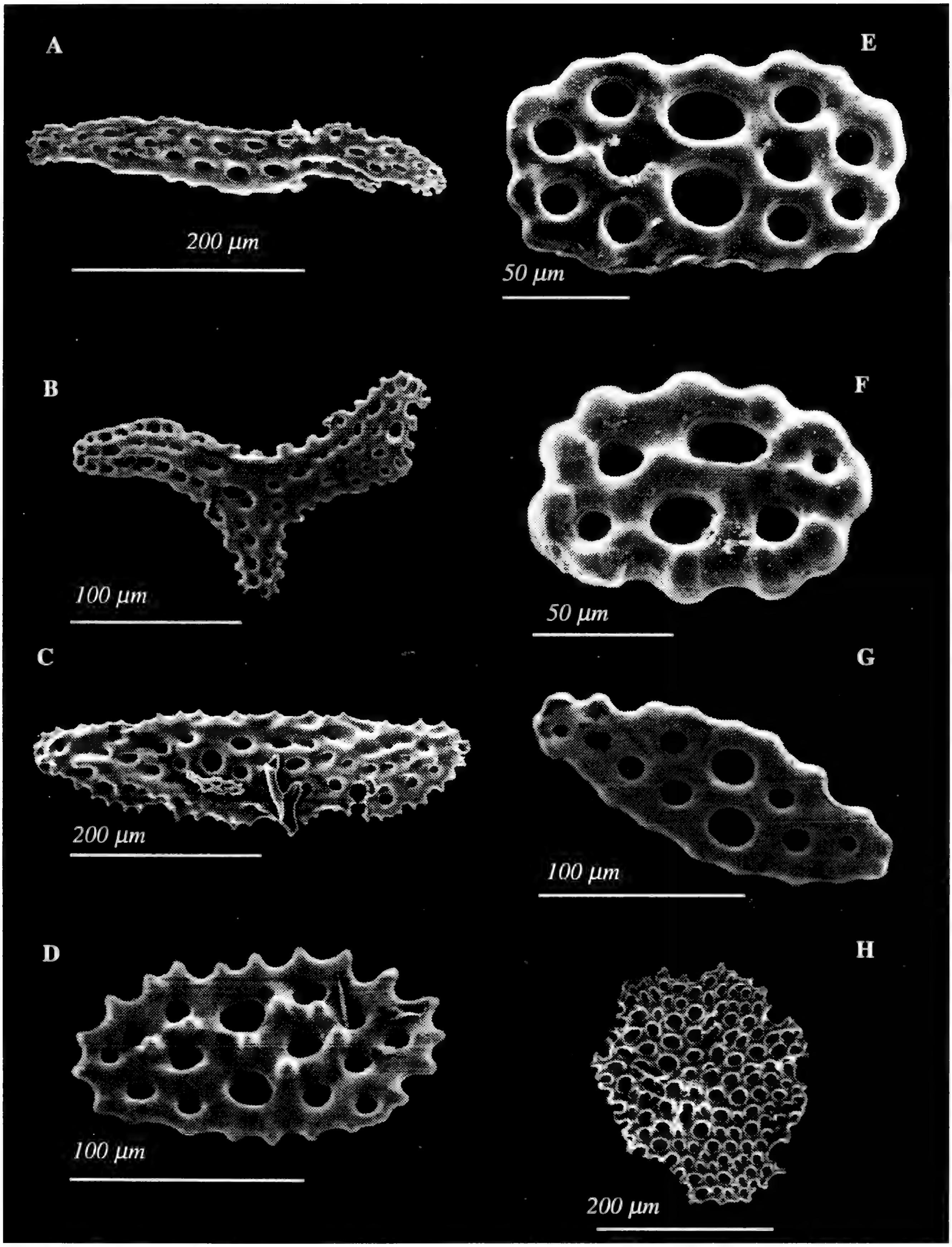

Fig. 4. Ossicles of *Cucumaria flamma.* (a–d) tentacle ossicles; (e–g) ventral skin ossicles; (h) end plate of podia. All from holotype (USNM E48072).

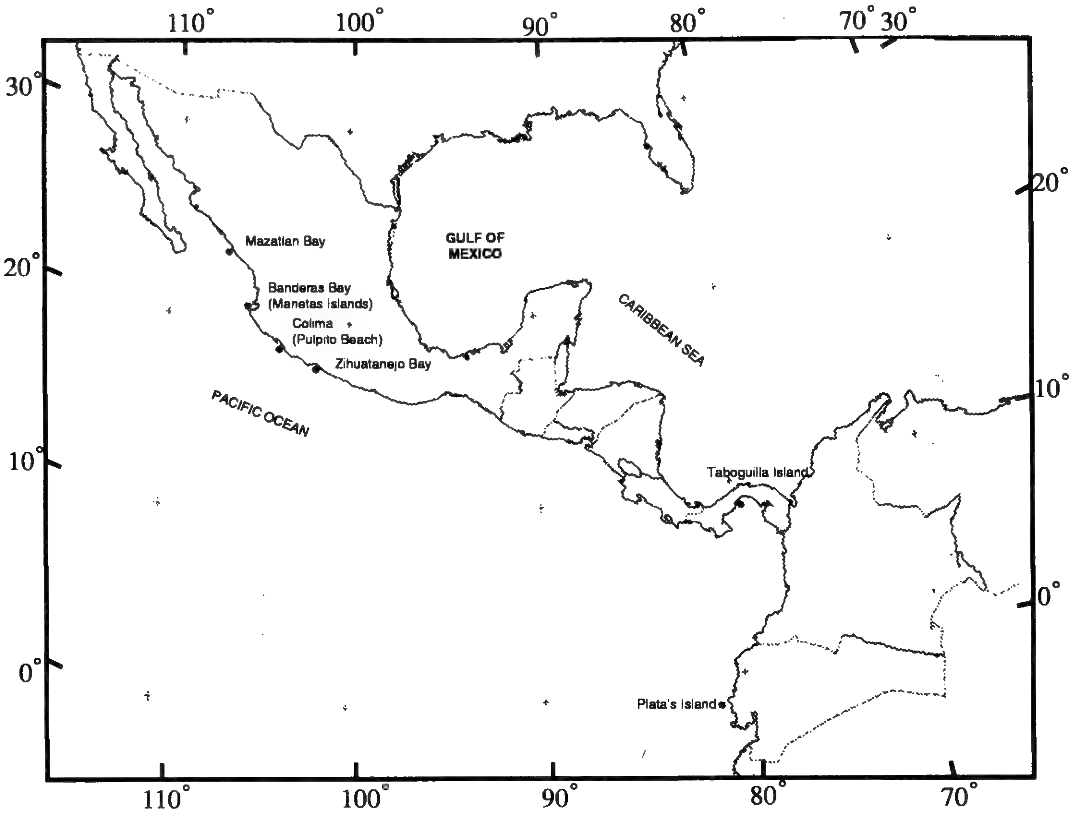

Fig. 5. Collection sites for *Cucumaria flamma.*

plates and smooth buttons with two central holes (Fig. 3a–d). Introvert with star-shaped (~340 μm) and elongated perforated plates (200 μm) (Fig. 3e, f). Tentacle ossicles perforated, robust rods, three-branched, curved or elongated, and scarce oval perforated plates, with scalloped margins (Fig. 4a–d). Ventral skin ossicles: abundant knobbed buttons (110–150 μm) and smooth perforated plates (200 μm). Knobbed buttons usually with four or sometimes six holes (Fig. 4e–g). Curved perforated rods in podia, end plates of 270–290 μm in diameter (Fig. 4h). Skin ossicles seem to disappear as the animal grows.

Etymology.—The specific epithet *flamma* in Latin means "flame, blaze or fire". It is here used as a noun in apposition and refers to the color of the skin and the tentacle crown of live specimens.

Distribution and habitat.—*Cucumaria flamma* is known from the Mexican Central Pacific, from Mazatlán, Sinaloa (23°15′39″N, 106°28′38″W) to Isla de la Plata, Ecuador (1°16′N, 81°06′W), (Fig. 5). It ranges in depth from 4 to 12 m. The majority of collections are from less than 10 m. Usually occurs on rocky substrates, in cavities and holes.

Discussion

Cucumaria flamma is distributed from Sinaloa, Mexico (in the mouth of the Gulf of California) to Isla de la Plata, Ecuador. As far as we know, eight species of the genus that could share this distribution area are: *C. frondosa japonica* (Gunnerus, 1767); *C. miniata* (Brandt, 1835); *C. piperata* (Stimpson, 1864); *C. pseudocurata* Deichmann, 1938; *C. salma* Yingst, 1972; *C. crax* Deichmann, 1941; *C. pallida* Kirkendale & Lambert, 1995 and *C. vegae* Théel, 1886 (Deichmann 1938, 1941; Bergen 1996; Lambert 1997). *C. flamma* is the largest of the *Cucumaria* species on Mexican coasts. It has the typical *Cucumaria* shape (Fig. 1a, b). It can attain a length of 150 mm and longer, depending on its state of relaxation.

Externally, *C. flamma* is similar to *C. miniata,* but the arrangement of the tube feet distinguishes them. *C. miniata* has five bands of tube feet separated by broad expanses of smooth skin, and occasional scattered tube feet. *C. flamma* has very widely dispersed tube feet not arranged in bands, particularly abundant in the ventral region. No other cucumariid exhibits the anteroposterior dorsal groove characteristic of *C. flamma.*

Cucumaria flamma is allied to *C. pseudocurata* in the shape of the smooth buttons ossicles of the body wall with two central holes, but those of *C. flamma* have broad and knobbed edges. The buttons of *C. pseudocurata* are smaller (about one-third of diameter) than those of *C. flamma. C. pseudocurata* also resembles *C. flamma* in the shape of the calcareous ring, but the radial plates in *C. pseudocurata* are slender, longer and with long anterior prolongations in comparison to *C. flamma,* that have broad radial plates with short anterior prolongations.

The knobbed plate ossicles present in the body wall may be reminiscent of *Cucumaria lubrica* H. L. Clark (formally *Pseudocnus lubricus*); Lambert (1997, 1998a) placed this species in the genus *Pseudocnus* based on the distribution of tube feet, the complex button ossicles and DNA evidence.

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A new species of rainfrog of the *Eleutherodactylus cruentus* group from eastern Honduras (Amphibia: Anura: Leptodactylidae)

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Abstract.—A new species of *Eleutherodactylus* (*E. operosus*) of the *E. cruentus* group is described from eastern Honduras. The new species differs from the remaining species in this group by the following combination of characters: heels with one small pustular tubercle; outer tarsus smooth; tubercles absent on upper eyelids; discs of fingers III–IV narrower than tympanum; disc covers and pads on fingers III–IV and all toes somewhat truncated; tympanum distinct in females; loreal region long; vomerine teeth present; dorsal surfaces brown in life; groin mottled, without distinct spots; groin and anterior and ventral surfaces of thighs brown in life; and heels pale copper in life. The forests around the known locality for the new species are under heavy human assault, even though the region is part of the Río Plátano Biosphere Reserve.

Frogs of the genus *Eleutherodactylus* (s.l.) constitute the largest genus of vertebrates with about 600 valid species currently recognized. The genus has an extensive geographic range from Arizona, U.S.A., to southern Ecuador on the Pacific slope and from Texas, USA, to Bolivia and southern Brazil on the Atlantic slope, including the West Indies.

Most mainland species belong to one of two lineages (Lynch 1986, Savage 1987), the Middle American clade (I; *Craugastor*) or the South American clade (II; *Eleutherodactylus* s.s.). These two groups are recognized on the basis of distinctive synapomorphies in the jaw muscles (Lynch 1986, Savage 1987) and karyotypes (DeWeese 1976, Savage 1987).

The majority of species found in North and Central America belong to clade I, but 14 forms, mostly confined to lower Central America, are representatives of clade II. Within that clade, twelve Central American species, characterized externally by having strongly areolate ventral integument, no toe webs, and toe III much shorter than toe V, with the tip of the latter reaching the level of the distal subarticular tubercle on toe IV, may be referred to the *Eleutherodactylus martinicensis* series (Lynch & Duellman 1997). Prior to the present report only one member of this series, *E. ridens,* was known to range as far north as Honduras.

In July 1997, JRM and LDW collected a single subadult female *Eleutherodactylus* sharing the ventral skin texture and toe features of the *E. martinicensis* series during three nights of searching the environs of a small stream in northeastern Olancho, Honduras. This specimen differed significantly from *E. ridens* in several characters and appeared to represent an undescribed species. Thus, in July–August 1998, JRM and LDW returned to the same stream hoping to collect additional material of this *Eleutherodactylus.* Despite six nights of searching along a broader area of the stream and surrounding forest, JRM and LDW were able to secure only one additional subadult female of this form. The second specimen

Fig. 1. Subadult female holotype of *Eleutherodactylus operosus* (USNM 530555), SVL 18.8 mm.

agrees in all details with the first specimen and both differ significantly from all known Central American species of the *E. martinicensis* series. Given the difficulty in collecting these frogs, plus the fact that JRM and LDW are extremely unlikely to ever return to this rapidly deforested locality, we describe the new taxon herein.

Materials and Methods

Measurements were made to the nearest 0.1 mm with dial calipers under a dissecting microscope. Comparative material examined is listed in Appendix I. Comparative data for *E. museous* was taken from Ibáñez et al. (1994). Abbreviations used are EL (eye length), EN (anterior border of eye to posterior edge of nostril; equals loreal length), HL (head length; tip of snout to angle of jaw), HW (greatest width of head), SHL (shank length), SL (snout length; anterior border of eye to tip of snout), SVL (snout-vent-length), and TPL (tympanum length). Disc terminology follows that of Savage (1987, 1997) and color codes are those of Smithe (1975–1981). Museum abbreviations follow those of Leviton et al. (1985), except for CRE (Costa Rican Expeditions, presently being catalogued into the LACM collection).

Systematics

Eleutherodactylus operosus, new species

Fig. 1

Holotype.—National Museum of Natural History (USNM) 530555, a subadult female, from near a small dam along a small tributary of the Quebrada de Las Márias (15°18′N, 85°21′W), about 12 airline km NNE La Colonia, Departamento de Olancho, Honduras, 680 m elev., collected 31 Jul 1998 by J. R. McCranie, K. L. Williams, and L. D. Wilson. Original number LDW 11354.

Paratype.—USNM 530556, a subadult female with the same data as the holotype, except collected 31 Jul 1997 by J. R. McCranie and L. D. Wilson.

Diagnosis.—Eleutherodactylus opero-

sus is referred to the *E. cruentus* group (sensu Savage 1980) within the *E. martinicensis* series by having large digital discs, non-triangular shaped disc pads, finger I shorter than finger II, and lacking toe webs. Eight valid Central American species (*E. altae, E. caryophyllaceus, E. cruentus, E. moro, E. museous, E. pardalis, E. ridens,* and *E. taeniatus*) belong to this group, which is a subset of the large (about 150 species) *E. unistrigatus* species group (sensu Lynch & Duellman 1997). *Eleutherodactylus operosus* differs from both *E. cruentus* and *E. museous* (character states for latter two species in parentheses) by having the heels with one small pustular tubercle (a distinct well-developed pointed tubercle), the outer tarsus smooth (two to four well-developed tubercles), no tubercles on the upper eyelids (distinct well-developed pointed tubercles), the discs of fingers III–IV narrower than the tympanum length (broader than tympanum length), and the groin region lacking distinct spots (usually one to several distinct yellow spots in *E. cruentus*; a black spot in *E. museous*). *Eleutherodactylus operosus* differs from *E. altae* and *E. pardalis* in having an essentially brown ground color with darker markings (nearly uniformly black), the groin area mottled dark brown and pale brown (groin marked with a large pale spot; spot red in life in *E. altae,* silvery-white in life in *E. pardalis*), and the anterior thigh surface dark brown with some pale brown mottling (marked with dark vertical bars separating large pale areas of the same color as spots in groin). *Eleutherodactylus operosus* differs from *E. caryophyllaceus* by lacking a superciliary tubercle (enlarged pointed superciliary tubercle located on free margin of upper eyelid) and by having the heel with one small pustular tubercle (distinct well-developed pointed tubercle). *Eleutherodactylus operosus* is distinguished from *E. moro* by having brown dorsal surfaces in life (green), the heels pale copper in life (no red on hind limbs), and the disc covers and pads on fingers III–IV and all toes somewhat truncated (round). *Eleutherodactylus operosus* is distinguished from *E. ridens* by having the disc covers somewhat truncate (round), the heel with one small pustular tubercle (heels smooth to rugose), the upper eyelids smooth or rugose (one to several low tubercles), the groin and anterior and ventral surfaces of the thighs brown in life (these surfaces some shade of red in life), ventral surfaces of head and body with sparse brown flecking from chin to anterior portion of belly (ventral surfaces moderately to heavily flecked with brown), and a long loreal region (EN/EL >1.00 versus <0.90 in females). The new form differs from *E. taeniatus* in having the posterior surface of the thighs dark brown with small distinct pale spots (essentially uniformly pale brown), a smaller tympanum (TPL/EL 0.30–0.31 versus 0.45–0.48 in females), and a longer loreal region (EN/EL 1.04–1.09 versus 0.88–1.00 in females).

Description of holotype (stored in alcohol after formalin fixation).—A subadult female with the following measurements (percentages of SVL in parentheses): SVL 18.8 mm; HL 7.7 mm (41.0); HW 6.7 mm (35.6); EL 2.2 mm (11.7); SL 3.4 mm (18.1); EN 2.4 mm (12.8); TPL 0.7 mm (3.7); SHL 11.3 mm (60.1); and FL 8.1 mm (43.1). Snout long, nearly rounded in dorsal aspect, vertical with rounded upper end in profile; top of head flat; canthus rounded, distinct; loreal region concave; upper lip not flared; nostrils directed laterally, situated at point about two-thirds distance between anterior border of eye and tip of snout; cranial crests absent; supratympanic fold weak, narrowly obscuring upper edge of tympanum; tympanum indistinct, located posterior to lower half of eye, separated from eye by distance about equal to tympanum length; upper arm more slender than moderately slender forearm; transverse dermal fold present on upper surface of wrist; transverse dermal fold absent on elbow; tubercles or dermal ridge absent along posterior ventrolateral edge of forearm; finger discs strongly expanded (disc on finger III about 3.0 times width of digit just proximal to disc); disc covers on fingers somewhat truncated; disc pads on fingers truncate; subarticular tubercles on fingers round, conical to pungent; supernumerary tubercles absent on fingers; palmar tubercle low, bifid, larger than thenar tubercle; 3–4 accessory palmar tubercles present; thenar tubercle ovoid to elongate, elevated, barely visible from above; pollex not enlarged; relative length of fingers I < II < IV < III; fingers unwebbed, bearing weak lateral keels on fingers II–IV; heels broadly overlapping when hind limbs held at right angles to body; weak vertical dermal fold present on outer lateral edge of heel; heels bearing a single, small pustular tubercle; tubercles or dermal ridge absent along posterior ventrolateral edge of tarsus; inner tarsal fold absent, although one low elongated tubercle present on one leg at about one-third length of tarsus; subarticular tubercles on toes round, globular; supernumerary tubercles absent on toes; 8–10 very small plantar tubercles present; inner metatarsal tubercle elongate, elevated, visible from above; outer metatarsal tubercle absent; relative length of toes I < II < III < V < IV, disc on toe V extending to level of distal subarticular tubercle on toe IV; toe discs moderately expanded (disc on toe IV about 2.5 times width of digit just proximal to disc); disc covers on toes somewhat truncated; disc pads on toes somewhat truncated; toes unwebbed, bearing very weak lateral keels; inguinal gland not evident; vent opening directed posteroventrally near upper level of thighs, skin below vent granular; skin of dorsal surfaces smooth to weakly granular, including that of upper eyelids; distinct ridge extending posteriorly from upper eyelids to level above axilla, ridge broken posteriorly with small laterally offset portion just posterior to level of axilla; suprascapular fold absent; dorsolateral ridges absent; skin of throat, chest, and ventral surface of thighs smooth, that of belly coarsely areolate; ventral disc absent; pupil horizontally elliptical; palpebral membrane translucent, unpatterned; tongue ovoid, barely notched posteriorly, free posteriorly for about one-half of its length; vomerine teeth on very low, ovoid ridges located posteromedially to ovoid choanae, tooth patches separated by distance greater than width of either patch; maxillary teeth present.

Color in life: dorsal surfaces of head and body Hair Brown (119A), with raised Mahogany Red (132B) postocular ridge; dorsal surface of forelimbs Hair Brown (119A); dorsal surface of hind limbs Army Brown (219B), with Sepia (219) crossbars; heels pale copper; groin mottled Hair Brown (119A) and Army Brown (219B); chin transparent with small brown punctations; belly colorless with small white punctations; iris yellowish brown on upper half, bronze with brown reticulations on lower half.

Color in alcohol: dorsal surfaces of head and body brown with darker brown outlining postocular ridge; dorsal surfaces of limbs pale brown with distinct, dark brown crossbars; lateral surface of head barred with pale brown and dark brown; posterior surface of thighs dark brown, with distinct pale brown spots; anterior surface of thighs dark brown, with some pale brown mottling; heel region very pale brown; ventral surfaces of head, body, and thighs pale cream-colored, with sparse brown flecking from chin to anterior portion of belly, flecking more pronounced on thighs.

Variation in paratype.—The paratype agrees well with the holotype in all morphological characters and in color pattern, except that the heel tubercles are not as well developed and the vomerine tooth patches are better developed than in the holotype. The following measurements (percentages of SVL in parentheses) were recorded: SVL 20.2 mm; HL 8.1 mm (40.1); HW 6.8 mm (33.7); EL 2.6 mm (12.9); SL 3.8 mm (18.8); EN 2.7 mm (13.4); TPL 0.8 mm

(4.0); SHL 11.9 (58.9); and FL 8.6 mm (42.6).

Natural history notes.—Both specimens were taken at night from vegetation about 1.5 m above the ground along a trail near where it crosses a small stream at 680 m elevation. Although the specimens were taken in different years, both were found at nearly the identical spot along the trail. The locality is in the Premontane Wet Forest formation of Holdridge (1967). The vegetation in the immediate vicinity was in a nearly pristine condition in 1997 and 1998. However, the area alongside this stream was completely deforested at 660 m, as were most of the hillsides surrounding the forest on both sides of the portion of the stream where *E. operosus* was collected. Also, considerably more deforestation was evident along this stream on JRM's and LDW's second trip in 1998 than was evident in 1997. This extensive deforestation is occurring even though the region is part of the "protected" Río Plátano Biosphere Reserve. Other species of *Eleutherodactylus* collected in the environs of this trail and stream were *E. epochthidius, E. fitzingeri, E. mimus, E. ridens,* and *Eleutherodactylus* sp. (*E. rugulosus* group). Males of *E. fitzingeri* and *E. ridens* could be located by their advertisement call. No other species of *Eleutherodactylus* were heard to call at this locality.

Etymology.—The name *operosus* is a Latin word meaning laborious or difficult (Brown 1991). The name is used in reference to the difficulty experienced in efforts to collect a series of these frogs.

Remarks.—Lynch & Duellman (1997) referred all species in the *E. martinicensis* series to two subdivisions, the *E. diastema* group (now composed of seven species, Savage 1997) and the *E. unistrigatus* group (about 150 species). It is clear that the latter is a composite that will be further divided into additional species groups as knowledge increases. The species placed here in the *E. cruentus* group are the same as those included by Savage (1980), with the exclusion of *E. cerasinus,* transferred by Lynch & Duellman (1997) to the *E. conspicillatus* series, and the additions of *E. museous, E. operosus,* and *E. taeniatus.* It remains to be seen if the *E. cruentus* group, as utilized here, is monophyletic, but for the present it conveniently clusters all Central American species of the *E. martinicensis* series, aside from *E. diastema* and its allies, belonging to the South American clade into a single group.

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Appendix I
Comparative Material Examined

Eleutherodactylus altae. Costa Rica—San José: CRE 3181, 3212, 3380–81, 7048.

Eleutherodactylus caryophyllaceus. Costa Rica—Cartago: CRE 7053, 7058 (2), 7060, 7075, 7095. San José: CRE 7035, 7048.

Eleutherodactylus cruentus. Costa Rica—Alajuela: CRE 693, 696, 767, 2929, 2932, 7014. Cartago: CRE 191, 2284. San José: CRE 490, 3181, 6467–68.

Eleutherodactylus moro. Costa Rica—San José: CRE 765, UCR 6000.

Eleutherodactylus pardalis. Costa Rica—Puntarenas: CRE 916 (2), 919, 3182 (2), 3485, 3488, 7224, LACM 119586. San José: CRE 7097.

Eleutherodactylus ridens. Honduras—Atlántida: FMNH 236380, SMF 77632–33, USNM 514529–50. Colón: BMNH 1985.1232, 1985.1453, LSUMZ 33647, UMMZ 89461, USNM 514551–54. Olancho: SMF 78781–82, USNM 343720–22, 344791, 514555–59, 530557–60.

Eleutherodactylus taeniatus. Colombia—Chocó: LACM 50551, 73208, 73212, 73222–23.

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A new species of arboreal viper (Serpentes: Viperidae: *Atheris*) from Cameroon, Africa

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Abstract.—A distinctive new species of the arboreal viper genus *Atheris* (*A. broadleyi*) is described from Cameroon, Africa. The new taxon inhabits moist evergreen and semideciduous transition forest in southern Cameroon, Congo, Central African Republic and Gabon. The new species previously has been confused with the widespread *A. squamigera,* but is distinguished from this species and other congeners by a combination of scale characteristics and a unique color pattern.

In a recent review, Broadley (1998) commented on an unusual color morph of *Atheris squamigera* from southern Cameroon. Perret & Mertens (1957) had previously mentioned the same population of *Atheris* from Moloundou in the extreme southeast of the country, and suggested that additional material was needed to ascertain this population's taxonomic status. Both of these descriptions agree with a series of *Atheris* I obtained during a herpetological survey of the proposed Lac Lobeké protected area of extreme southeastern Cameroon. Comparison of this material with museum specimens from Cameroon, Democratic Republic of the Congo, Central African Republic (CAR), topotypic *A. anisolepis* Mocquard (1887) and the holotype of *A. squamigera* (Hallowell, 1856) reveals that the southern, inland Cameroon population is distinct from all other *Atheris* species.

Methods

Specimens of the new *Atheris* were fixed in 3.7% formalin within 24 hr of collection. Specimens were transferred into 70% ethanol within two months after preservation.

Snout-vent length (SVL) and tail length (TL) were measured to the nearest mm using a meter stick. Other standard measurements were taken to the nearest 0.1 mm using dial calipers held under a dissecting microscope. Features of scalation were examined by holding preserved specimens under a dissecting microscope. Scale terminology generally follows Klauber (1956). Suprarostrals and interorbitals are used in keeping with Broadley (1998) for other members of the genus. Interrictal counts refer to scales across the back of the head between the posterior supralabials. Anterior body dorsal scale row counts were made approximately one head-length posterior to the head. Posterior body dorsal scale row counts were made approximately one head-length anterior to the vent. Color descriptions in preservative and life are based on a published standard (Smithe 1975). Institutional abbreviations refer to Academy of Natural Sciences of Philadelphia (ANSP), American Museum of Natural History (AMNH), University of Texas at Arlington Live Collection (DPL), University of Texas at Arlington Collection of Vertebrates (UTA). A list of specimens examined is given in the Appendix.

Systematic Account

During the summer of 1994 I made herpetological collections at various proposed

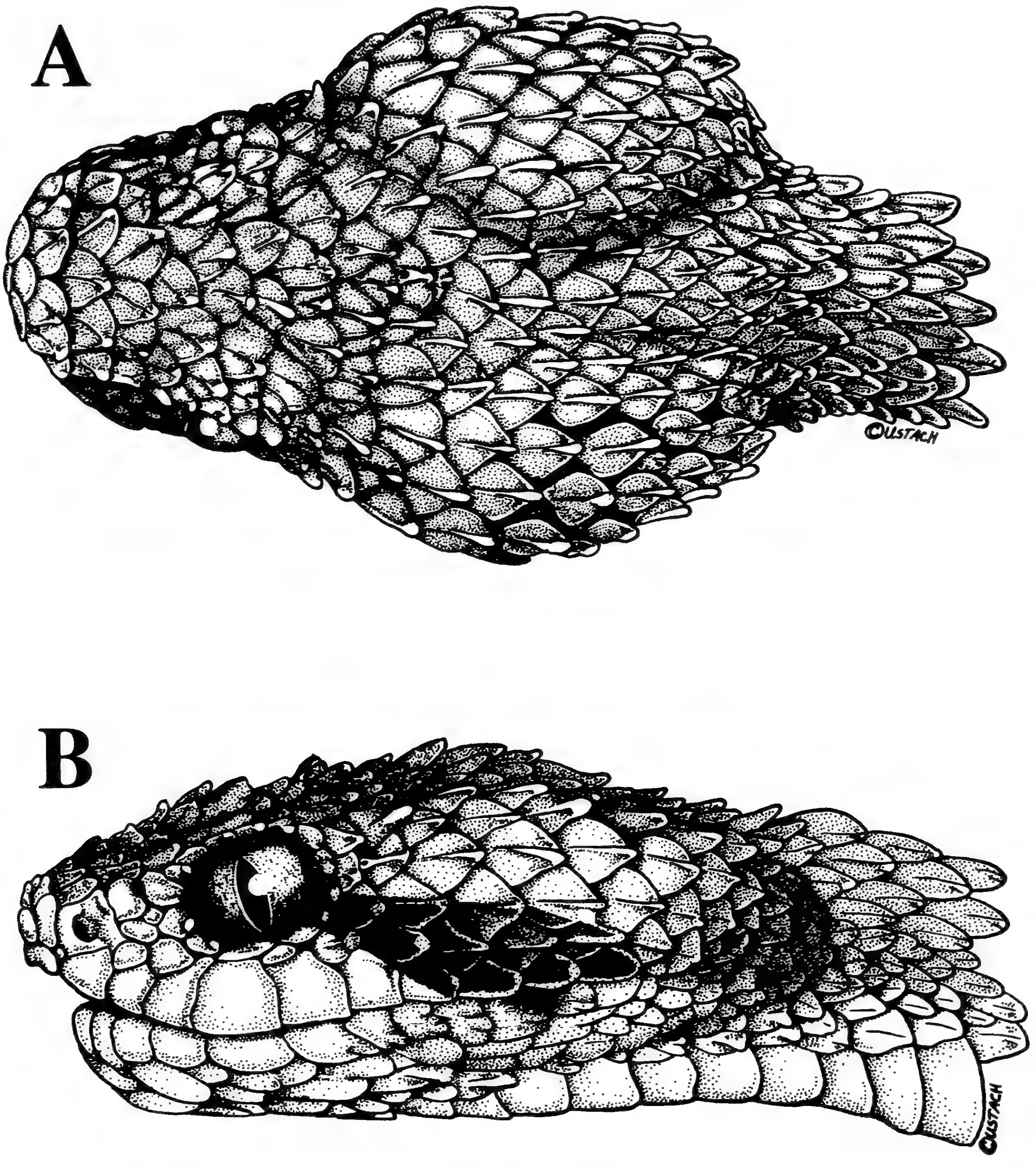

Fig. 1. (A) Dorsal and, (B) left lateral aspect of *Atheris broadleyi* holotype, UTA R-37801, head length 29.0 mm.

and existing protected areas throughout Cameroon. Specimens of *Atheris* taken at Lac Lobeké confirm long-standing impressions that this population is distinct. I propose that this new snake be known as

Atheris broadleyi, new species
Figs. 1–2 and 5 (A)

Atheris squamigera squamigera.—Perret & Mertens, 1957:597
Atheris squamigera ssp. Perret, 1961:137
Atheris squamigera.—Broadley, 1998: fig. 8

Holotype.—University of Texas at Arlington Collection of Vertebrates (UTA) R-37801, mature female collected vicinity Lipondji village, East Province, Cameroon (2°23′05″N, 15°25′41″E), 1 Jun 1994 by D. P. Lawson (original field number DPL 3608).

Fig. 2. *Atheris broadleyi,* adult male from the type-locality, ca. 525 mm SVL, DPL 3646. Photo by D. P. Lawson.

Paratypes.—UTA R-37798-37800 and 44911-21, 10 adult and 4 juvenile females from the type-locality, collected between May and December 1994, UTA R-44957, an adult female collected in the vicinity Mbanjani village, East Province, Cameroon (ca. 5 road km south of the type-locality), 7 Sep 1997, and ANSP 20334, an adult male from Nola, Central African Republic (3°32′22″N, 16°02′51″E), collected 27 Oct 1934 by J. A. G. Rehn of the G. Vanderbilt Africa Expedition.

Definition and diagnosis.—A species of *Atheris* distinguished from all other members of the genus by the following combination of characters: lateral scales without serrated keel; supralabials in contact with suboculars (not separated by one or more scale rows); 14–18 interrictals; interorbitals keeled; rostral 3.5 to 4 times broader than high; scales in loreal region smooth or with only slight keel or knob; a dark postocular stripe persisting in adults; maximum total length of 765 mm or more; and a dark tail tip in adult females.

Specifically, *Atheris broadleyi* appears to be most similar to *A. squamigera,* but differs consistently by the combination of: a distinctive and consistent dorsal color pattern of citrine to greenish olive; checked black, white and sky blue venter, and a dark postocular stripe; more oculars (mode of 15 versus modes of 12–14, see Table 1); and, greater length of 765 mm or more (versus 650 mm maximum for Cameroon *A. squamigera*). Additionally, *A. broadleyi* usually has more ventrals (mean of 162 ± 3.3 versus 157 ± 3.6) and fewer subcaudals (mean of 51 ± 4.9 versus 52 ± 3.2), and more infralabials (mode of 11 versus 10) than *A. squamigera.*

Atheris broadleyi lacks serrated keels on its lateral scales differentiating it from an East African group comprised of *A. ceratophora, A. desaixi, A. katagensis, A. nitschei,* and *A. rungweensis* with pronounced serrations on the lateral scales. Elongate supraocular scales forming a horn-like projection over the eye further distinguish *Atheris ceratophora.* Similarly, *Atheris broadleyi* lacks lanceolate or acuminate dorsal scales and fused lateral scale rows, differentiating it from the distinctive East African *A. hispida* and *A. acuminata. Atheris broadleyi* is distinguished from *A. chlorechis* by having fewer interrictals (14–18 versus 23 or more) and fewer mid-body dorsal scale rows (17–23 versus 25–36). In addition to differences in color pattern, *Atheris broadleyi* is distinguished from *A. anisolepis* by having completely keeled interorbitals (smooth in *A. anisolepis*), supralabials in contact with oculars (separated by a scale row in *A. anisolepis*), and usually fewer suprarostrals.

Description of holotype.—Rostral flattened, dorsal margin slightly concave medially, 3.5 times broader than high, contacting anteriormost supralabials, three unkeeled suprarostrals and divided left nasal; medial suprarostral the smallest, 1.3 times wider than high, right and left suprarostrals as wide as high; right and left nasals partially divided above the nares, left nasal further divided at anteriormost edge forming a separate small scale; nares large, covering approximately 30% of nasal, directed laterally and slightly posteriorly; internasals 5, strongly keeled, medial scale lying directly above medial suprarostral but not separating two innermost internasals; interrictals 17; interorbitals 6, strongly keeled, those not contacting oculars enlarged and irregularly shaped; oculars 15/13, supra- and postoculars keeled, terminating in blunt knobs, suboculars and ventralmost preocular dorsoventrally compressed, knobbed but not keeled, two dorsalmost preoculars feebly knobbed, enlarged, extending anteriorly into loreal region; oculars separated from nasals by 6/5 smooth or feebly knobbed scales loosely arranged in three rows of 1/1, 1/2, 4/2; supralabials 11/10, 3–5 contacting suboculars; infralabials 11/11, 5–10 on each side feebly keeled, anteriormost in contact at the midline, separating mental from 5 pairs of chin shields; mental 2.3 times wider than deep; gulars strongly keeled; ventrals 159; subcaudals 50, entire; anal entire; dorsal scales about twice as long as wide, becoming shorter posteriorly, in 19-21-16 rows; keel on dorsals increasing in height from base, declining rapidly at apex, ending in slight knob; paraventrals larger than other dorsals, keeled, angled slightly ventrally.

Measurements (mm): SVL 550; tail length 110; eye diameter 5.1; head length 29; head width 21.2; distance from anterior margin of eye to nares 4.7 mm, to tip of snout 6.8 mm.

Color in preservative (ethanol after formalin) has not changed appreciably from life: dorsum of head uniformly citrine with olive-yellow keels; sides of head spectrum yellow extending onto lateral aspect of neck; face straw yellow; a diffuse dark stripe extending from the ventral posterior margin of the eye caudad to the rictus, incorporating the last three supralabials and posterior margin of the eighth, barely extending onto the last three infralabials; dorsum of body citrine anteriorly becoming greenish olive posteriorly, broken by 29 black-bordered sulphur yellow crossbands, crossbands on anterior half of body do not meet on midline, becoming indistinct on neck, posterior 15 crossbands conspicuous, complete across the dorsum; tail with 9 moderately distinct, complete crossbands; tail tip black; interstitial skin color varied, corresponds to dorsal color pattern; throat and neck white; venter sky blue, irregularly suffused with white anteriorly, becoming increasingly darker posteriorly; white blotch on lateral portion of every third and/or fourth (occasionally second) ventral scale extending onto paraventral, blotches become more pronounced as venter darkens posteriorly, forming a checkered pattern; ventral color extends onto paraventrals and occasionally onto adjacent dorsal scale.

Variation.—The 15 paratypes closely resemble the holotype in color, pattern, and scalation. Posterior portions of the venter in some individuals (including the only male in the type series) are more uniformly dark than that of the holotype, but always have distinct white lateral blotches. Specimens from the western extent of the range (see below) may be less boldly patterned, and are almost uniformly citrine/greenish olive with barely discernable crossbands and postocular stripe (DPL 5508). Juveniles less than 300 mm SVL (UTA R-37798, 44913, 44918, 44920) have white tail tips, and remnants of a pale tail tip are present in two subadult specimens (UTA R-44915 and 44919). UTA R-37799 is the largest of the series (768 mm total length), UTA R-37798 the smallest (247 mm total length). One to three isolated scales are present in the interoculabial region in five of the paratypes, but do not completely separate oculars and supralabials. Scales in the loreal region are smooth in eight specimens and feebly knobbed in seven.

The paratypes exhibit the following variation (means and standard deviations in parentheses, modes in brackets, see Table 1): ventrals 157–169 (162 ± 3.3); subcaudals 45–59 [50]; midbody dorsal scale rows 17–23 (20 ± 1.6); anterior body dorsal scale rows 16–21 [19]; posterior body dorsal scale rows 13–18 [16]; ratio rostral width to height 3.2–5 (3.9 ± 0.5); ratio medial suprarostral width to height 1–2.2 (1.2 ± 0.3); ratio right suprarostral width to height 0.65–1.3 (0.91 ± 0.2); suprarostrals 3–7 [3]; internasals 3–5 [5]; interorbitals 3–8 [6]; oculars 12–16 [15]; total scales in loreal region 3–7 (5.3 ± 1.2) [6]; supralabials 9–12 [10]; infralabials 9–12 [11]; ratio of mental width to depth 1.3–2.5 (2 ± 0.3); chin shields 4–7 [5]; interrictals 14–18 [17]; ratio eye diameter to head length 0.15–0.24 (0.18 ± 0.02); ratio head length to SVL 0.05–0.07 (0.06 ± 0.01); ratio head width to head length 0.64–0.84 (0.78 ± 0.05); ratio eye-nares to head length 0.13–0.16 (0.15 ± 0.01); ratio eye-snout to head length 0.21–0.27 (0.24 ± 0.01).

Distribution.—Atheris broadleyi is known from southern Cameroon from the Nyong River just southeast of Yaounde (11°11′12″E, 3°27′38″N, DPL 5508), south through the Dja Forest Reserve (Broadley 1998) and east at least as far as the Sangha region of the Central African Republic (Fig. 3). This distribution corresponds to a region previously mapped for Cameroon as moist evergreen and semideciduous forest (transition forest) comprised of *Baillonella toxisperma* and *Gilbertiodendron dewevrei* (CENADEFOR 1985). This region also features palm swamps and large scrub grassland clearings associated with seasonal high water tables (D. Thomas, pers. comm.). The distribution of *Atheris broadleyi* presumably follows this forest type into northern Gabon and Congo.

Atheris broadleyi was the most common snake in the Lac Lobeké, Cameroon survey, but does not appear in a slightly larger collection from the vicinity of Oesso, Congo, just across the Sangha River (Kate Jackson, pers. comm.). *Atheris broadleyi* is abundant near the type-locality. Local collectors obtained 24 specimens in 48 hours, indicating remarkable densities for a snake by Central African forest standards.

Etymology.—The specific epithet is a patronym for Donald G. Broadley in recognition of his considerable contributions to the herpetology of Africa in general, and

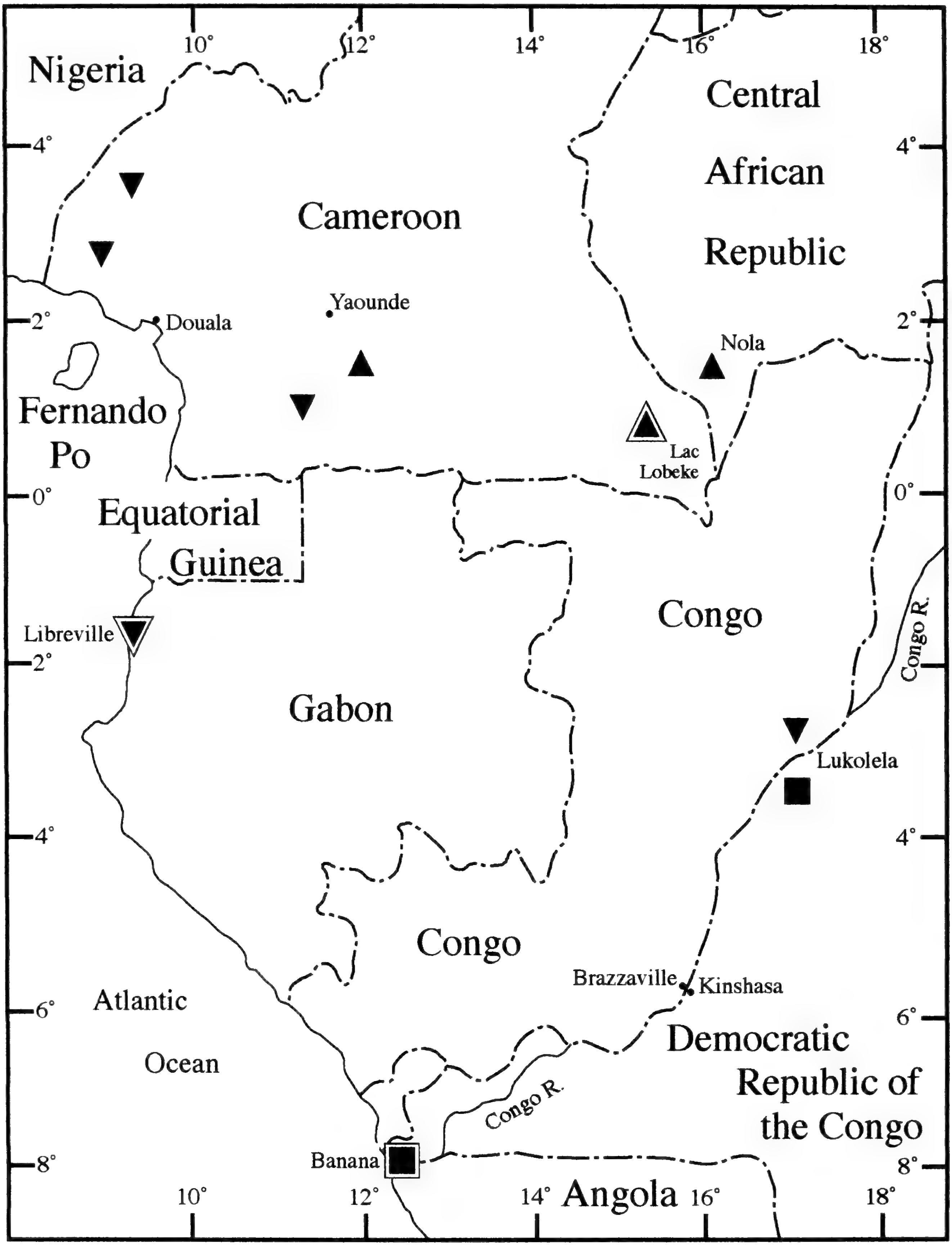

Fig. 3. Localities of *Atheris broadleyi* (triangles), *A. squamigera* (inverted triangles), and *A. anisolepis* (squares) in west Central Africa. Outlined symbols indicate type-localities.

his recent clarifications of the genus *Atheris* in particular.

Comparisons.—Broadley (1998) provided a key to the species of *Atheris* by which *A. broadleyi* is readily diagnosed from all members of the genus except *A. anisolepis* and the widely distributed and highly variable *A. squamigera. Atheris broadleyi* is also distinctly allopatric from all but *A. squamigera.* Although recognized in recent treatments (e.g., McDairmid et al. 1999, Broadley 1998, Trape & Roux-Estève 1995), *A. anisolepis* is similar to *A. squamigera* and its validity remains uncertain (Broadley 1998). Descriptive statistics and differences among *A. broadleyi, A. anisolepis* and *A. squamigera* are summarized in Table 1. For the purpose of comparisons with the new taxon, information for four populations of *A. squamigera* is presented separately in Table 1. *Atheris squamigera* is widely distributed in forests from Senegal to western Kenya (Spawls and Branch 1995). As evidenced by this species description and the intraspecific variability of *A. squamigera* (Table 1), previous descriptions of this taxon may have inadvertently increased the reported variation in many characters by combining distinct species with *A. squamigera.*

With the exception of occasional specimens which uniformly darken in preservative over time, color and pattern features of *Atheris* in preservative closely resemble those in life (pers. obs.). *Atheris squamigera* are most often apple green to turquoise blue with yellow crossbands above and yellow, green or blue ventrally (Fig. 4, Schmidt 1923, pers. obs.). Occasional specimens of *A. squamigera* from the Cameroon-Nigeria frontier (UTA R-44963, 44926, Stuck-Stirn 1979, Lawson 1993) and Congo (AMNH 45940, 51840), and specimens of *A. anisolepis* (AMNH 11898–99) are uniform spectrum yellow sparsely flecked with yellow-green spots. *Atheris squamigera* from the Congo River above Kinshasa (AMNH 45940, 45943, 45945, 51840) may be uniform yellow, turquoise green, violet or a mottled combination of yellow and violet. Unlike *A. squamigera, A. broadleyi* appears to be highly consistent in color pattern.

South-central Cameroon is an area of possible sympatry between *Atheris broadleyi* and *A. squamigera* for which material is available. Specimens from Metet and Bitye (AMNH 5254, 51841–43) have a pronounced, dark postorbital stripe and several features of scutellation overlapping *A. broadleyi.* I have referred the south-central Cameroon material to *Atheris squamigera* on the basis of dorsal color pattern and scutellation. However, this area lies at the transition between the coastal moist evergreen forest of *A. squamigera* and the inland transition forest of *A. broadleyi,* and may represent an integration zone between the taxa (Fig. 3). Collections from other areas of possible sympatry at the southern limit of *A. broadleyi* are lacking.

In addition to differences in color and scalation, *Atheris broadleyi* differs from Cameroon *A. squamigera* in behavior and reproduction. Both in the field and in captivity, *A. broadleyi* are more aggressive, active and alert than *A. squamigera,* striking readily and repeatedly with little provocation (pers. obs.). Neonate *Atheris broadleyi* (Fig. 5 A) resemble the adults in coloration, but have a pale colored tail tip that disappears as they mature. This is in contrast to *A. squamigera* from western Cameroon that produce almost uniform charcoal-black offspring with pale green eyes and a pale tail tip (Fig. 5 B). These neonates attain the apple green or turquoise blue adult coloration with successive post-natal sheds. The pale tail tip persists in female *A. squamigera* from western Cameroon, but is lost in males from this population as they mature.

A pair of *Atheris broadleyi* collected as adults at the type-locality in 1994 and maintained in captivity in the United States have reproduced twice. Courtship and copulations were observed between 28 June and 11 July 1995, and 13 young (one deformed) were born on 10 February 1996. Courtship

Table 1.—Comparison of characteristics among *Atheris broadleyi, A. anisolepis,* and selected populations of *A. squamigera.* Mean values in parentheses, mode in brackets. Color descriptions are based on preserved material supported by observations of live *A. broadleyi* and Cameroon *A. squamigera.* * indicates values for *A. anisolepis* reported by Broadley (1998) that are outside the range seen in material examined in the current study.

Characteristic	*Atheris broadleyi* $n = 16$	*Atheris squamigera* western Cameroon $n = 13$	*Atheris squamigera* Kakamega Kenya $n = 5$	*Atheris squamigera* Congo $n = 4$	*Atheris anisolepis* $n = 3$
Ventrals	157–169 (162)	149–163 (157)	153–160 (156)	152–156 (154)	150–162
Subcaudals	45–61 (51)	50–60 (55)	50–57 (53)	57–63 (59)	46–55*
Maximum total length in mm	768	629	738	403	650*
Supralabials	9–12 [10]	8–11 [10]	8–11 [10]	9–11 [9]	9–13
Infralabials	9–12 [11]	8–12 [10]	10–12 [10]	9–10 [10]	10–14*
Rostral width/rostral height	(3.9)	(4.3)	(3.7)	(4.1)	(3.2)
Suprarostrals	3–7, median never fused to internasal	3–7, median often fused to internasal	3	3–5	6–8
Interoculars	3–8 (5.8)	6–10 (6.8)	4–8 (6.2)	6 (6)	6–8*
Total oculars	12–16 [15]	11–16 [14]	13–15 [13]	12–15 [12]	12*–17*
Loreal scales	smooth	keeled	keeled	keeled	smooth
Adult female tail color	dark	white	white	NA	white?
Dorsal color pattern	Citrine to greenish olive w/crossbands	Green w/yellow crossbands or uniform yellow	Greeen w/yellow crossbands	Uniform green, yellow, or mottled violet and yellow	Uniform yellow or green
Postorbital stripe	present	usually absent	absent	absent	absent

Fig. 4. *Atheris squamigera,* adult male from vicinity Nguti, Southwest Province, Cameroon, ca. 375 mm SVL, DPL 5348. Photo by D. P. Lawson.

was observed on 13 July 1996, but no offspring were produced that year. Courtship was observed again on 10 June 1997 and continued for approximately one week. Five live and three stillborn young were produced on 17 February 1998. The male was observed courting and trying to copulate approximately one week prior to parturition. Specimens of *A. squamigera* from western Cameroon maintained under similar captive conditions to the *A. broadleyi* above have been observed in courtship in September–October and have given birth in April (pers. obs.). Pitman (1974) reported similar timing of reproduction for *A. squamigera* in Uganda.

Like its congeners, *Atheris broadleyi* is primarily nocturnal (Spawls and Branch 1995, pers. obs.). Specimens have been found as they were either active on the ground during or following evening rains, or coiled among vine tangles, sitting in apparent ambush along arboreal rodent runways (pers. obs.). The few direct observations of this species in the wild occurred at the forest edge.

There is a preponderance of females in samples of both *Atheris broadleyi* and *A. squamigera* from Cameroon indicating a strong collecting bias or skewed sex ratio in the populations. Males of both species are considerably smaller than females. Males and females of *A. broadleyi* are much longer and more robust than their *A. squamigera* counterparts (Table 1, Figs. 2 and 4).

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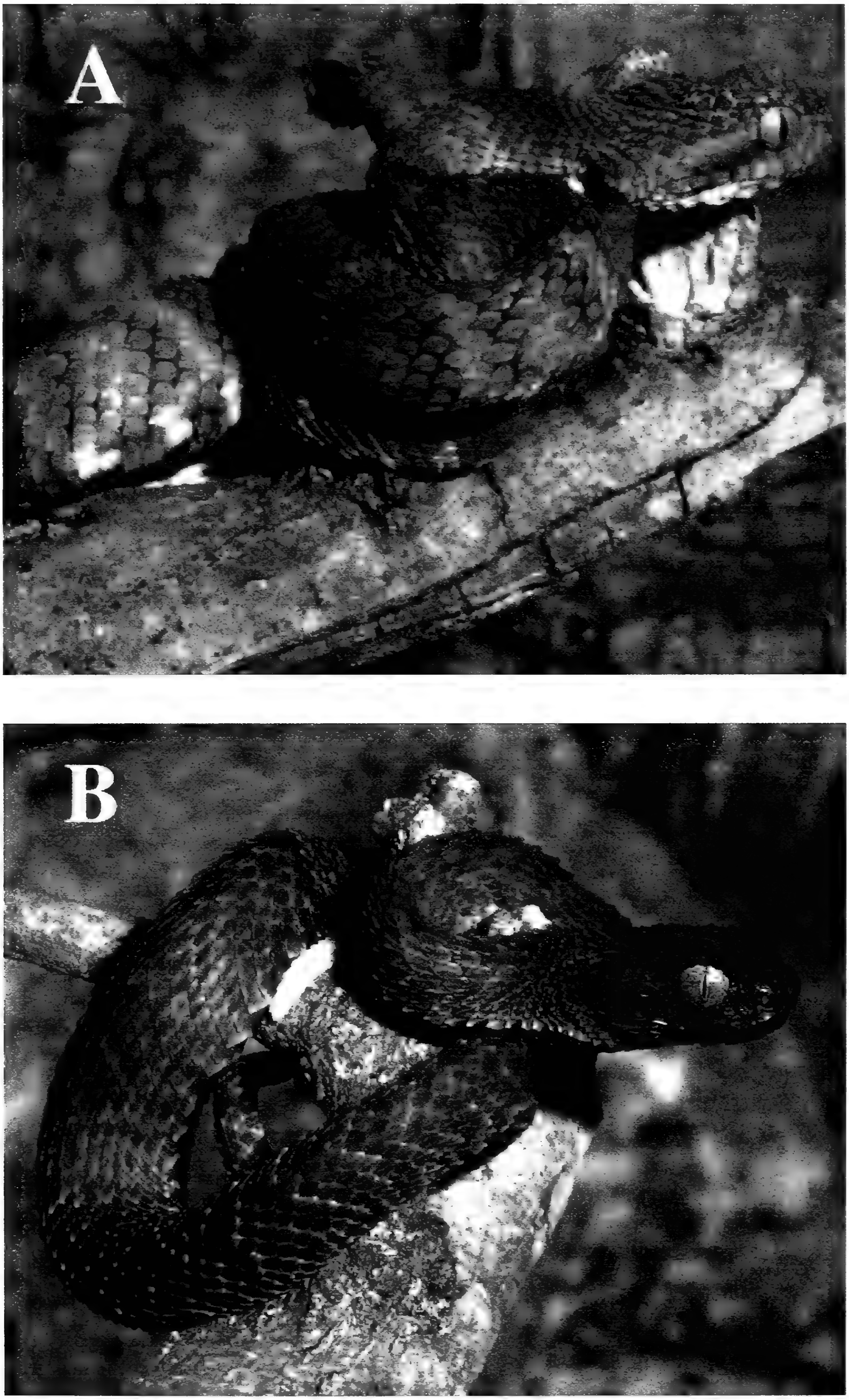

Fig. 5. (A) Neonate *Atheris broadleyi* born to parents from the type-locality; (B) Neonate *A. squamigera* from wild-caught gravid female DPL 5318, Banyang-Mbo Wildlife Sanctuary, Southwest Province, Cameroon. Photos by J. A. Campbell.

drawing of the holotype, and M. Fost documented captive behavior and reproduction. I thank J. A. Powell and M. D. Powell for their friendship and logistic support in Cameroon, and P. Elkan and J. Ako for their help in the field. Field work was funded by the Wildlife Conservation Society through a grant from the U.S. Agency for International Development. Cameroon permits were issued by the Ministry of Environment and Forest. I also thank L. Ford (AMNH) and T. Daeschler (ANSP) for the loan of specimens examined in this study.

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Appendix
Specimens Examined

Atheris anisolepis (3): Democratic Republic Of The Congo: Banana, Lower Congo; AMNH 11898–99. Kukolela, Congo R.; AMNH 45941.

Atheris broadleyi (5): Cameroon: East Province; DPL 3646, 3657, 5300, 5302. Center Province; DPL 5508.

Atheris squamigera (28): Cameroon: Bitye; AMNH 5254. Metet; AMNH 51841–43. Southwest Province; UTA R-31346, 44922–930, 44963, 45003–04. Democratic Republic Of The Congo: Lukolela, Congo R.; AMNH 45940, 45943, 45945, 51840. Gabon: ANSP 27253. Near the River Gaboon, Guinea; ANSP 6949 Holotype. Kenya: Kakamega; UTA R-12782, 13037, 19510, 26612, 32074.

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Taxonomic notes on hummingbirds (Aves: Trochilidae)
2. *Popelairia letitiae* (Bourcier & Mulsant, 1852) is a valid species

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Abstract.—*Popelairia letitiae* (Bourcier & Mulsant, 1852), known from two specimens supposedly from Bolivia, appears to be a valid species. Analysis of plumage color and morphometrics indicates that *P. letitiae* does not represent an immature plumage or geographic variant of *Discosura longicauda,* although this species and *P. letitiae* may be sister taxa. No credible evidence for a hybrid origin of *P. letitiae* was discovered. "Letitia's Coquette" is proposed as the common English name for *P. letitiae.*

Known from two specimens of vague provenance, *Popelairia letitiae* (Bourcier & Mulsant, 1852), has been neither observed nor collected during the 20th century. This fact alone is reason enough to question the taxonomic validity of Letitia's Coquette, as many nominal trochiline taxa of comparable rarity have proven to be hybrids (Meyer de Schauensee 1947; Graves 1996, 1997a, 1997b, 1998a). Nonetheless, the systematic status of *P. letitiae* remains unchallenged (Mulsant & Verreaux 1876, Elliot 1878, Boucard 1893, Cory 1918, Simon 1921, Peters 1945, Morony et al. 1975, Sibley & Monroe 1990), although Salvin (1892) may have been the last taxonomic authority to critically examine the type specimen. The relevance of this issue was brought to the forefront by the inclusion of *P. letitiae* in a recent survey of threatened avian species (Collar et al. 1992). Here I offer an appraisal of the systematic status of *P. letitiae.*

Despite its current placement in the genus *Popelairia* (Peters 1945, Morony et al. 1975, Sibley & Monroe 1990), *letitiae* more closely resembles *Discosura longicauda* in plumage color (Elliot 1878). Generic limits in the Trochilidae are based primarily on male plumage traits (Taylor 1909). This has resulted in a proliferation of genera (n = 109), more than 1/4 of which are monospecific (Sibley & Monroe 1990). Zimmer (1950) advocated merging all band-rumped coquettes and thorntails in a single genus, *Lophornis.* Even under a narrow interpretation of generic limits, *Popelairia* would have been merged with *Discosura* if not for the racket-tipped rectrices of the latter (Elliot 1878). In that eventuality, *Popelairia* Reichenbach 1854 would become a junior synonym of *Discosura* Bonaparte 1850. In order to avoid nomenclatural confusion, however, I use the binomial, *Popelairia letitiae,* throughout this paper.

Methods

The type of *Popelairia letitiae* (BMNH 1888.7.25.83 in The Natural History Museum, formerly British Museum of Natural History) was obtained from John Gould, who procured it from Bourcier (Gould 1858, Warren 1966). A second specimen in the American Museum of Natural History (AMNH 38060) was part of the Daniel Giraud Elliot collection cataloged in 1888 (fide Paul Sweet). Both specimens appear to be males in definitive plumage as judged by their brilliant gorgets, crowns, elongated rectrices, and unstriated maxillary ramphothecae (Figs. 1–3). I compared them with male specimens of all species of hum-

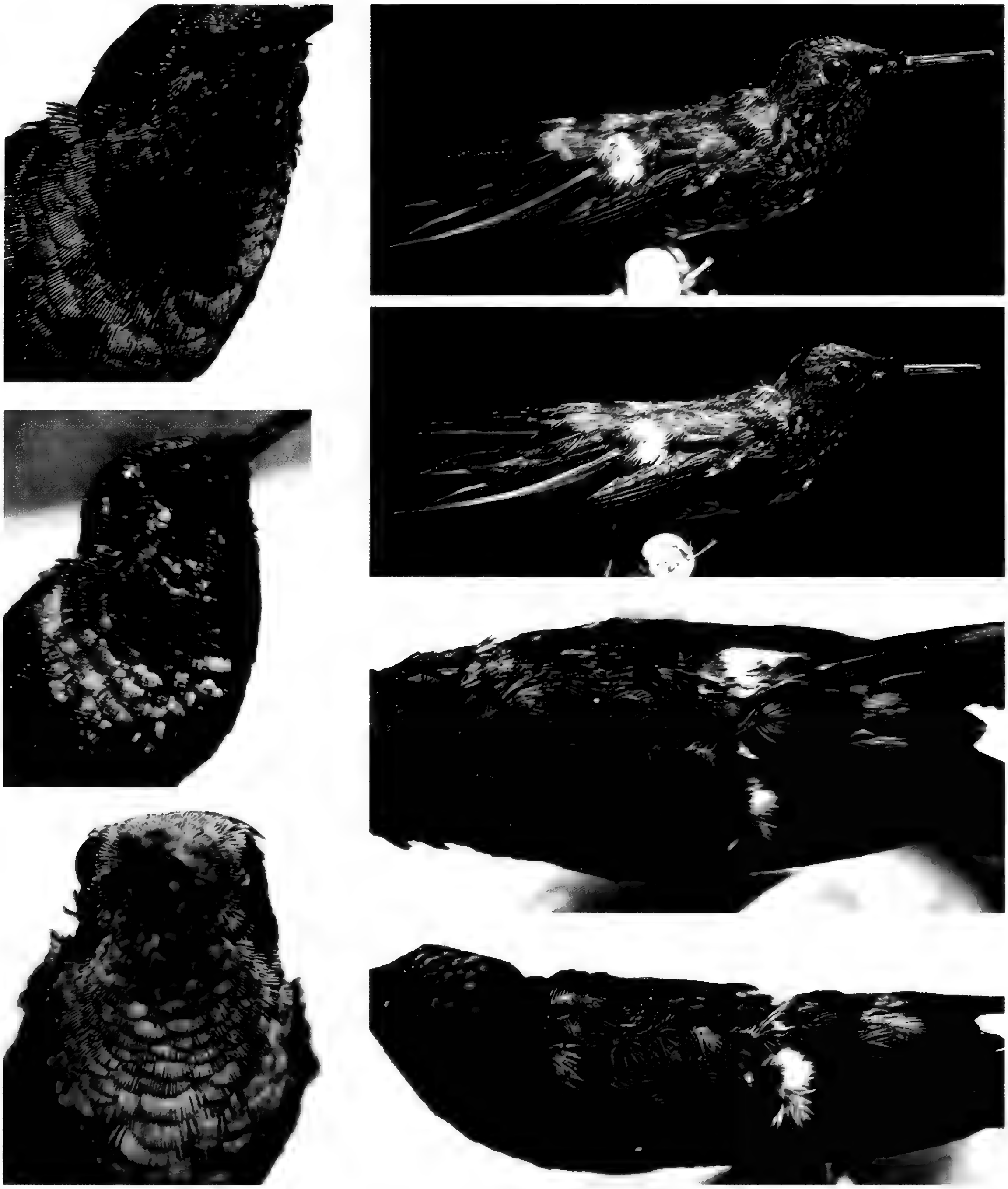

Fig. 1. Multiple exposures of the type specimen (BMNH 1888.7.25.83) of *Popelairia letitiae* (Bourcier & Mulsant, 1852).

mingbirds deposited in The Natural History Museum and the American Museum of Natural History. It was not possible to compare directly the two specimens. However, I compared photographs of the AMNH specimen of *P. letitiae* with the type specimen (BMNH), and vice versa. Because previous characterizations of *P. letitiae* were brief and somewhat contradictory, I provide a more detailed description in Appendix 1. Measurements of wing chord, bill length (from anterior extension of feathers), and rectrix length (from point of insertion of central rectrices to the tip of each rectrix) were made with digital calipers and rounded to the nearest 0.1 mm. Rectrices are numbered from innermost (R1) to outermost (R5) (Table 1).

I evaluated the color of the plumage (forecrown, back above white band, rump below white band, upper throat, lower side of throat, lower breast along midline) with

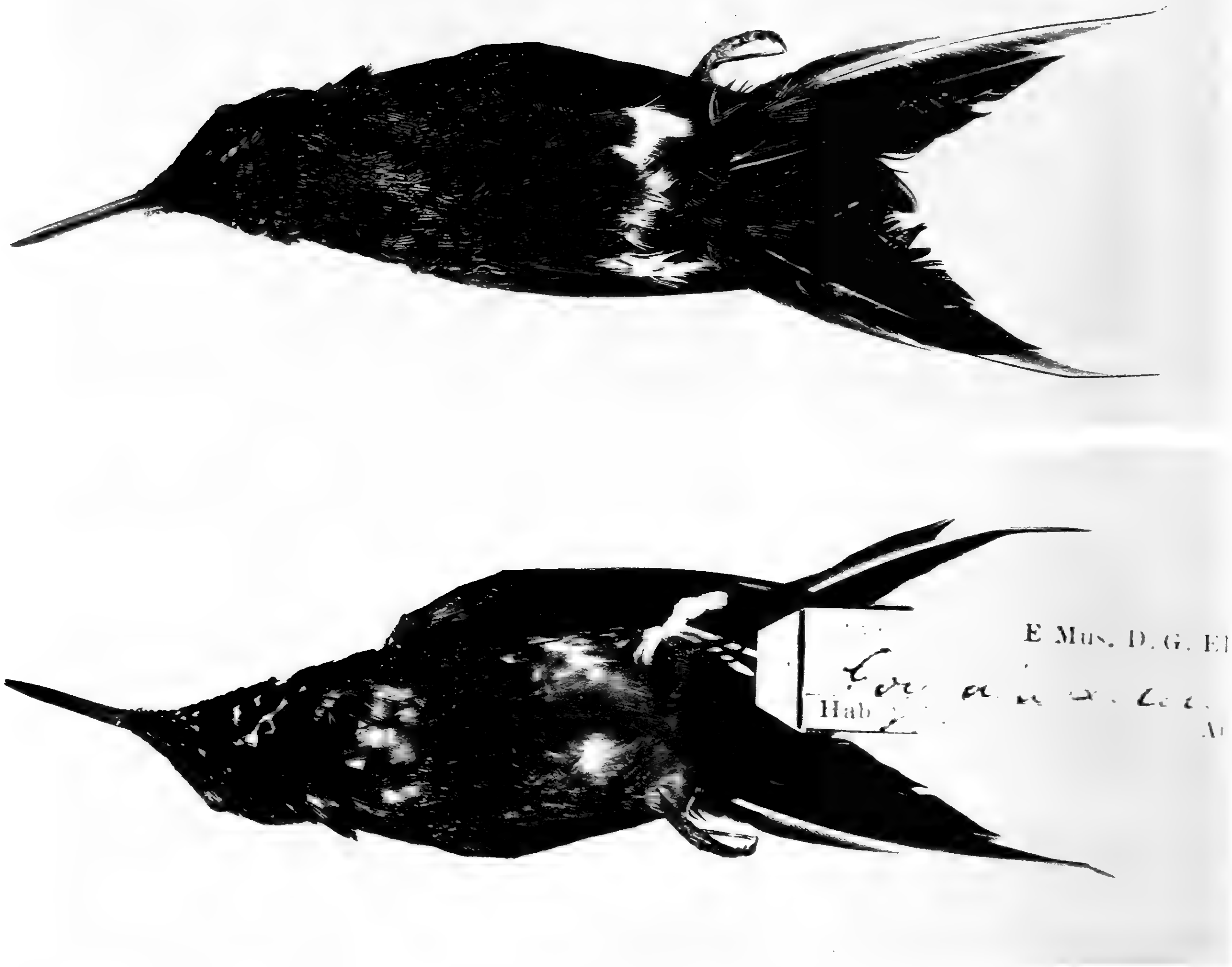

Fig. 2. Dorsal and ventral views of Elliot's specimen of *Popelairia letitiae* (AMNH 38060).

Fig. 3. Lateral view of Elliot's specimen of *Popelairia letitiae* (AMNH 38060).

Table 1.—Measurements (mm) of the two known specimens of *Popelairia letitiae* and male specimens of *Discosura longicauda* (range; mean ± standard deviation) in definitive plumage.

	Popelairia letitiae		
	BMNH 1888.7.25.83	AMNH 38060	*Discosura longicauda* $n = 15$[a]
Wing Chord	37.8	38.0	42.1–47.5 (45.2 ± 1.6)
Bill length	10.5	10.9	10.2–12.4 (11.4 ± 0.6)
Rectrix 1	14.8	Missing	15.2–19.2 (16.7 ± 0.9)
Rectrix 2	19.7	16.1	24.3–28.2 (26.0 ± 1.1)
Rectrix 3	26.7	22.5	29.2–33.6 (32.0 ± 1.2)
Rectrix 4	30.7	29.3	32.3–37.5 (35.0 ± 1.4)
Rectrix 5	36.2	38.9	49.9–56.0 (52.5 ± 2.0)

[a] Bahia, Brazil ($n = 4$), Brazil ($n = 2$), ''Cayenne'' ($n = 3$), ''British Guiana'' ($n = 1$), Guyana ($n = 4$), locality unknown ($n = 1$).

[b] Tip (~0.2–0.4 mm) missing.

a calibrated colorimeter (CR-221 Chroma Meter, Minolta Corporation) equipped with a 3.0 mm aperture. The measuring head of the CP-221 uses 45° circumferential illumination. Light from the pulsed xenon arc lamp is projected onto the specimen surface by optical fibers arranged in a circle around the measurement axis to provide diffuse, even lighting over the measuring area. Only light reflected perpendicular to the specimen surface is collected for color analysis. Colorimetric data from iridescent gorget feathers are acutely dependent on the angle of measurement, the curvature of the gorget surface in museum skins, and the degree of pressure applied to the plumage surface by the Chroma Meter aperture. In order to reduce measurement variation, I held the aperture flush with the plumage surface without depressing the plumage surface. The default setting for the CR-221 Chroma Meter displays mean values derived from three sequential, in situ measurements. I repeated this procedure three times for each area of plumage, removing the aperture between trials. Thus, each datum summarized in Table 2 represents the mean of three independent measurements, each of which represents the average of three sequential default measurements.

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

I considered four hypotheses: *Popelairia letitiae* represents (1) an immature plumage of *Discosura longicauda*; (2) a geographic variant of *D. longicauda*; (3) a hybrid; or (4) a valid species. In investigating the possibility of hybridization, I considered the band-rumped coquettes and thorntails that occur in South America (i.e., *Lophornis ornatus, L. gouldii, L. magnificus, L. delattrei, L. stictolophus, L. chalybeus, L. pavoninus, Popelairia popelairii, P. langsdorfii, P.*

Table 2.—*L a b* opponent color coordinates for plumage characters of the two known specimens of *Popelairia letitiae*: L = lightness; a/−a = red/green; b/−b = yellow/blue.

		BMNH BMNH 1888.7.25.83			AMNH 38060		
Plumage character	Color[a]	*L*	*a*	*b*	*L*	*a*	*b*
Forecrown	golden-green	19.9	−5.7	12.0	23.1	−4.0	13.3
Lower back above band	coppery-bronze	24.5	4.3	15.0	21.4	5.0	10.5
Rump below band	coppery-bronze	25.1	9.2	20.1	19.6	8.5	11.4
Upper throat	golden-green	11.6	−0.2	4.5	16.8	−3.4	8.9
Lower throat (side)	golden-green	13.9	−1.3	9.0	13.4	−0.5	6.7
Lower breast (midline)	bronze-green	25.6	2.1	15.8	22.9	3.9	10.7

[a] General color observed when specimen is held in a position that yields the greatest apparent brilliance.

conversii, Discosura longicauda) as potential parental species (taxonomy of Sibley & Monroe 1990). Fewer than half (23 of 55) of the possible pairwise combinations of the aforementioned species actually occur in nature (i.e., species sympatric at the resolution of 1° × 1° latitude-longitude blocks). Unless otherwise noted, assessments of plumage characters refer to those of males in definitive plumage. Assumptions and methods of hybrid diagnosis follow Graves (1990) and Graves & Zusi (1990).

Results

Immature plumage or geographic variant of Discosura longicauda?—A review of plumage and mensural characters demonstrates that *Popelairia letitiae* is not an immature of *Discosura longicauda.* Immature males of *D. longicauda* possess rounded rectrices (USNM 328627, AMNH 46737) that are replaced in subsequent molts by sharply attenuated (R2–R4) and racket-tipped (R5) rectrices. The outer rectrices (R4–R5) of *Popelairia letitiae* are sharply attenuated and lack rackets. *P. letitiae* also differs from *D. longicauda* in lacking a black chin spot, in possessing a yellowish-brown mandibular ramphotheca (black in *D. longicauda*), coppery-bronze back plumage (green in *D. longicauda*), white rump band (buff in sub-definitive plumages of *Discosura longicauda*), coppery-bronze rump (green in definitive plumages, purplish-black in sub-definitive plumages of *D. longicauda*), and dull bronze-green lower breast and abdomen (spangled with iridescent golden-bronze disks in both definitive and sub-definitive plumages of *D. longicauda*). Finally, bill length is similar in *P. letitiae* and *D. longicauda,* but the wing and rectrices are substantially shorter in *P. letitiae* (Table 1). The qualitative differences between *P. letitiae* and *D. longicauda* far exceed the magnitude of geographic variation exhibited within species of *Popelairia* and *Lophornis,* and approximate the level of morphological divergence observed among the largely allopatric rufous-crested species of *Lophornis* (Zimmer 1950).

Hybrid?—I failed to discover convincing evidence for a hybrid origin of *Popelairia letitiae.* Among the pool of potential parental species, the pale mandibular ramphotheca (possibly orange in life) of *P. letitiae* is shared with the rufous-crested species of *Lophornis* (*ornatus, gouldii, magnificus, delattrei, stictolophus*). These same species also exhibit varying amounts of rufous in the gorget. Because rufous pigmentation appears to be inherited in a codominant fashion in hummingbird hybrids (see Banks & Johnson 1961, Graves & Newfield 1996), I would expect *Lophornis* hybrids in definitive plumage to exhibit traces of ochraceous or rufous pigments in crown and gorget feathers. However, none were found in *P. letitiae* (10× magnification). This forcefully suggests that *P. letitiae* shares no immediate genealogical relationship with the rufous-crested species of *Lophornis.* Likewise, I could see no manifestation of a coronal apterium (blue in life) present in *L. chalybeus* (Ruschi 1962) or the elongated and spectacularly spotted auriculars of *L. pavoninus* in either specimen of *P. letitiae.* Further, none of the pairwise species combinations drawn from the subset consisting of *Discosura longicauda* and *Popelairia* (*popelairii, langsdorfii, conversii*) could have produced the suite of characters exhibited by *P. letitiae* (e.g., pale mandibular ramphotheca, coppery-bronze rump).

Additional evidence arguing against the hybrid hypothesis is provided by feather length and shape, both of which appear to be controlled polygenically in hummingbird hybrids (Banks & Johnson 1961, Graves 1990). *Lophornis ornatus, L. gouldii, L. magnificus, L. delattrei,* and *L. stictolophus* possess elongated crests (>11 mm), and *L. chalybeus* and *L. gouldii* have lateral gorget feathers that exceed 15 mm in length. Crown (4.3–5.5 mm) and lateral gorget feathers (6.8–7.0 mm) of *P. letitiae* are rounded, similar in size and shape to those of *Discosura longicauda.* These data provide further grounds for excluding *Lophornis* species from the pool of potential parental species. All combinations of species drawn from the subset of thorntails (*Popelairia popelairii, P. langsdorfii, P. conversii*) and *Discosura longicauda* can again be eliminated from consideration because their outer rectrices are substantially longer than those of *P. letitiae.*

The two specimens of *Popelairia letitiae* are similar in size and shape (Table 1). Wing length differs by 0.5%, whereas the difference in rectrix lengths vary from 4.7% (R4) to 22.4% (R2). These values fall within the normal range of variation found among museum samples of trochiline hummingbirds (e.g., Graves 1996, 1997a, 1998c). Plumage pattern and color are nearly identical, agreeing in such minor characters as tibial feathering and undertail coverts (Table 2, Appendix 1). These observations are consistent with the hypothesis that *P. letitiae* is a valid species.

In conclusion, analysis of plumage and size characters indicates that *Popelairia letitiae* does not represent an immature plumage or geographic variant of *Discosura longicauda,* although the close resemblance of the two suggests a sister species relationship. As noted in the introduction, the very rarity of *P. letitiae* in museum collections raises the specter of hybridization. However, based on known patterns of phenotypic inheritance in trochiline hybrids (Banks & Johnson 1961; Graves 1990, 1998c, 1999; Graves & Zusi 1990) and the characteristics of phenotypic variants (e.g., Graves 1998b), the possibility that *P. letitiae* represents a hybrid seems remote. Barring discovery of contradictory data, *P. letitiae* should be regarded a valid species.

Geographic origin.—Both specimens of *Popelairia letitiae* were thought to have been collected in "Bolivia" (Bourcier & Mulsant 1852, Elliot 1878), and Remsen & Traylor (1989) suggested "northeastern Bolivia" as a possible site. The purveyor of the type specimen is unknown (Bourcier & Mulsant 1852), whereas "Verreaux" was listed as the collector of the AMNH specimen. Both are relaxed taxidermy mounts prepared in a similar style, perhaps by the Verreaux brothers, who operated a thriving import/export business in natural history specimens in Paris during the middle decades of the 19th century.

Collecting localities inscribed on labels of 19th century hummingbird specimens are frequently unreliable (Berlioz & Jouanin 1944). For example, in the same paper in which *Popelairia letitiae* was described, Bourcier & Mulsant (1852) reported the type locality of *Ramphodon dohrnii* as "la République de l'Équateur," although this species is apparently restricted to the Atlantic coastal forest of Brazil. Consequently, it would be unwise to confine a contemporary search for *P. letitiae* to Bolivia.

Common English name.—Bourcier & Mulsant (1852:144) dedicated *Popelairia* *letitiae* to the "jeune enfant de M^{me} la marquise Delgallo, fille de l'un des ornithologistes les plus célèbres de l'Europe, M. Le prince Charles Bonaparte." The authors offered no common name and Gould (1858) referred to the taxon simply as "Letitia" in his Monograph of the Trochilidae. Sixty years later, Cory (1918) proposed "Letitia's Thorn-bill." The group name "thornbill" is now restricted to short-billed species in two related Andean genera, *Chalcostigma* and *Ramphomicron* (Sibley & Monroe 1990). No other common English name was used in taxonomic literature until Meyer de Schaunsee (1966) coined a new name, "Coppery Thorntail," which has been used sporadically since then (e.g., Collar et al. 1992). Meyer de Schauensee's name was inappropriate because other species in the complex possess "coppery" plumage, and because *Popelairia letitiae* does not possess a "thorntail" on par with those of the so-called thorntails (*Popelairia popelairii, P. langsdorfii, P. conversii*). I recommend "coquette" as a group name for the small band-rumped species currently placed in the genera, *Lophornis, Popelairia,* and *Discosura* (Sibley & Monroe 1990), and the common English name, "Letitia's Coquette," for *Popelairia letitiae.*

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Appendix 1

Description of male *Popelairia letitiae* in definitive plumage based on the two known specimens (type, BMNH 1888.7.25.83; AMNH 38060). Characterization of structural colors is unusually subjective as color seen by the observer varies according to the angle of inspection and direction of light. Color descriptions were made under natural light.

Forecrown and crown (to a line drawn behind the eyes) are brilliant golden-green. The crown color blends smoothly into dark bronze-green on the hindneck and back. Crown feathers are of moderate length (4.3–5.5 mm long) and rounded. The mantle emits a coppery-bronze iridescence when viewed in direct light. Wing coverts are the same color as back plumage. A narrow white band crosses the lower back. Band feathers are gray, broadly tipped with silky white barbs (especially apparent at the sides). The white band is bordered posteriorly by a coppery-bronze (coppery-purple or coppery-red at some angles) rump, which in turn is bordered by bronze-green uppertail coverts.

The chin to upper breast is brilliant golden-green (about the same as crown; see Table 2), with coppery-gold reflections at the sides of the throat (when viewed head-on). Iridescent terminal disks are bordered proximally by a narrow subterminal bronze-green zone, a broader band of dull white (obscured by imbricated feather tips), and finally by gray basal barbs. Obscured portions of gorget feathers become progressively grayer toward the sides of the throat; the outer vane of lateral gorget feathers is gray below the iridescent disk. Lateral gorget feathers are of moderate length (6.8–7.0 mm), the iridescent disks are slightly wider (~2.8–3.1 mm) than long (~2.3–2.4 mm). Green terminal disks are reduced or absent along the posterior border of the gorget, producing a mottled green and white pectoral band. The breast below the pectoral band is bronze-green along the midline. This area is burnished with coppery-gold (AMNH specimen) and a few spangles of coppery-red immediately below the pectoral band. Feathers of the lower belly and sides are broadly tipped with buffy-white and grayish-white barbs. Vent feathers are dark gray, tipped with white. The undertail coverts are dark green with gray bases and rufous tips. Tibial feathers are of moderate length (reaching about half way to the base of the hallux), dark gray, tipped with a mixture of white and cinnamomeous barbs.

The outermost rectrix (R5) is brownish-black with a bluish sheen on the medial vane. A pale stripe bordering the rachis becomes wider and buffier near the base of the shaft. Dorsal rachis color is pale cinnamomeous, becoming browner distally. The inner rectrices (R2–R4) are similar in color and pattern. The outer vanes of R4 & R3 in the AMNH specimen are faintly glossed with bronzy-green. Both vanes of R2 in the AMNH specimen are glossed with bronze-green (less pronounced in the type). There is a small V-shaped buffy spot at the tip of R2 in both specimens. The innermost pair of rectrices is absent in the AMNH specimen. Those of the BMNH specimen are bronze-green, broadly tipped with black, and faintly marked with terminal V-shaped cinnamomeous spot. From below, the medial vanes are bluish-black (R3–R5); the rachises are white, becoming very pale buffy-white proximally. The remiges, which lack emarginations or markedly thickened rachises, are black with faint purple and bronze glossing under strong light.

The maxillary ramphotheca is black becoming dark brown at the nares. The nares are completely obscured by adpressed feathers. The mandibular ramphotheca is brownish-yellow (slightly darker in the type) becoming dark brown about half way to the bill tip. Scutes of toes and tarsometatarsus are medium brown—less heavily melanized than in *Popelairia langsdorfii* or *Discosura longicauda*.

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Identification and distribution of cotton rats, genus *Sigmodon* (Muridae: Sigmodontinae), of Nayarit, México

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Abstract.—Morphological, chromosomal, distributional, and ecological data are presented for three species of *Sigmodon* (*S. alleni, S. arizonae,* and *S. mascotensis*) from the state of Nayarit, México. The species were collected in all possible pairwise combinations of sympatry, including the first record of such documented for *S. arizonae* and *S. mascotensis.* Emphasis is devoted to the discrimination of *S. arizonae* and *S. mascotensis,* from each other and from typical *S. hispidus,* using qualitative features of the skin and skull and morphometric analyses of craniodental measurements. Based on these results and examination of type specimens, additional synonyms of *S. mascotensis* are identified, with reassignment of two forms, *tonalensis* Bailey (1902) and *obvelatus* Russell (1952), currently mistaken as subspecies of *S. hispidus. Sigmodon mascotensis* emerges as a species distributed from southern Nayarit and Zacatecas to extreme western Chiapas, where it inhabits deciduous or semideciduous tropical vegetation having a pronounced dry season. These reallocations and other reidentifications remove any documentation for *S. hispidus* along the entire Pacific versant of México.

A useful form of research communication that sees less application today is the brief expeditionary account or short faunal note. Aside from the practical enhancements in knowledge of a taxon's distribution and habitat, such reports offer the advantage of bringing regionally focussed nomenclatural clarity to complex taxonomic problems that seem incomprehensible over a broader geographic scale. One recalls that the prolific literature appearing over the past two decades on the *Peromyscus boylii* group emanated from Hooper's (1955) immemorable commentary in "Notes on Mammals of Western México," in which he recorded the sympatric occurrence of various "morphological types" of *boylii* at several collecting localities in Jalisco, Nayarit, and Sinaloa (see systematic reviews by Carleton 1989, and Bradley et al. 1996).

The regional focus here is Nayarit, México, and the taxon of interest is the genus *Sigmodon,* the ecologically abundant cotton rats that inhabit open landscapes from the southern United States, through México and Middle America, to northern South America (Hall 1981, Voss 1992). Situated along coastal westcentral México, the state of Nayarit encloses a varied topography and diverse natural environments, a biogeographical setting that has proven pivotal for illuminating the systematics of other small mammals (for example, Fisher & Bogan 1977, Gardner 1977, Bogan 1978, Diersing & Wilson 1980, Carleton et al. 1982, Wilson 1991).

The excellent series of Nayarit cotton rats collected by personnel of the U.S. Fish and Wildlife Service in the middle 1970s warrant report in view of Zimmerman's (1970) seminal report on *Sigmodon* taxonomy. His study, and the subsequent contributions of

Severinghaus & Hoffmeister (1978) and Hoffmeister (1986), revealed the greater species diversity and distributional complexity of *Sigmodon* found in the southwestern United States and northwestern México. In this report, we document the kinds and distribution of *Sigmodon* species in Nayarit (*S. alleni, S. arizonae,* and *S. mascotensis*); review morphological and chromosomal characteristics for identifying the species, with emphasis on discrimination of *S. arizonae* and *S. mascotensis*; and amplify the known geographic range of *S. mascotensis* in western México, including the reallocation of forms currently classified as subspecies of *S. hispidus* (namely, *Sigmodon hispidus tonalensis* Bailey, 1902, and *Sigmodon hispidus obvelatus* Russell, 1952).

Materials and Methods

The 214 specimens of Nayarit *Sigmodon* that form the nucleus of this report are contained in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM, the abbreviation for the former United States National Museum). A few originated from the pioneering Biological Survey of México conducted by E. A. Goldman and E. W. Nelson (1897 expedition to Tepic; see Goldman 1951), but most were collected recently (1975–1977) by personnel associated with the U.S. Fish and Wildlife Service (now part of the USGS Patuxent Wildlife Research Center), pursuant to a faunal analysis of Nayarit mammals. Other specimens reported here, including holotypes and type series, are housed in the American Museum of Natural History, New York (AMNH); the Field Museum of Natural History, Chicago (FMNH); Museum of Natural History, University of Kansas, Lawrence (KU); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); The Museum, Michigan State University, East Lansing (MSU); and Texas Cooperative Wildlife Collections, College Station (TCWC).

Table 1.—Gazetteer of collecting localities (see Fig. 1).

Locality	Elevation (meters)	Coordinates N/W
1. Tacote, 1.4 mi N	15	22°38′/105°27′
2. Río Canas, near La Concha	20	21°31′/105°26′
3. Acaponeta	46–75	22°29′/105°21′
4. Cuautla, 1 mi S	0	22°12′/105°38′
5. Santa Cruz, 6 km S	0	21°56′/105°35′
6. Playa Colorado	0	21°53′/105°34′
7. Playa Los Corchos, 4 mi E	0	21°43′/105°25′
8. San Blas	0	21°32′/105°17′
9. Aticama, 4 km S	50	21°27′/105°11′
10. Chacala	30	21°10′/105°13′
11. Lo de Marcos, 1 mi S	0	20°57′/105°21′
12. El Venado, 3.5 mi E	100	22°57′/104°57′
13. Arroyo de Jiguite	100	21°49′/104°48′
14. El Casco, 1.2 mi S	60	21°45′/104°51′
15. La Villita, 1 km S	760	21°35′/104°56′
16. Tepic	1000	21°30′/104°53′
17. San Pedro Lagunillas, 2 mi E	1300	21°12′/104°43′
18. Estanzuela	1380	21°16′/104°28′
19. Coapan, 1.8 mi NW	1560	21°09′/104°29′
20. Ahuacatlán, 8 mi S	1500	20°58′/104°28′
21. Mesa del Nayar	1300	22°12′/104°39′
22. Ocota Airstrip	1900	21°50′/104°13′
23. Rancho Sapotito	1100	21°20′/103°58′

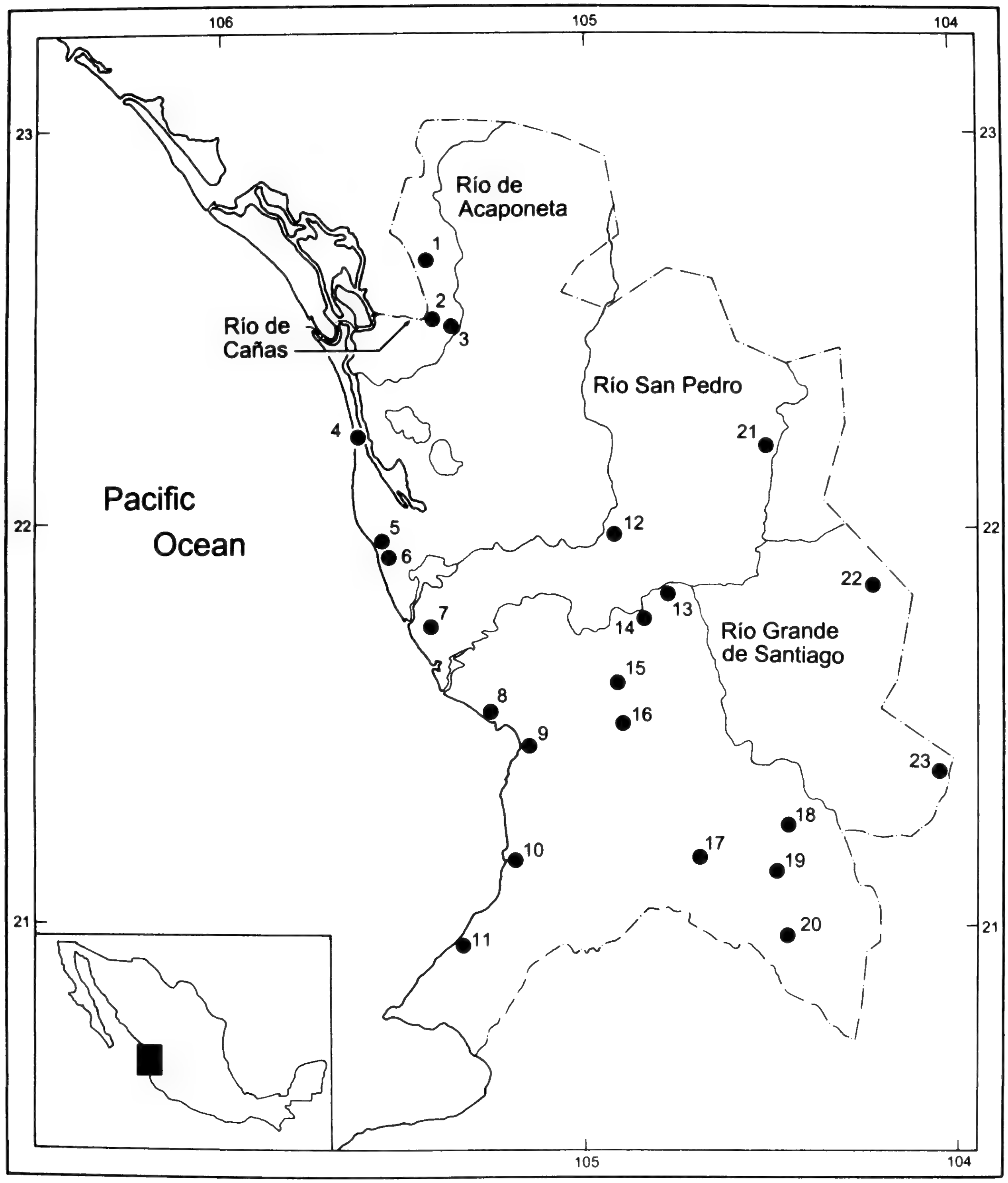

Fig. 1. State of Nayarit, México, illustrating collecting localities of *Sigmodon* specimens housed in the National Museum of Natural History (numbers refer to sites listed in Table 1).

Twenty-three Nayarit localities are represented in the preserved material (Table 1, Fig. 1). Coordinates of collecting sites were later determined from 1:50,000 topographic maps used by the field teams and annotated with the localities visited; most elevations were recorded in the field with an altimeter and later verified against the same topographic series.

Animals were generally preserved as conventional study skins and skulls but also as complete skeletons and formalin-fixed, whole carcasses stored in alcohol. Preparation of standard chromosomal spreads, definition of fundamental number (FN), and descriptive terminology for chromosomal morphology follow Patton (1967) and Gardner & Patton (1976). The 32 voucher specimens for the karyotypic variation reported are contained in USNM and represent the localities listed next.

Sigmodon alleni: Nayarit, Arroyo de Jiguite, Río Santiago, 1 ♂ (523935); 4 km S Aticama, 1 ♂ (524480), 2 ♀ (524478, 524479); Chacala, 1 ♀ (523934); 1.2 mi S El Casco, 1 ♀ (511699); 1 mi S Lo de Marcos, 1 ♂ (523943), 3 ♀ (523940–523942).

S. arizonae: Nayarit, Mesa del Nayar, 1 ♀ (511700); Ocota Airstrip, 2 ♂ (523948, 523950), 4 ♀ (523946, 523947, 523949, 523951). Sinaloa, Microondas La Muralla, 1 ♂ (524487), 1 ♀ (524486).

S. mascotensis: Nayarit, 8 mi S Ahuacatlán 1 ♂ (523953), 2 ♀ (523952, 523954); Arroyo de Jiguite, Río Santiago, 4 ♂ (523962, 523963, 523965, 523966), 1 ♀ (523964); Rancho Sapotito, 2 ♂ (511703, 511704), 3 ♀ (511702, 511705, 511706).

We recorded 5 external, 18 cranial, and 3 dental dimensions (in millimeters, mm) to summarize patterns of variation within and between the populations sampled. Total length, length of tail vertebrae, hindfoot length, length of pinna from notch, and mass (weight in grams, g) were transcribed from skin labels. Crania were viewed under a dissecting microscope when measuring the 21 craniodental variables to 0.01 mm with hand-held, digital calipers accurate to 0.03 mm. These measurements, their abbreviations as used in tables and figures, and their landmark definitions where clarification is necessary, include (see Carleton and Musser, 1995, for illustration of most anatomical endpoints): occipitonasal length (ONL); zygomatic breadth (ZB); least interorbital breadth (IOB); breadth of braincase (BBC)—taken behind the squamosal root of the zygomatic arches, the caliper's jaws resting on the squamosal bones just above the flange (inferior temporal ridge) extending from the arches; breadth across occipital condyles (BOC); depth of braincase (DBC); distance between temporal ridges (DTR)—vertical distance between the dorsal margin of the superior temporal ridge and the ventral edge of the inferior temporal ridge (see Fig. 8); length of rostrum (LR)—measured oblique to the midlongitudinal cranial axis, from the innermost bevel of the right zygomatic notch to the end of the nasals at their midsagittal junction; breadth of rostrum (BR)—distance across the lateralmost convexity of the nasolacrimal capsules; postpalatal length (PPL); length of bony palate (LBP); breadth of bony palate (BBP); length of incisive foramen (LIF); length of diastema (LD); breadth of zygomatic plate (BZP); length of zygomatic spine (LZS)—distance between the anterior orbital rim and the tip of the zygomatic spine; length of auditory bulla (LAB); coronal length of maxillary toothrow (LM1-3); coronal width of upper first molar (WM1); depth of upper incisor (DI); depth of mandible (DM)—distance, taken on the lateral surface of the dentary, from the rim of the m1 alveolus to the ventralmost projection of the mental symphysis.

Relative age was coarsely indexed by degree of molar wear according to the four age-classes recognized by Carleton and Musser (1989)—juvenile (J), young (Y), full (A), and old-adult (O). The distinction between juvenile and young adult cohorts based on upper third molar eruption constituted a more objective criterion of age recognition than did the assignment of individuals among the three adult classes based on gradations of wear. Among specimens with annotation of their reproductive state, many we assigned as young or full adult based on tooth wear exhibited signs of reproductive maturity (testis scrotal, evidence of lactation, counts of embryos or embryo scars), whereas those classified as juveniles did not.

To augment sample sizes for the various morphometric comparisons, Nayarit specimens were grouped into eight analytical samples (operational taxonomic units, OTUs), as defined below (locality numbers correspond to those identified in Table 1 and Fig. 1). To provide a comparative standard, we included a homogeneous series of *Sigmodon hispidus,* sensu stricto, as a ninth OTU (U.S.A., Florida, Wakulla Co., St. Marks National Wildlife Refuge; *n* = 53; USNM 526059–526106, 527358, 527359, 527362–527364). Since most collectors at this locality also participated in the Nayarit survey, one can expect procedural conformity in the measurement of external variables.

Sigmodon alleni: OTU 1, *n* = 20, localities 8–15.

S. arizonae: OTU 2, *n* = 9, localities 2–7; OTU 3, *n* = 25, locality 17; OTU 4, *n* = 6, locality 22.

S. mascotensis: OTU 5, *n* = 27, locality 13; OTU 6, *n* = 46, locality 17; OTU 7, *n* = 12, localities 18–20; OTU 8, *n* = 6, locality 23.

S. hispidus: OTU 9, *n* = 53, Florida.

Standard descriptive statistics (mean, range, standard deviation) were obtained for the OTUs. Principal components and canonical variates were extracted from the variance-covariance matrix and computed using natural logarithmic transformations of the 21 craniodental variables. Loadings are expressed as Pearson product-moment correlation coefficients of the principal components or canonical variates with the original skeletal and dental variables. All univariate and multivariate computations were generated using Systat (Version 7.0, 1997), a series of statistical routines programmed for microcomputers.

Discrimination of Nayarit *Sigmodon* and Comparisons with *Sigmodon hispidus*

Intrasample age and sex variation.—Field and lab workers who study *Sigmodon* populations have regularly commented on the considerable ontogenetic variation encountered (e.g., Chipman 1965, Baker 1969, Voss 1992, Zelditch et al. 1992). Cotton rats are highly precocial and weaned animals soon enter the trappable population; seasonal differences in age composition of a population, as well as differences in growth rates between age cohorts, may be remarkable (Layne 1974, Slade et al. 1984). In view of such demographic factors, we found age variation to be equally conspicuous in all species samples of *Sigmodon* reported here, an impression quickly formed from superficial observation of crania and their wide range in size, shape, and rugosity. Casual visual impressions are reinforced by statistical comparisons among age groups in the large sample of *S. hispidus* (Table 2). Nearly all measurements display regular, incremental increases in size across the four age classes we defined, producing age-correlated differences that contribute substantially to nongeographic variation within our locality samples. Notable exceptions include dimensions of the molars (LM1-3, WM1), which once erupted decrease in crown height with occlusal use but do not grow in size; in contrast, girth of the incisor (DI) enlarges appreciably as cotton rats age.

The contribution of sexual dimorphism to intrasample variation, on the other hand, is hardly apparent, at least given the unbalanced nature of analyzable material usually consolidated from museum collections. Only two (IOB, DTR) of the 21 craniodental measurements yielded significant differences according to sex (Table 2), and these are sufficiently infrequent and incidental to suggest sampling error as an explanation.

Other than procedural elimination of the youngest age class, juveniles, we did not adjust for size in the morphometric analyses. Although variation attributable to postweaning growth may be substantial within samples of *Sigmodon,* it is typically negligible relative to the interspecific contrasts that proved to be taxonomically important. In this respect, patterns of morphometric differentiation among cotton rats, their con-

Table 2.—Arithmetic means of craniodental variables and results of one-way *ANOVAs* for sex and age cohorts in a large sample of *Sigmodon hispidus* from Florida (OTU 9, $n = 53$).

	Sex			Age				
Variable	M (31)	F (22)	*f* (sex)	J (3)	Y (13)	A (29)	O (8)	*f* (age)
ONL	34.8	34.3	1.0	30.2	32.8	34.9	37.0	33.1***
ZB	19.5	19.3	1.5	17.2	18.7	19.5	20.3	21.7***
IOB	5.2	5.1	4.2*	4.8	5.0	5.2	5.3	7.8***
BBC	14.4	14.2	2.1	13.5	14.2	14.4	14.7	8.3***
BOC	7.5	7.5	0.4	7.5	7.4	7.4	7.7	1.9
DBC	10.7	10.7	0.5	10.1	10.6	10.7	11.2	8.6***
DTR	3.1	2.9	7.2**	2.4	3.0	3.1	3.3	12.4***
LR	11.6	11.5	0.2	9.8	10.9	11.7	12.5	21.4***
BR	6.7	6.6	0.9	6.1	6.3	6.7	7.3	22.8***
PPL	12.2	12.0	0.4	10.5	11.3	12.2	13.3	34.1***
LBP	6.6	6.5	1.7	6.1	6.3	6.7	6.7	6.2**
BBP	7.7	7.7	0.2	7.0	7.5	7.8	8.1	24.1***
LIF	7.8	7.7	0.1	6.7	7.3	7.9	8.5	19.8***
LD	9.6	9.3	1.1	8.1	8.7	9.7	10.5	31.5***
BZP	3.9	3.7	2.8	3.2	3.7	3.9	4.1	9.7***
LZS	4.6	4.4	1.3	3.6	4.3	4.6	4.9	11.3***
LAB	6.3	6.3	0.0	6.1	6.1	6.4	6.5	6.3**
LM1–3	6.4	6.4	0.2	6.4	6.4	6.4	6.3	0.5
WM1	2.1	2.1	0.5	2.1	2.1	2.1	2.1	0.5
DI	2.0	2.0	0.4	1.6	1.9	2.0	2.1	49.0***
DM	6.4	6.3	1.6	5.6	6.1	6.5	6.6	14.9***

* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$.

spicuous age variety notwithstanding, are much like those derived for other closely related, congeneric species of New World muroids (e.g., Carleton & Musser 1989, 1995; Voss & Marcus 1992, Hoofer et al. 1999).

Morphometric variation.—Covariation patterns derived from the 21 original craniodental variables suggest two kinds of large *Sigmodon* among Nayarit populations (Fig. 2). These clusters correspond to the species *S. arizonae* and *S. mascotensis* (Figs. 3, 4), identifications independently corroborated by agreement of karyotyped specimens with currently understood differences in diploid number (2N = 22 or 28; Zimmerman 1970) and by contrasts in certain qualitative features (see below). The "correct" phenetic association of relevant holotypes—*arizonae, major,* and *mascotensis* (Fig. 2)—bolsters the use of these names for the Nayarit populations. Greater size in all dimensions accounts for separation of *S. mascotensis* and *S. arizonae* on the first principal component (loadings uniformly large and positive—Table 3); the generous proportions of the latter's molars provide most discrimination on the second component (LM1-3 and WM1 correlations relatively large and negative). The resulting constellations of specimen scores conform to the now familiar ordination pattern evidenced between morphologically similar, closely related (congeneric) species of Muroidea; furthermore, their elongate spread and orientation, oblique to the bivariate plot of PC I and PC II, suggest the interplay of consistent interspecific shape differences and age-related size increases (Voss et al. 1990, 1992). Included among our samples is one locality where the two species were collected in sympatry (2 mi E San Pedro Lagunillas).

Unambiguous specific discrimination is preserved in the discriminant function analysis of the eight OTUs representing *S. ar-*

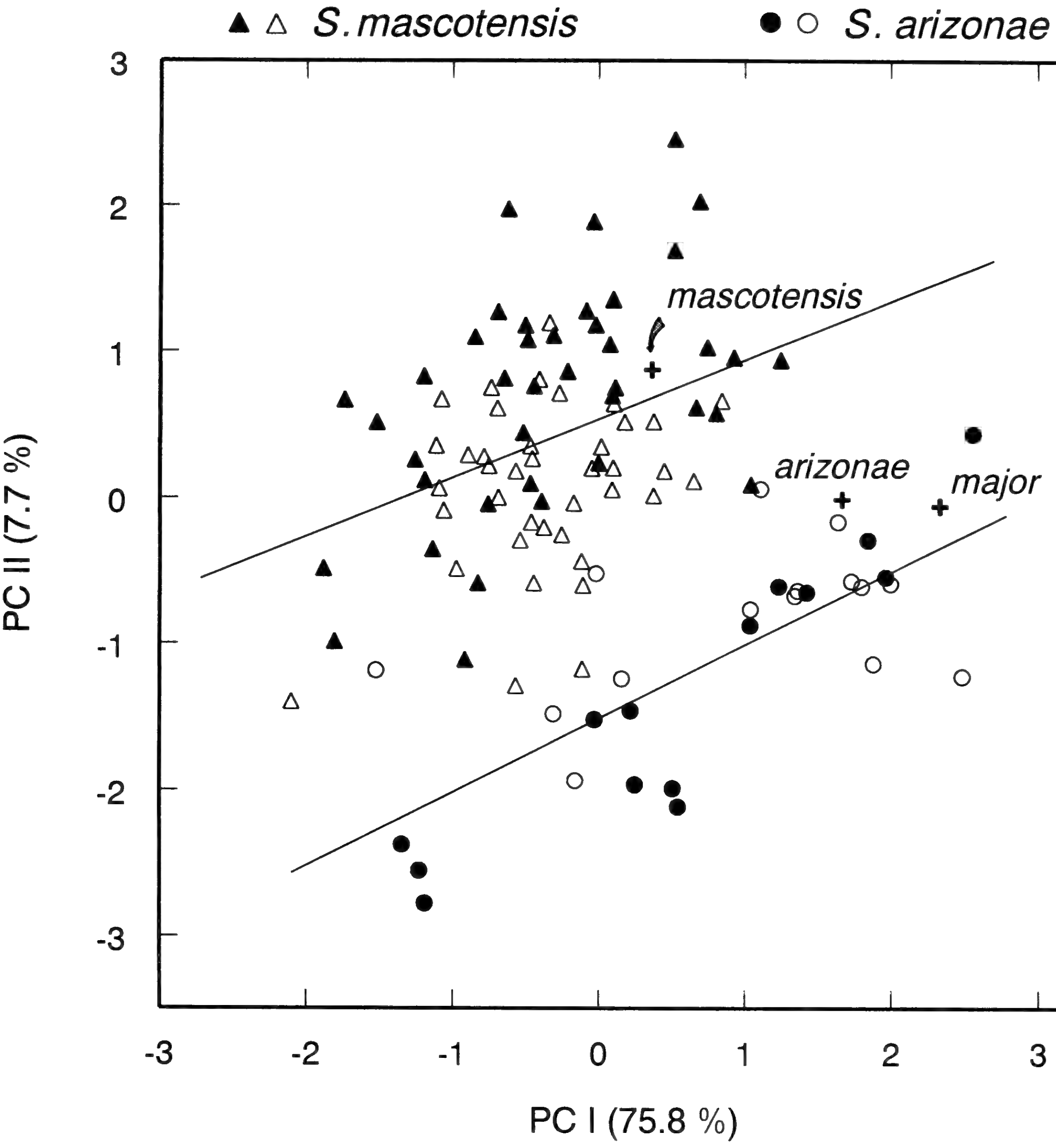

Fig. 2. Plot of first and second principal components extracted from analysis of 21 log-transformed craniodental variables measured on intact specimens of Nayarit *Sigmodon arizonae* (n = 29) and *S. mascotensis* (n = 79). Open symbols indicate specimens collected in close proximity at 2 mi E San Pedro Lagunillas, 1300 m; crosses refer to relevant type specimens discussed in the text. Regression lines of PC II on PC I differ significantly between species in their y-intercepts (0.54 versus −1.50; F = 144.9, $P < 0.001$) but not their slopes (0.42 versus 0.51; F = 0.3, $P = 0.553$). See Table 3.

izonae, S. mascotensis, and *S. hispidus* (Fig. 5). Separation of Floridian *S. hispidus* on the first canonical variate extracted primarily results from differences in three variables (Table 4)—the larger size of the auditory bullae (LAB), the narrower distance between the temporal ridges (DTR), and, perhaps in correlation with the latter, the shallower braincase (DBC). LAB also generated the largest *f*-value in one-way analyses of variance of the 21 craniodental measurements among the three species. Less conspicuously, the relatively greater length of the facial region in *S. hispidus* is reflected in the moderate, positive loadings for lengths of rostrum and incisive foramen, whose univariate means match those of the bigger *S. arizonae.* The generally larger values and comparable range (mostly −0.5 to −0.7) of correlations on the second ca-

Table 3.—Results of principal component analysis and one-way *ANOVAs* performed on all intact specimens of *Sigmodon arizonae* ($n = 29$) and *S. mascotensis* ($n = 79$) from Nayarit, México (see Fig. 2).

Variable	Correlations PC I	PC II	*ANOVAs* *f* (species)
ONL	0.97	0.15	20.9***
ZB	0.98	0.02	55.1***
IOB	0.75	0.07	4.1*
BBC	0.88	−0.20	70.0***
BOC	0.78	−0.22	32.1***
DBC	0.81	0.08	21.0***
DTR	0.82	−0.01	50.0***
LR	0.94	0.16	19.4***
BR	0.95	0.16	17.8***
PPL	0.96	0.13	23.9***
LBP	0.78	0.13	8.1**
BBP	0.94	−0.13	41.9***
LIF	0.94	0.01	44.3***
LD	0.96	0.18	22.9***
BZP	0.86	0.28	2.7
LZS	0.88	0.16	12.9***
LAB	0.85	−0.33	144.5***
LM1–3	0.64	−0.70	189.3***
WM1	0.53	−0.79	206.6***
DI	0.92	0.15	11.1**
DM	0.97	0.10	28.2***
Eigenvalue	15.9	1.6	
% Variance	75.8	7.7	

* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$.

nonical variate are more suggestive of general size and again underscore the robust proportions of *S. arizonae* apparent in visual inspection of skulls; the substantial dimensions of its molars (LM1-3, WM1) are particularly noteworthy in this regard. Samples of *S. mascotensis* approximate that of *S. hispidus* on the second axis.

A posteriori classifications of type specimens historically associated with the *S. hispidus* complex, as implemented in discriminant function analysis of the same eight OTUs, accord with some present taxonomic alignments and dispute others. The nomenclatural significance of these statistical assignments is considered in the Discussion and Taxonomic Summary (Fig. 17, Table 6—see below).

Sorting examples of Nayarit *S. alleni* from those of *S. arizonae* and *S. mascotensis* is straightforward based on pelage color (see below) or diploid number (2N = 52; Zimmerman 1970). Yet in cranial size and discrete characteristics, *S. alleni* (Fig. 6) unexpectedly proved somewhat difficult to distinguish from *S. mascotensis*; for example, most univariate measurements of the two overlap extensively (Appendix) and disclose relatively few significant differences between means (Table 5). Principal component analysis of log-transformed variables nonetheless supplied clear separation of the two species based on crania alone (Fig. 7). The variables most influencing discrimination represent measurements taken on the braincase (DBC, DTR), zygoma (LZS), and molars (LM1-3, WM1), each of which is notably greater in *S. mascotensis* (Table 5; Appendix). Holotypes of interest within the region appropriately associate with their respective Nayarit populations, those of *mascotensis* and *colimae* more so and that of *alleni* less so. Although the disposition of the type specimen of *alleni* was somewhat peripheral as divulged in PCA, discriminant function analysis based on all nine OTUs (not illustrated) indisputably placed the holotype with the Nayarit sample of the taxon.

Although external dimensions were excluded from multivariate examination, they generally reflect the same pattern of interspecific size contrasts noted for craniodental variables and supply helpful guidance for first-approximation field or museum identification (Appendix). The absolutely short and relatively narrow hind foot of *S. alleni,* for example, readily separates that species from young examples of *S. mascotensis.* As noted by Bailey (1902), hindfoot size and tail length, absolute and relative, help to distinguish *S. mascotensis* from examples of *S. h. hispidus* and *h. berlandieri.* Relative length of tail in *S. mascotensis* (TL ca. 45% of TOTL) also exceeds that in the larger-bodied *S. arizonae* (TL ca. 40% of TOTL), a species which otherwise stands apart for its exceptional mass and size in all other external variables quantified.

Fig. 3. Dorsal and ventral cranial views (about 1.75×) of adult *Sigmodon*: left pair, *S. mascotensis* (USNM 510026), a male from 2 mi E San Pedro Lagunillas, Nayarit; middle pair, *S. hispidus berlandieri* (USNM 157382), a male from 8 mi E Deming, New México; and right pair, *S. arizonae* (USNM 510040), a female from 2 mi E San Pedro Lagunillas, Nayarit.

Qualitative cranial traits.—Zimmerman (1970) identified several consistent cranial differences among *Sigmodon* populations that corresponded to the chromosomal contrasts he documented and to the three species he recognized among his samples—namely, *S. hispidus, S. arizonae,* and *S. mascotensis.* Other useful qualitative traits were advanced by Severinghaus & Hoffmeister (1978) and Hoffmeister (1986), particularly for separation of *S. hispidus* from *S. arizonae* in the southwestern United States. We here extend the utility of select cranial features to the Nayarit populations formerly included under *S. hispidus.*

The vertical distance between the supe-

Fig. 4. Lateral cranial view of adult *Sigmodon*: top, *S. mascotensis*; middle, *S. hispidus berlandieri*; and bottom, *S. arizonae* (same specimen numbers as in Fig. 3).

rior and inferior temporal ridges (the latter called the occipital crest by Zimmerman 1970) provides a reliable means for discriminating examples of *S. hispidus* from those of *S. arizonae* and *S. mascotensis.* As noted by Zimmerman, this distance is visibly narrower in *S. hispidus* relative to the latter two (see Appendix), a difference underscored by our multivariate results in which distance between the temporal ridges (DTR) heavily influenced the separation of OTUs along the first canonical variate (Fig. 5, Table 4). The temporal ridges, together with the lateral arc of the transversely oriented lambdoidal ridge, define the size and shape of the temporal fossa, an area on the lateral wall of the braincase from which originates the temporalis, an important masticatory muscle (Rinker 1954). In *S. hispidus* (and *S. alleni*), the temporal fossa tapers conspicuously toward the rear of the skull, forming a trapezoidal shape over the posterior half of the parietal and squamosal bones; whereas, the fossa in *S. mascotensis* and *S. arizonae* occupies a larger area, approximately rectangular in outline on the lateral braincase wall (Fig. 8). As expected for osseus features that provide muscular attachment, some change in fossa shape accompanies individual aging, such that juvenile animals of all three species exhibit a stronger rearward convergence of the superior and inferior temporal ridges; consequently, the size and shape differences noted are best appreciated when comparing crania of similar age classes.

The anterodorsal edge of the zygomatic plate forms a spinous process in all *Sigmodon* examined here, but its projection, and the degree of concavity imparted to the plate's anterior border, can aid specific identification, as demonstrated by Severinghaus and Hoffmeister (1978) for Arizonan populations of *S. hispidus* and *S. arizonae.* Among Nayarit samples, the spine is longest and most acute in specimens of *S. arizonae,* shortest in those of *S. alleni.* Configuration of the anterior zygoma in *S. mascotensis* more closely resembles *S. arizonae* but is not so extreme. Such interspecific contrasts are partially conveyed by certain variable loadings (BZP, LZS) generated from principal component and discriminant function analyses (Tables 3, 4), as well as by their mean differences (Appendix). Nevertheless, the expression of the spinous process has a strong age component (Table 2), which must be considered when comparing and identifying individuals. In *S. hispidus,* compared with *S. arizonae,* the spinous process is not only shorter, but its dorsal border appears wider and its tip is usually blunt (Severinghaus & Hoffmeister 1978:868, fig. 1; Hoffmeister 1986). In some individuals of *S. hispidus,* the spinous process is even expanded anteriorly to produce a knoblike

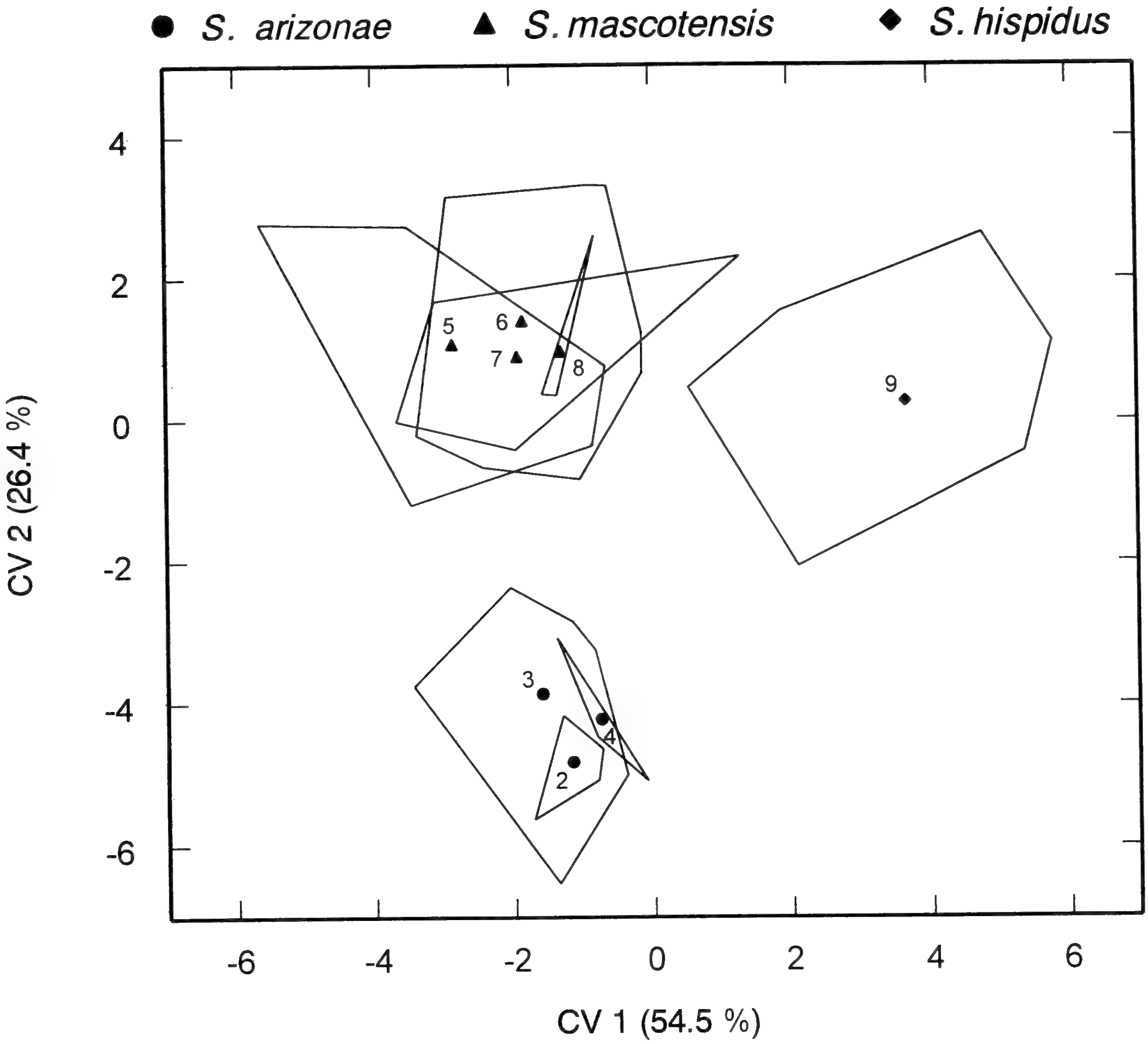

Fig. 5. Plot of the first and second canonical variates extracted from discriminant function analysis of eight samples of *Sigmodon arizonae* (OTUs 2–4), *S. mascotensis* (OTUs 5–8), and *S. hispidus* (OTU 9). Each of the eight OTU centroids is surrounded by a polygon that encloses maximal dispersion of sample scores. See Table 4.

tip. The contrast is similar in kind, if somewhat less pronounced in degree, between samples of *S. hispidus* and *S. mascotensis.*

The relative volume of the auditory bullae, difficult to capture accurately in a linear dimension (i.e., LAB) but easy to see in side-by-side comparisons of skulls, is another feature that separates *S. hispidus* from both *S. arizonae* and *S. mascotensis*—noticeably more inflated in the former and less so in the latter two (Fig. 3). Still, LAB contributed even more heavily than distance between the temporal ridges (DTR) to the segregation of the *S. hispidus* sample along the first canonical variate (Fig. 5, Table 4). Voss (1992) characterized the auditory bullae of *S. hispidus* as "small," but his taxonomic context involved contrast with the manifestly rotund capsules possessed by South American *S. peruanus,* a species indigenous to dry habitats in western Ecuador and northwestern Perú. Within the genus, the auditory bullae in members of the *S. hispidus* complex may be loosely graded as medium-sized, those of *S. alleni, S. arizonae,* and *S. mascotensis* as small, and those of *S. peruanus* as large.

The anatomy of the posterior palatal re-

Table 4.—Results of discriminant function analysis and one-way *ANOVAs* performed on eight OTUs representing intact specimens of *Sigmodon arizonae* ($n = 29$) and *S. mascotensis* ($n = 79$) from Nayarit, México, and *S. hispidus* ($n = 50$) from Florida, U.S.A. (see Fig. 5).

Variable	Correlations CV 1	CV 2	*ANOVAs* *f* (OTU)
ONL	0.28	−0.57	15.8***
ZB	0.08	−0.74	19.4***
IOB	0.30	−0.35	3.9**
BBC	0.24	−0.67	13.9***
BOC	−0.19	−0.57	10.0***
DBC	−0.43	−0.58	16.8***
DTR	−0.58	−0.61	35.8***
LR	0.35	−0.53	14.1***
BR	0.13	−0.53	9.4***
PPL	0.19	−0.61	17.2***
LBP	0.38	−0.35	8.2***
BBP	0.33	−0.46	17.0***
LIF	0.40	−0.60	19.9***
LD	0.30	−0.55	14.1***
BZP	0.10	−0.36	5.4***
LZS	−0.03	−0.53	10.4***
LAB	0.77	−0.55	73.3***
LM1–3	0.22	−0.78	38.3***
WM1	0.21	−0.79	32.3***
DI	0.31	−0.43	7.7***
DM	0.33	−0.58	15.1***
Canonical correlations	0.94	0.89	
Eigenvalue	7.9	3.8	
% Variance	54.5	26.4	

** = $P \leq 0.01$; *** = $P \leq 0.001$.

gion affords several points of contrast that aid specific separation. In examples of *S. arizonae,* the palatine bones are distinctly keeled and terminate medially as a pronounced spine that projects into the mesopterygoid fossa (Fig. 9). A well formed mesopterygoid spine is atypical of *S. mascotensis* skulls (Figs. 9, 10), although the posterior border of their palatines may be gently curved or occasionally bluntly pointed. Even in the latter condition, however, the bony palate is relatively flat, unmarked by the conspicuous palatal gutters and raised keel observed in specimens of *S. arizonae.* The ventral opening of the foramen ovale, situated at the posterolateral corner of the parapterygoid fossa, is notably large in most *S. arizonae* and smaller in *S. mascotensis* (Figs. 9, 10). Although we opportunistically used a 0.9 mm-diameter probe to convey this difference, some objective measure of foraminal area would better underscore the size distinction between the species. With regard to both palatal construction and size of the foramen ovale, the Floridian sample of *S. hispidus* resembles *S. arizonae,* but its variability is greater, at least according to the character states we have defined.

Another useful characteristic, one not mentioned by Zimmerman (1970) or Severinghaus & Hoffmeister (1978), involves the occurrence of an oval-shaped vacuity or fenestra on the parapterygoid fossa. Such an opening, situated just laterad to the pterygoid process and astride the palatine-pterygoid suture (Fig. 9), occurs commonly in samples of *S. mascotensis* (ca. 70%) but uncommonly in specimens of *S. arizonae* and *S. hispidus* (<25%). Nevertheless, this

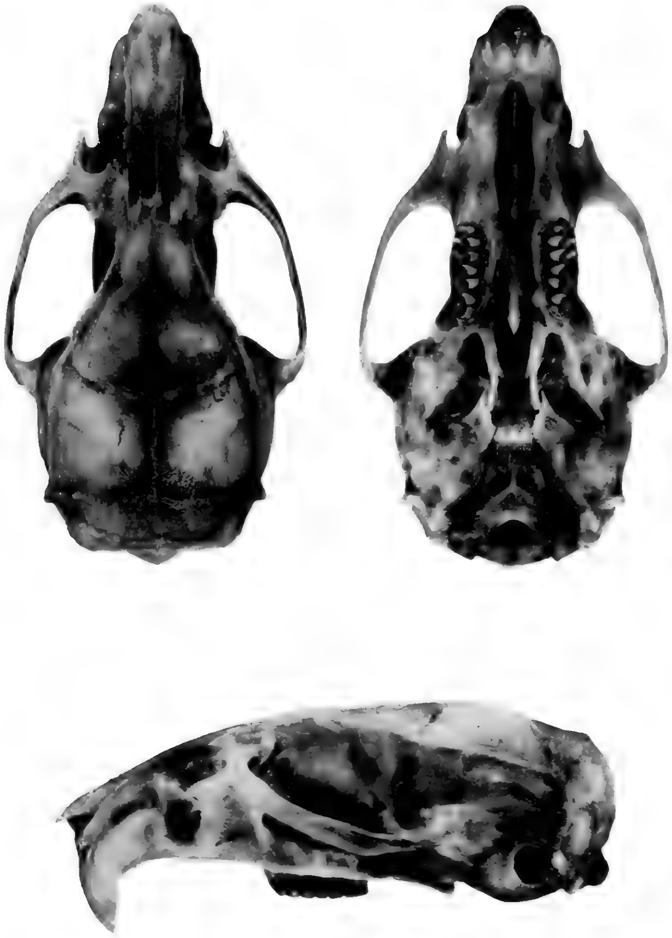

Fig. 6. Dorsal, ventral, and lateral cranial views (about 1.75×) of an adult *Sigmodon alleni* (USNM 524479), a female from 4 km S Aticama, Nayarit.

character varies in all three species, so that the fenestra's presence or absence is not alone decisive for identification but informative when applied in combination with other qualitative and quantitative variables. In some individuals, especially those of *S. mascotensis,* the position of a presumptive fenestra is suggested by an oval area of thin, translucent bone ("Present, covered" per histogram, Fig. 11). By its location and orientation, the parapterygoid fenestra appears to correspond to the path of the anastomotic artery that crosses the dorsal surface of the pterygoid plate to supply the distal cephalic circulation in muroids having a reduced stapedial branch, as is true in most *Sigmodon* (Bugge 1970, Voss 1992, and see Carleton and Musser 1989: fig. 21). Why the impression of this artery's passage should usually ossify fully in some *Sigmodon* species but not in others is unknown; the opening, however, does not appear to transmit nerves or blood vessels.

With regard to the typical conditions we reviewed above for *S. arizonae, S. hispidus,* and *S. mascotensis,* our series of *S. alleni* present an interesting mosaic of conditions. Like examples of *S. mascotensis,* the foramen ovale is small and the parapterygoid fenestra is typically present (on both sides in 10 individuals; one side in 2; and absent in 3); a mesopterygoid spine is usually present but small with shallow palatal corrugations. The temporal fossa, on the other hand, is narrow, convergent posteriorly in the manner of *S. hispidus.* The spinous process is short, slightly overhanging the zygomatic plate and tapering to a point (not wide and blunt as in *S. hispidus*). The auditory bullae of *S. alleni* are absolutely the smallest of the four species we have examined (Appendix) and in proportion nearly match the capsules of *S. mascotensis.*

As for other cranial features noted by Zimmerman (1978) or Severinghaus & Hoffmeister (1978), we subjectively assessed their variability apropos the Nayarit samples, but did not attempt to quantify their diagnostic utility because of their shape complexity or definitional arbitrariness (e.g., curvature of the lateral nasal margins, width of the presphenoid, shape of the occipital shield). Of these, the angularity (*S. hispidus*) or not (*S. arizonae* and *S. mascotensis*) of the dorsal rim of the occipital shield, as described by Severinghaus and Hoffmeister (1978), seems to provide consistent contrast, at least for the regional examples we examined.

Pelage color and texture.—Among the three species of Nayarit *Sigmodon, S. alleni* visually stands apart based on the uniformly rich brown color, occasionally with rufous- or cinnamon-brown tones, of its dorsal pelage. The common name, brown cotton rat, is aptly descriptive of the species. Rufescent tints are most evident over the rump, with medium brown on the middle dorsum that fades on the flanks to create a paler tawny hue. In texture, the dorsal fur of *S.*

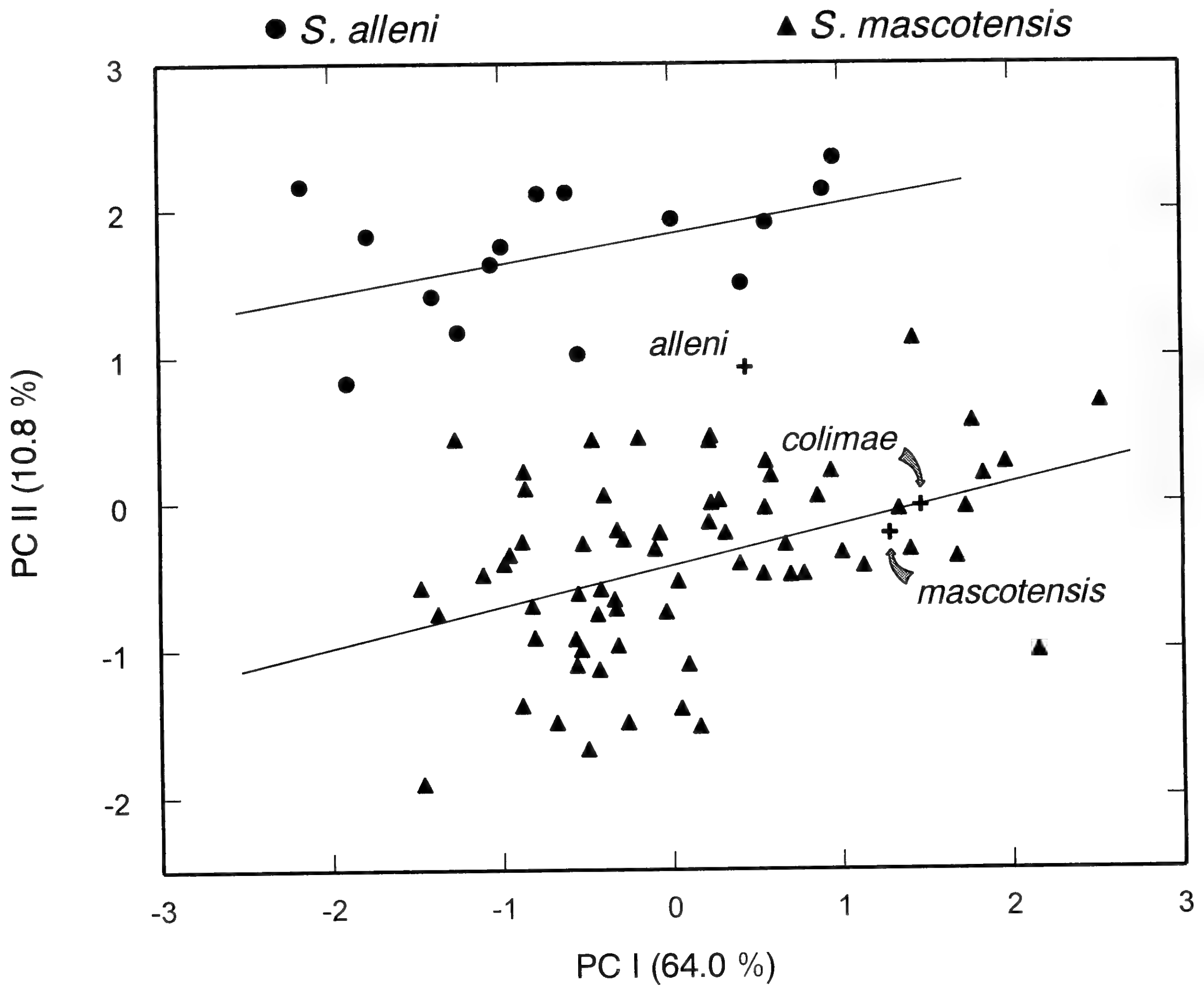

Fig. 7. Plot of first and second principal components extracted from analysis of 21 log-transformed craniodental variables measured on intact specimens of Nayarit *Sigmodon alleni* ($n = 15$) and *S. mascotensis* ($n = 79$). Crosses indicate relevant type specimens discussed in the text. Regression lines of PC II on PC I differ significantly between species in their y-intercepts (1.84 versus −0.42; $F = 156.0$, $P < 0.001$) but not their slopes (0.18 versus 0.28; $F = 0.4$, $P = 0.544$). See Table 5.

alleni is comparatively soft and fine, only slightly stiff to the touch; guard hairs on the rump are mostly unicolored and project little above the cover hairs.

The upperparts of *S. mascotensis* and *S. arizonae* suggest some shade of brown: typically a paler saturation, brighter tone, and distinctly grayish hue in the former species; and a darker saturation, more somber cast, and yellowish hue in the latter. In specimens of *S. arizonae,* there is greater intermixture of darkly tipped cover hairs over the mid-dorsum, which contrasts more noticeably with the yellow browns of the flanks; in examples of *S. mascotensis,* the grayish brown pelage color is usually evenly expressed across the dorsum. The subtle difference in shade of brown also results from the band colors of their agouti-patterned cover hairs: the basal band a pale plumbeous gray and middle band medium buff in *S. mascotensis* versus a dark gray basal band and deep buff middle band in *S. arizonae.* The chromatic accent of the buffy middle bands against the darker bases and tips of the cover hairs imparts a more grizzled or flecked appearance to the upperparts of *S. arizonae* and *S. mascotensis*; in individuals of *S. alleni,* the middle band is ochraceous and less dramatically set off from the umber tips. In further contrast to *S. alleni,* the dorsal fur in the two larger

Table 5.—Results of principal component analysis and one-way *ANOVAs* performed on all intact specimens of *Sigmodon alleni* (n = 15) and *S. mascotensis* (n = 79) from Nayarit, México (see Fig. 7).

Variable	Correlations		*ANOVAs*
	PC I	PC II	*f* (species)
ONL	0.93	0.24	0.5
ZB	0.95	0.01	11.5**
IOB	0.48	0.27	0.8
BBC	0.73	−0.03	9.6**
BOC	0.44	−0.10	6.7*
DBC	0.61	−0.43	51.1***
DTR	0.78	−0.44	48.5***
LR	0.85	0.39	0.5
BR	0.82	0.37	1.0
PPL	0.90	0.26	0.5
LBP	0.44	0.17	0.0
BBP	0.85	0.03	5.5*
LIF	0.87	0.19	2.6
LD	0.89	0.36	0.0
BZP	0.85	0.08	3.0
LZS	0.77	−0.44	47.1***
LAB	0.67	−0.13	12.1**
LM1–3	0.42	−0.49	46.4***
WM1	0.43	−0.52	56.6***
DI	0.87	0.17	2.1
DM	0.90	0.23	0.4
Eigenvalue	0.073	0.012	
% Variance	64.0	10.8	

* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$.

species is coarser and sparser, especially so in *S. arizonae,* and can be tactually appreciated as hispid. Guard hairs are conspicuously longer than the cover hairs over the rump and consist of both monocolored black and agouti-banded types.

Ventral cover hairs of all three species are bicolored, having a plumbeous gray base and a pale tip. The general appearance of the ventrum and the color differences observed between species principally depends upon the pigmentation of the tips. In *S. alleni,* the tips are buffy to pale ochraceous and the bases dull plumbeous, imparting a somber, dark gray color to the venter. In *S. mascotensis,* the cover hairs terminate in pure white, creating a light gray impression and conveying brighter tones than the underparts of the other species, especially *S. alleni.* Ventral pelage color is more variable in *S. arizonae*; some individuals have a predominance of pale buffy tips, while in others they are dull white. The overall impression is one of dull to medium gray, in contrast to the brighter grays of *S. mascotensis.*

The upper surfaces of the hindfeet are generally well haired in all three species but

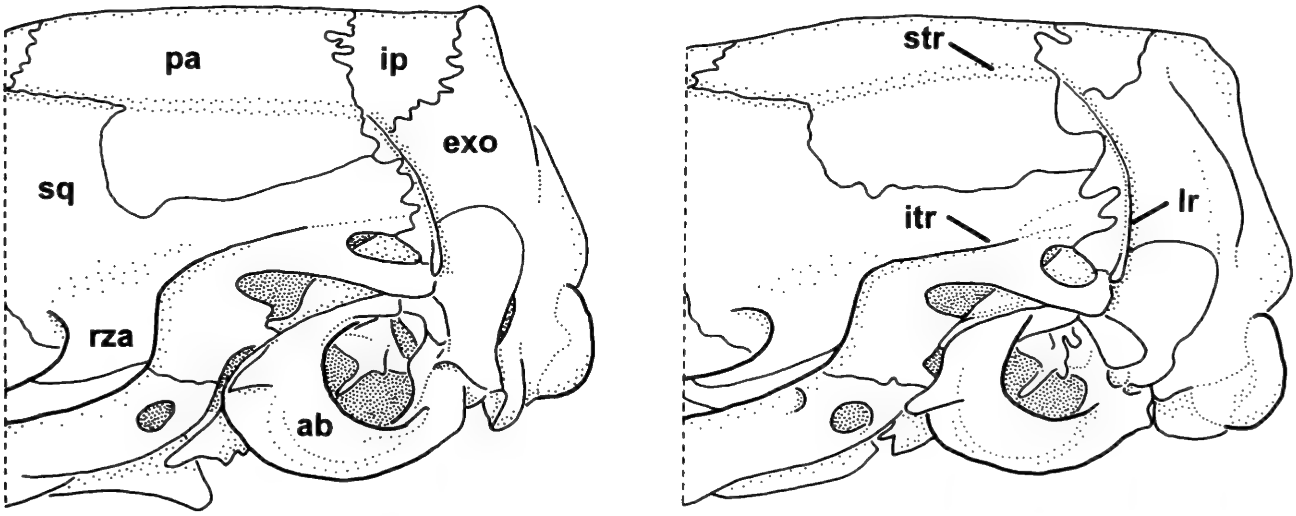

Fig. 8. Left lateral view of the temporal region in adult examples of *Sigmodon hispidus* (left; USNM 526071, Florida, St. Marks National Wildlife Refuge) and *S. mascotensis* (right; USNM 523954, Nayarit, 8 mi S Ahuacatlán). Abbreviations: ab, auditory bullae; exo, exoccipital; ip, interparietal; itr, inferior temporal ridge; lr, lambdoidal ridge; pa, parietal; rza, squamosal root of the zygomatic arch; sq, squamosal; str, superior temporal ridge. The superior temporal, inferior temporal, and lambdoidal ridges outline a trapezoidal shape of the temporal region in *S. hispidus* in contrast to the rectangular shape observed in *S. arizonae* and *S. mascotensis.* The distance between the temporal ridges (DTR) was measured between the points of the arrows denoting the superior (str) and inferior (itr) ridges.

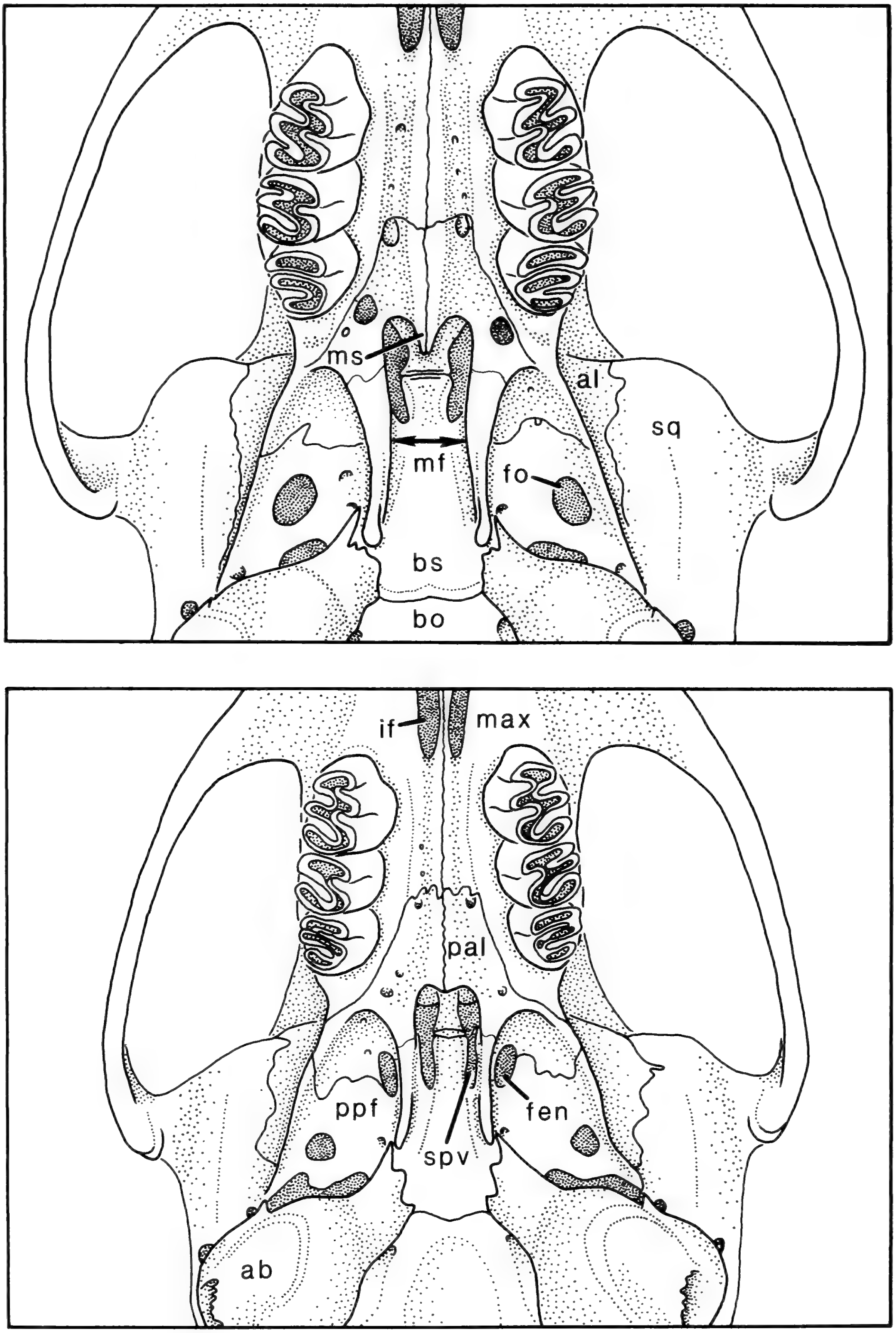

Fig. 9. Ventral view of the bony palate and adjoining parapterygoid and mesopterygoid fossae in Nayarit examples of *Sigmodon arizonae* (top; USNM 510012, 2 mi E San Pedro Lagunillas) and *S. mascotensis* (bottom; USNM 510022, 2 mi E San Pedro Lagunillas). Abbreviations: ab, auditory bullae; al, alisphenoid bone; bo, basioccipital bone; bs, basisphenoid bone; fen, fenestra of parapterygoid fossa; fo, foramen ovale; if, incisive foramen; max, maxillary bone; mf, mesopterygoid fossa; ms, mesopterygoid spine; pal, palatine bone; ppf, parapterygoid fossa; spv, sphenopalatine vacuity; sq, squamosal bone. In *S. arizonae,* as compared with *S.*

chromatic differences are apparent. Hairs covering the dorsal metatarsus and phalanges of *S. alleni* have dusky bases with buffy to pale ochraceous tips, such that hindfoot color generally blends with the reddish-brown appearance of the dorsum. Like the hairs of its ventral pelage, those on the hindfeet of *S. mascotensis* have plumbeous gray bases and bright white tips; thus, the feet appear pale gray and distinctly contrast with the grayish browns of the rump. Upper surfaces of the hindfeet of *S. arizonae* appear medium gray to dull brown over the metatarsum and grayer on the phalanges, blending with the dorsum more so than in *S. mascotensis* but less so compared with *S. alleni.*

Although Bailey (1902) characterized all of these taxa as having semi-naked and coarsely annulated tails, we found clear differences in caudal pilosity and scutellation. Epidermal scales appear dark brown, above and below, in all three; consequently, expression of bicoloration issues from the interplay of hair color, density, and length. None of the species, however, possesses a truly bicolored tail (e.g., like that of *Peromyscus maniculatus*) with sharp linear demarcation between dark dorsal and pale ventral surfaces. Instead, transition from darker dorsal to the paler undersurface is gradual. In examples of *S. alleni,* the tail is sparsely covered, the caudal hairs extending over 2–3 annuli; the color is dark brown dorsally and slightly paler below, bicoloration weakly expressed and effectively unicolor in some individuals; caudal scales are small but typically visible to the naked eye given the relatively sparse investiture of hairs. Individuals of *S. mascotensis* possess a similarly fine scalar pattern, but caudal hairs are longer, about 4 annuli in length, and scutellation is mostly obscured. This species most nearly approaches a bicolored condition, brown above and pale gray below. In samples of *S. arizonae,* the tail is dark brown above and grades imperceptibly to paler brown below. Caudal scales are noticeably larger, and the annulations accordingly coarser and readily evident macroscopically. Paradoxically, the annulation pattern remains visibly appreciable in *S. arizonae* even though its caudal hairs are absolutely longer (about 4–5 annuli) in contrast to those of *S. mascotensis.* The impression of semi-nakedness arises from the sparser density of caudal hairs, arranged in triplets as in the other species but more widely spaced as a result of the larger tail scales.

Chromosomal variation.—Three well marked chromosomal formulae are apparent among Nayarit *Sigmodon.* The diploid number (2N) of *S. arizonae* is 22, consisting of largely biarmed chromosomes (fundamental number, FN, = 38). The autosomes number four pairs of very large metacentrics and submetacentrics, two pairs of large subtelocentrics, two pairs of medium-sized metacentrics, one pair of small submetacentrics, and a single pair of small acrocentrics (Fig. 12). The X chromosome is a medium-sized acrocentric; the Y, a small acrocentric with discernible secondary arms, is the smallest element in the complement. This karyotype is identical to that described by Zimmerman (1970) for the 22-chromosome cotton rats he studied from Arizona, Sinaloa, and Nayarit.

The diploid number in examples of *S. mascotensis* is invariantly 28, nearly all of the autosomes uniarmed (FN = 28). Autosomes consist of 12 pairs of acrocentrics, gradated in size from medium to large, and one pair of small subtelocentrics (Fig. 12). The X chromosome is a medium-sized ac-

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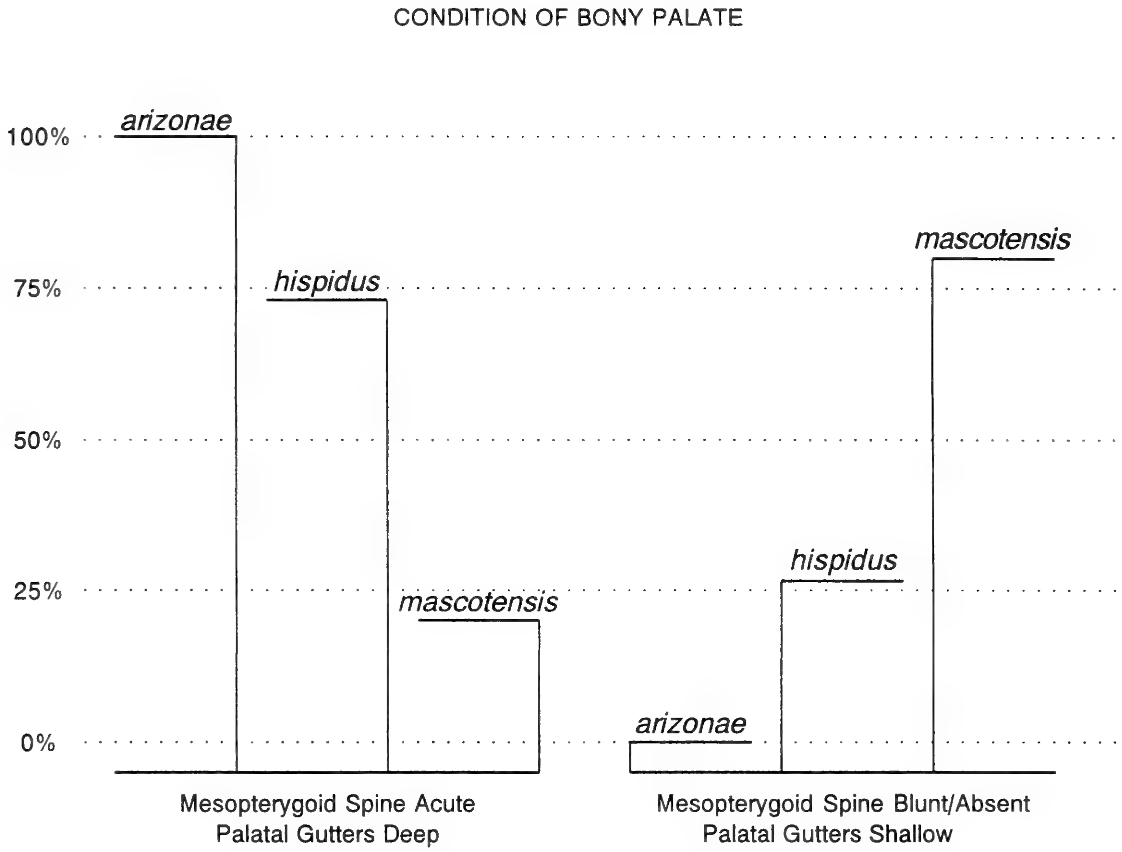
mascotensis, note the occurrence of a pronounced mesopterygoid spine, the conspicuously larger size of the foramen ovale, and the absence of a parapterygoid fenestra.



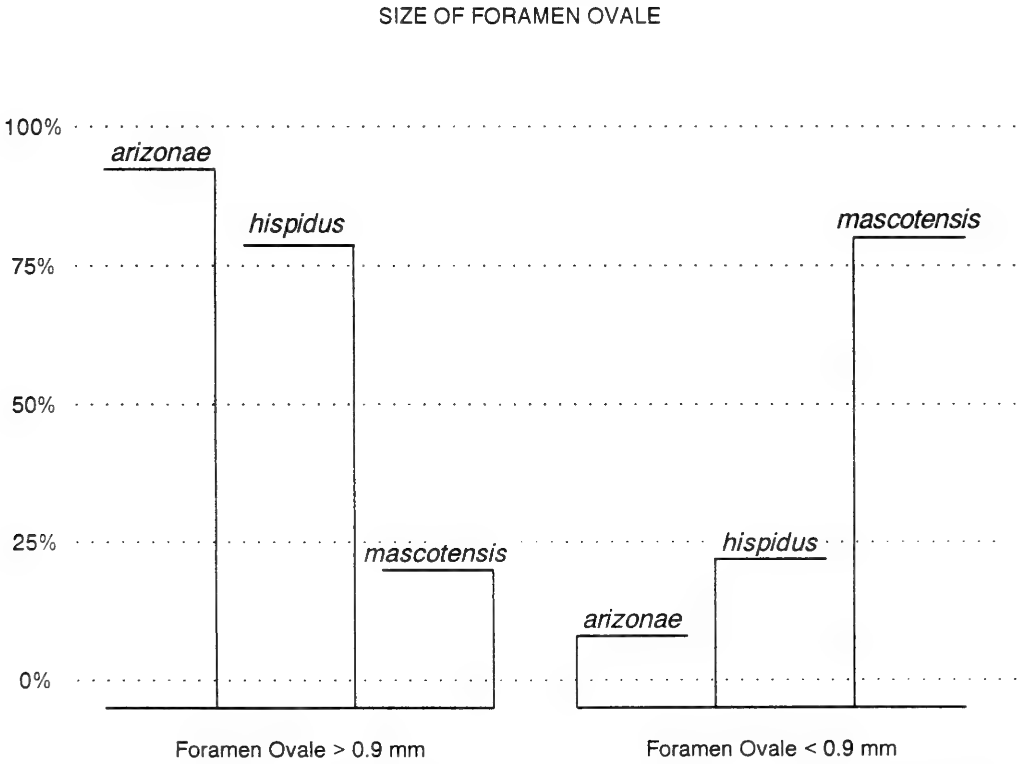


Fig. 10. Percent occurrence of certain qualitative cranial characters in samples of *Sigmodon arizonae* ($n = 36–40$) and *S. mascotensis* ($n = 88–91$) from Nayarit, México, and in *S. hispidus* ($n = 53$) from Florida, U.S.A. Top, condition of the bony palate; bottom, size of the foramen ovale (See Fig. 9 for illustration and text for description of character states).

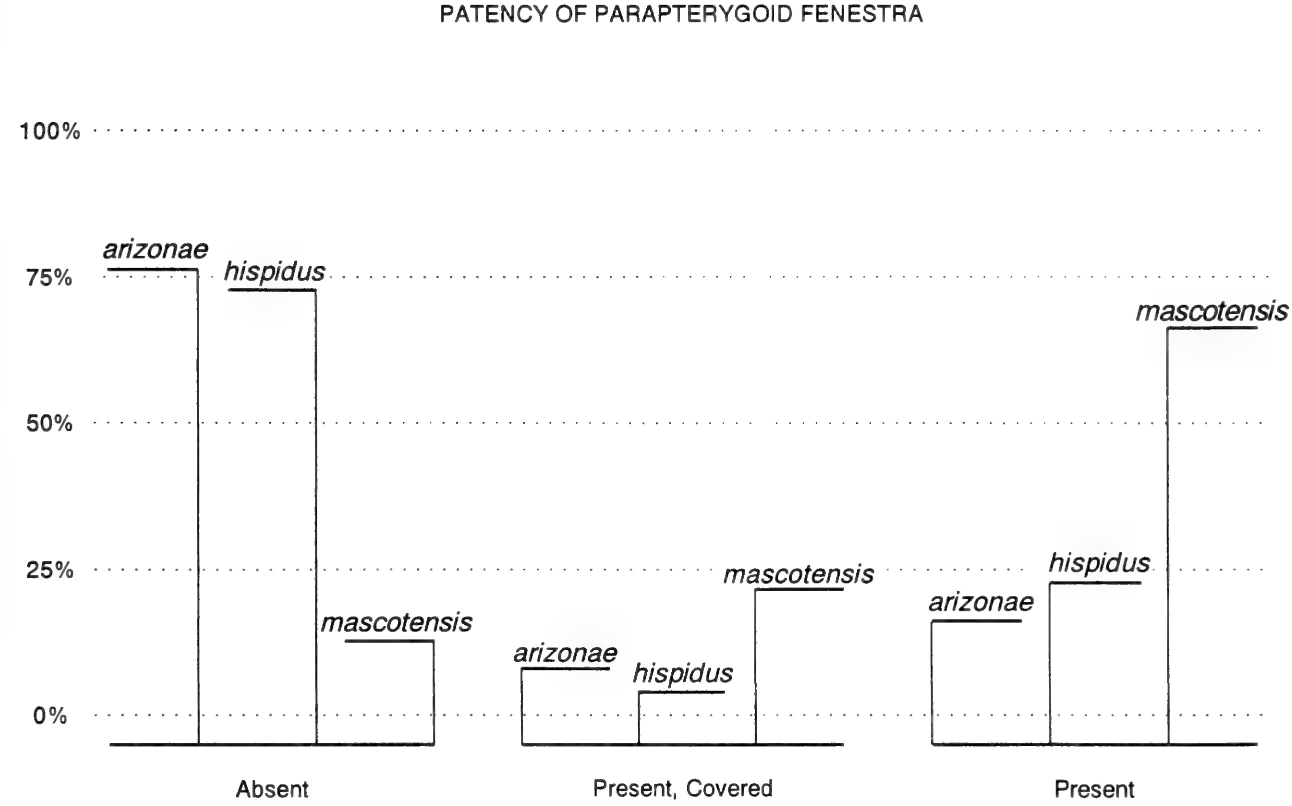


Fig. 11. Percent occurrence of character states of the right parapterygoid fenestra in samples of *Sigmodon arizonae* ($n = 38$) and *S. mascotensis* ($n = 86$) from Nayarit, México, and in *S. hispidus* ($n = 52$) from Florida, U.S.A. (See Fig. 9 for illustration and text for description of character states).

rocentric; the Y, a tiny acrocentric, is smaller than any of the autosomal acrocentrics. A female (USNM 511706) from Rancho Sapotito is heteromorphic for a centric fusion involving two similarly sized larger acrocentrics; two other females and two males karyotyped from this locality possess typical karyotypes. Lee & Zimmerman (1969) noted similar examples of heteromorphic karyotypes resulting from centric fusion in *S. fulviventer,* and Zimmerman (1970) reported the same phenomenon in *S. hispidus.*

Zimmerman (1970) characterized all autosomes in *S. mascotensis* as acrocentric (that is, FN = 26), but we follow Elder (1980) in describing the smallest of these as subtelocentric (FN = 28). In most spreads, this pair has clearly discernible second arms (see Fig. 12), which Elder (1980) found to be heterochromatic in most of his C-banded preparations. Excepting this minor discrepancy in autosomal classification, the karyotype of Nayarit animals conforms to those described by Zimmerman (1970) from scattered localities in southern Jalisco, Michoacán, Guerrero, and western Oaxaca.

In *S. alleni,* the 2N is consistently 52 and the FN is typically 64. Autosomes in the 64-FN karyotype consist of one pair of large, four pairs of medium-sized, and one pair of small subtelocentrics; one pair of very small metacentrics; and 18 pairs of acrocentrics graded in size from small to medium (Fig. 13). At Lo de Marcos, two FNs, 64 and 66, are apparent. The autosomal complement in the 66-FN karyotype includes an additional pair of small submetacentrics and lacks a pair of acrocentrics. The X chromosome is a moderately large subtelocentric; the Y is a small subtelocentric. The karyotype Zimmerman (1970) reported for *S. alleni* from Michoacán is similar to our 64-FN pattern, except that the Y chromosome in our Nayarit samples appears to be smaller.

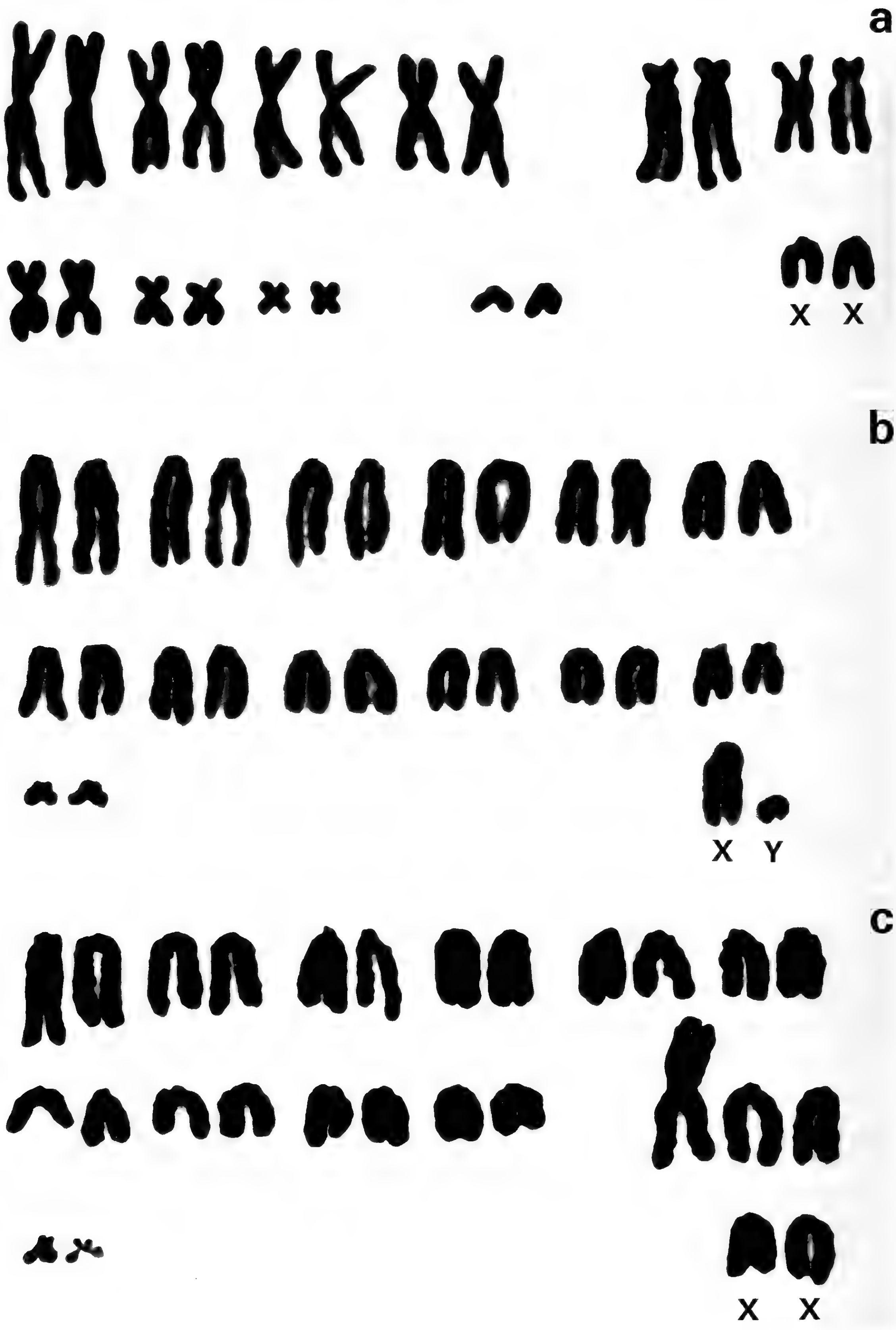


Fig. 12. Representative karyotypes of Nayarit *Sigmodon:* a, *S. arizonae* (USNM 511700), a female from Mesa del Nayar; b, *S. mascotensis* (USNM 523953), a male from 8 mi S Ahuacatlán; c, heteromorphic variant of *S. mascotensis* (USNM 511706), a female from Rancho Sapotito.

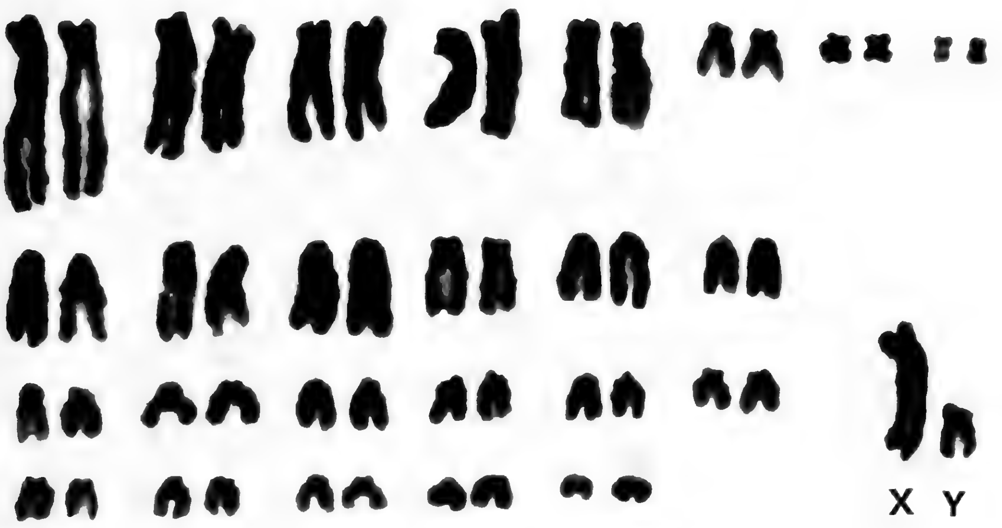


Fig. 13. Representative karyotype of *Sigmodon alleni* (USNM 523940), a male from 1 mi S Lo de Marcos.

Discussion

Bailey's (1902) revision of *Sigmodon* established the view that most North American populations with coarsely annulated, partially naked tails are geographic races of *S. hispidus,* including the distinctive complex of large-bodied cotton rats found in the southwestern U.S.A. and western México. His classification prevailed over subsequent decades and accommodated most new descriptions of taxonomic variety as subspecies (Miller 1924, Miller & Kellogg 1955, Hall & Kelson 1959). Zimmerman's (1970) fine synthesis of chromosomal and morphological information abruptly overturned this comfortable arrangement and resurrected both *S. arizonae* and *S. mascotensis* as valid species distinct from *S. hispidus.* The morphological basis for specific stature of these forms was amplified by Severinghaus & Hoffmeister (1978) and Hoffmeister (1986), who also refined our understanding of their intermingling distributions in the southwestern U.S.A. and northwestern México. Morphometric, morphological, and chromosomal differences observed among Nayarit populations of *Sigmodon* further corroborate the taxonomic insights and nomenclatural realignments advanced by Zimmerman (1970).

Examples of *S. alleni, S. arizonae,* and *S. mascotensis* were collected in all possible pairwise combinations of sympatry, but at no place were all three species documented. Of particular note is the co-occurrence now recorded for *S. arizonae* and *S. mascotensis* at a locality east of San Pedro Lagunillas in southcentral Nayarit. Although collected "sympatrically" in terms of bearing a single skin-tag provenience, the two species are apparently segregated according to microhabitat at this place. The vegetation in the vicinity includes succulent dicots, particularly water hyacinth, and marsh grasses bordering the small lake; and dryer brush, low sparse woodland, and bunchgrasses covering the hillsides that overlook the lake (Fig. 14). Most examples of *S. arizonae* originated from the former habitat and those of *S. mascotensis* from the latter (Fig. 15). Whether the two species at this place are entirely nonoverlapping in their microhabitat occurrence is unknown, since field identifications were tentative at the time of collection. Furthermore, whether the specific habitat affinities recorded at this one locality reflect general ecological differences of the species, particularly their humidity tolerances, will require extended site investigations.

The distinctive cranial and pelage features so apparent in Nayarit *S. mascotensis*

Fig. 14. Panoramic view of collecting site at the eastern side of the small lake San Pedro Lagunillas and two miles east of the village of the same name. Traplines were placed both along the emergent lakeside vegetation and on the dryer hillside and tableland.

encouraged our review of its distribution in western México. We concur with all species-group epithets so far allocated to the species by Zimmerman (1970) and Hall (1981): these are *atratus, colimae, inexoratus,* and *ischyrus.* Like Allen's (1897b) *S. mascotensis,* populations represented by each of these names are large, grayish brown cotton rats with strongly hispid fur and relatively long tails; their crania possess relatively small auditory bullae and expansive temporal fossae; the occurrence of parapterygoid fenestrae is common within locality samples, but a large foramen ovale, pronounced mesopterygoid spine, and deep palatal grooves are uncommon. The forms *tonalensis* Bailey (1902) and *obvelatus* Russell (1952), currently maintained as subspecies of *S. hispidus* (Hall 1981, Musser & Carleton 1993, Alvarez-Castañeda 1996), also fit well with this morphology and properly belong as junior synonyms of *S. mascotensis* (see remarks under Taxonomic Summary).

The emergent picture of *S. mascotensis* distribution reveals a species confined to western México, documented from southern Nayarit and Zacatecas to extreme western Chiapas (Fig. 16). Although its range boundaries appear convoluted and constituent populations are certainly discontinuous, the occurrence of the species corresponds closely to deciduous or semideciduous tropical woodlands having a pronounced dry season. Comments by collectors typically mention the semiarid to arid environment and-or xerophilous vegetational character of localities where *S. mascotensis* has been captured (Hooper 1947, 1957; Goldman 1951; Russell 1952; Goodwin 1969; Alvarez et al. 1987). According to Goldman's (1951) life-zone di-

Fig. 15. Microhabitat preferences of *Sigmodon* captured at 2 mi E San Pedro Lagunillas (see Fig. 14). Top: hillside covered with brush, low broken woodlands, and bunch grasses where examples of *S. mascotensis* were captured. Bottom: dense growth of water hyacinth fringing the lake and inhabited by *S. arizonae*.

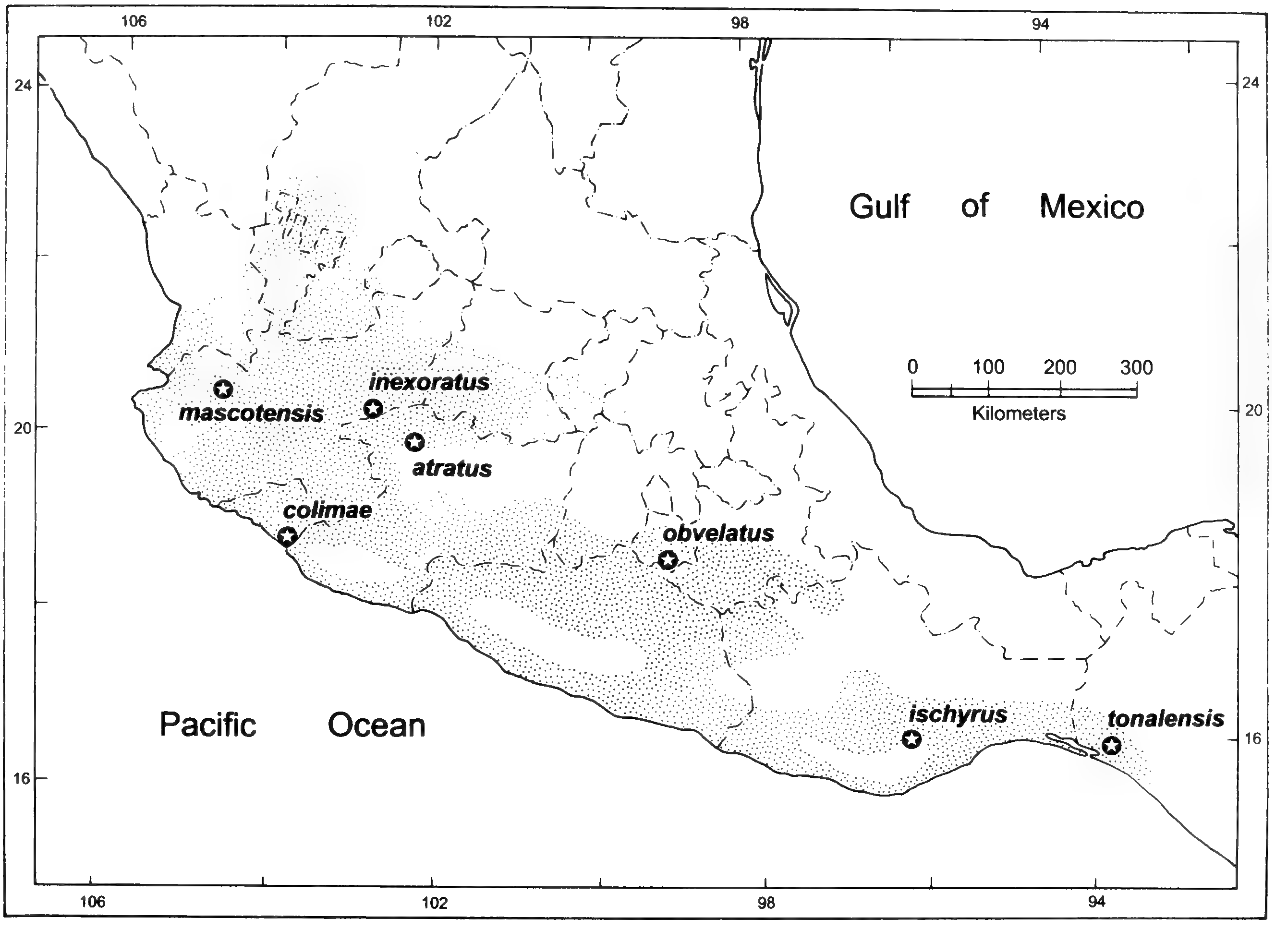


Fig. 16. Generalized distribution of *Sigmodon mascotensis* in western México based on specimens examined herein. Enclosed stars identify the type localities of the six species-group taxa that we view as regional synonyms of *S. mascotensis* Allen (1897), including two newly associated herein (*tonalensis* Bailey, 1902, and *obvelatus* Russell, 1952).

visions of México, nearly all of these distributional records represent either Arid Lower Tropical Subzone or Arid Upper Tropical Subzone, a few the Lower Austral Zone; by Leopold's (1959) categorization of broad vegetational units, they fall within Tropical Deciduous Forest and Arid Tropical Scrub. Not unexpectedly, in view of such climatic and vegetational associations, the geographic boundary of the species conforms well to certain biotic patterns distilled from distributions of the Méxican herpetofauna (Flores-Villela 1993).

The range of *S. mascotensis* collectively overlies three physiographic regions: Pacific coastal plain and the contiguous lowlands of the Isthmus of Tehuantepec; the drainage basin and surrounding tablelands of Lago de Chapala (Meseta Central de Anáhuac or Altiplano Sur), including the Tequisquiapan Valley; and the Balsas Basin, including the Tehuacán Valley. Except for those records in the Tehuacán valley of western Puebla, collecting sites of *S. mascotensis* predominantly occur within hydrologic systems that ultimately drain into the Pacific Ocean; the Río Salado of the Tehuacán Valley joins the Río Santa Domingo, a major effluent to the Gulf of México. The Tehuacán-Cuicatlán Valley is presently considered part of the same physiographic domain as the Balsas Basin (Sierra Madre del Sur Morphotectonic Province), but persuasive argument for past biotic connections drawn from geological evidence is elusive, given both the daunting complexity of México's physical landscapes and the continuing need for geologic-tectonic research (see review by Ferrusquía-Villafranca 1993).

Although our study is focussed on means

for interspecific discrimination, we are as much impressed by the morphological similarities that *S. arizonae* and *S. mascotensis* share, notably the configuration of the temporal fossa and degree of bullar inflation. Goodwin (1969:199) had earlier appreciated the fundamental affinity among these populations and summarized their external resemblances: "*Sigmodon h. mascotensis* is in a group of several subspecies of very large, long-tailed, coarse-haired cotton rats that range from Arizona [i.e., *arizonae*] in western North America south along the slopes and plains of the Pacific coast in México to Tonalá, Chiapas." Such general notions of kinship, along with their geographically complementary distributions, suggest a sister-group relationship, a hypothesis which has received more rigorous endorsement from traditional and banding chomosomal studies (Zimmerman 1970, Zimmerman & Sihvonen 1973, Elder 1980). Zimmerman (1970), for example, divided North and Middle American *Sigmodon* into two species groups based on a combination of diploid and fundamental numbers: those with a low range (2N = 22–30, FN = 26–38), consisting of *S. arizonae, S. fulviventer,* and *S. mascotensis*; and those with a high range (2N = 52–56, FN = 52–66), consisting of *S. alleni, S. hispidus, S. leucotis,* and *S. ochrognathus.* Assuming derivation from a *S. hispidus*-like ancestor, G-banding evidence supports the common ancestry of *S. arizonae* and *S. mascotensis* (Elder 1980). The phyletic affinity of *S. fulviventer* with *S. arizonae* and *S. mascotensis* as postulated by Zimmerman (1970) remains untested.

More importantly, our nomenclatural and distributional amendments of *S. mascotensis* bear on a taxonomically more entangled issue: what is *S. hispidus* proper? As now documented, populations of medium to large *Sigmodon* known to occur throughout the Pacific coastal lowlands and west-facing slopes from Sonora to western Chiapas, represent either the species *S. alleni, S. arizonae,* or *S. mascotensis.* Supposed western records for *S. hispidus* proper have proven incorrect upon reexamination. Specimens from Jalisco and Querétaro that had been assigned to *S. h. berlandieri* (Bailey 1902, Hall 1981) are in fact *S. mascotensis,* as enumerated below in the Taxonomic Summary; Goodwin's (1969) two vouchers (KU 63075, 63076) of *S. h. saturatus* in southern Oaxaca (1 mi NNW Soledad) are instead *S. alleni,* as corrected by Baker (1969). To our knowledge, these reidentifications, together with reallocation of *obvelatus* and *tonalensis* and their referred series, remove any documentation for *S. hispidus* along the entire Pacific versant of México.

The inability of discriminant coefficients to associate Middle American holotypes of nominal "*hispidus*" with Floridian *S. hispidus* indirectly attests the still composite nature of the species as arranged. While our selection of this Floridian population sample as a standard for *S. hispidus* proper was a reasonable choice, on geographic and morphologic grounds, our expectation of its agreement with Neotropical taxa proved wonderfully naive. Most holotypes representing such populations clustered among or nearer the Nayarit samples of *S. mascotensis* (Fig. 17) and were classified a posteriorly with that species (Table 6). None of these numerically probabilistic assignments, except Bailey's (1902) *tonalensis,* merits serious consideration as biological truth—the various taxa are not conspecific with *S. mascotensis* of western México. Those craniodental variables that heavily influenced multivariate separation among centroids—particularly LAB on the first canonical variate and LM1-3 and WM1 on the second—are small in most of the Middle American type specimens, as compared with typical *S. hispidus* (OTU 9). By default these were associated with examples of *S. mascotensis,* since among the eight predefined OTUs, individuals of that species possess the smallest bullae, shortest toothrows, and narrowest molars compared with typical *S. hispidus* or *S. arizonae* (Ap-

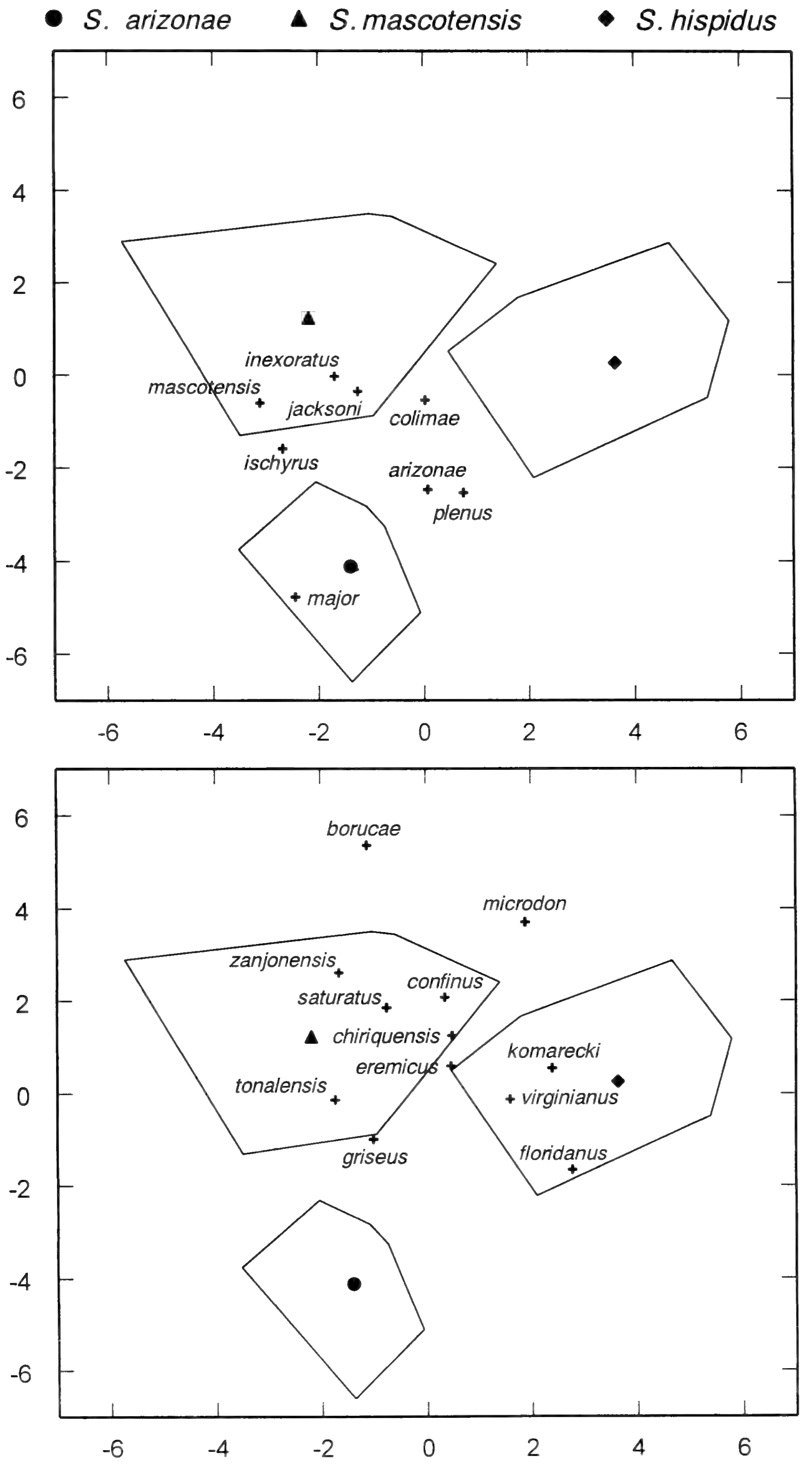


Fig. 17. Phenetic dispersion of type specimens of *Sigmodon* based on discriminant coefficients extracted from the same discriminant function analysis of eight samples of *Sigmodon arizonae* (OTUs 2–4), *S. mascotensis* (OTUs 5–8), and *S. hispidus* (OTU 9). Polygons in this instance enclose the maximal dispersion of all specimen scores around the grand centroid for each species (compare with Fig. 5). Top, type specimens of forms currently considered synonyms of *S. arizonae* (*jacksoni, plenus,* and *major*) and *S. mascotensis* (*colimae, inexoratus,* and *ischyrus*); bottom, type specimens of forms currently considered synonyms of *S. hispidus* (two groups plotted separately to avoid visual congestion). See Table 6 and text for discussion.

Table 6.—A posteriori classification of type specimens of *Sigmodon* derived from discriminant function analysis of OTUs 2–9 (see Fig. 17).

Holotype	Current classification	A posteriori OTU assignment	*P*
arizonae Mearns (AMNH 2370/1841)	*S. arizonae*	2 (*arizonae*)	0.71
major Bailey (USNM 96275)	*S. arizonae*	2 (*arizonae*)	0.99
jacksoni Goldman (USNM 214121)	*S. arizonae*	5 (*mascotensis*)	1.00
plenus Goldman (USNM 181086)	*S. arizonae*	3 (*arizonae*)	1.00
mascotensis Allen (AMNH 8321/6655)	*S. mascotensis*	8 (*mascotensis*)	1.00
colimae Allen (AMNH 2648/2318)	*S. mascotensis*	7 (*mascotensis*)	0.67
inexoratus Elliot (FMNH 8651)	*S. mascotensis*	7 (*mascotensis*)	1.00
ischyrus Goodwin (AMNH 10045)	*S. mascotensis*	5 (*mascotensis*)	0.73
borucae Allen (AMNH 171600)	*S. hispidus*	8 (*mascotensis*)	0.63
eremicus Mearns (USNM 60319)	*S. hispidus*	7 (*mascotensis*)	0.57
tonalensis Bailey (USNM 75144)	*S. hispidus*	8 (*mascotensis*)	1.00
saturatus Bailey (USNM 99998)	*S. hispidus*	5 (*mascotensis*)	0.70
microdon Bailey (USNM 108467)	*S. hispidus*	9 (*hispidus*)	0.92
chiriquensis Allen (AMNH 18789)	*S. hispidus*	7 (*mascotensis*)	0.65
griseus Allen (AMNH 28497)	*S. hispidus*	5 (*mascotensis*)	0.64
confinus Goldman (USNM 204241)	*S. hispidus*	5 (*mascotensis*)	0.69
zanjonensis Goodwin (AMNH 69277)	*S. hispidus*	7 (*mascotensis*)	0.98
floridanus Howell (USNM 261624)	*S. hispidus*	9 (*hispidus*)	1.00
virginianus Gardner (USNM 273535)	*S. hispidus*	9 (*hispidus*)	0.99
komareki Gardner (USNM 207210)	*S. hispidus*	9 (*hispidus*)	1.00

pendix). By way of instructive contrast, those holotypes originating from the southeastern U.S.A. (*floridanus, komareki, virginianus*) did group sensibly with the Floridian sample of *S. hispidus* (Table 6).

Members of the *hispidus* complex, so far as known from the southern U.S.A. to northwestern South America, possess a relatively narrow temporal fossa, tail notably shorter than head-and-body length, and a diploid number of 52 (Zimmerman & Lee 1968, Kiblisky 1969, Zimmerman 1970), but in pelage color and texture and in cranial form and size, they vary substantially. Based on our review of most relevant types and casual examination of museum series, typical *S. hispidus* appears to comprise those populations in the southeastern

U.S.A. (*floridanus, komareki, virginianus*), the southern Great Plains (*alfredi, texianus*), and the central plateau of northern México (*berlandieri*). To the southwest and south of this moiety, the taxonomic picture becomes muddled. Populations in Arizona—those bearing the names *confinus, eremicus,* and *jacksoni*—deserve additional systematic clarification, with respect to their synonymy as *S. hispidus,* as *S. arizonae,* or as something else (Zimmerman 1970, Hoffmeister 1986). Along the Gulf coast of eastern México, across the Isthmus of Tehuantepec, and into the lowlands of the Yucatán Peninsula and northern Guatemala, one finds a group of populations characterized by shorter fur, generally somber brown in color, shorter toothrows, and smaller auditory bullae. The oldest name for these is Saussure's (1860) *toltecus,* which may include the forms *saturatus, microdon,* and perhaps *furvus* (Bangs, 1903); Bailey (1902) had mentioned a *toltecus* group within his broad polytypic definition of *S. hispidus.* Hispid cotton rats described from the highlands of Chiapas and western Guatemala, *villae* and *zanjonensis,* respectively, resemble those of the *toltecus* complex in size but possess a longer, more brightly colored pelage; the elevation of the type locality of *zanjonensis,* ca. 2700 m, alone advises caution in accepting the homogeneity of populations now grouped under the epithet in conventional range maps (Hall 1981). The relationships of the Méxican *hispidus*-like forms to populations farther south in Central America—*griseus, borucae,* and *chiriquensis*—similarly invite detailed study. As noted by Voss (1992); Burmeister's (1854) *hirsutus,* whose type locality is in northern Venezuela, may assume importance in deciding nomenclatural issues that involve these southernmost populations of the *hispidus* complex.

The number and distribution of species still mistakenly subsumed under "*hispidus*" are topics that require much additional investigation, incorporating other kinds of data and fine-scale geographic sampling. Like Hooper's (1955) early perceptions of taxonomic differences among *Peromyscus boylii* populations, unraveling the intricate alpha systematic problems that yet surround *Sigmodon* will likely unfold from firm answers attained first on select regional bases.

Taxonomic Summary

Partial synonymies that trace first authorities for new name combinations are given below for *S. arizonae* and *S. mascotensis.* Species-group taxa given under *S. alleni* and *S. hispidus* are intended only as a list of the type specimens we examined, and are not a statement of junior synonyms demonstrated to be conspecific. For the latter, we include names that have been applied only to populations in the southwestern U.S.A., México, and Central America.

Sigmodon arizonae Mearns

Sigmodon hispidus arizonae Mearns, 1890: 287 (type locality—United States, Arizona, Yavapai County, 3 mi SE Camp Verde, Bell's Ranch [as restricted by Hoffmeister 1986]; holotype—AMNH 2370/1841).

Sigmodon arizonae, Zimmerman, 1970:435 (elevation to species).

Sigmodon hispidus major Bailey, 1902:109 (type locality—México, Sinaloa, Sierra de Choix, 50 mi NE Choix; holotype—USNM 96275).—Zimmerman, 1970:446 (synonymy with *S. arizonae*).—Hall, 1981:742 (retention as a subspecies of *S. arizonae*).

Sigmodon hispidus jacksoni Goldman, 1918:22 (type locality—United States, Arizona, Yavapai County, 3 mi N Fort Whipple, near Prescott, 5000 ft; holotype—USNM 214121).—Zimmerman, 1970:446 (synonymy with *S. arizonae*).—Hall, 1981:742 (retention as a subspecies of *S. arizonae*).

Sigmodon hispidus cienegae Howell, 1919: 161 (type locality—United States, Arizona, Pima County, 4 mi E Fort Lowell, Bullock's Ranch; holotype—A. B. Howell collection 1531).—Zimmerman, 1970: 446 (synonymy with *S. arizonae*).—Hall, 1981:741 (retention as a subspecies of *S. arizonae*).

Sigmodon hispidus plenus Goldman, 1928: 205 (type locality—United States, Arizona, Yuma County, Parker, 350 ft; holotype—USNM 181086).—Zimmerman, 1970:446 (synonymy with *S. arizonae*).—Hall, 1981:742 (retention as a subspecies of *S. arizonae*).

Distribution.—Extreme southeastern California and southcentral Arizona, U.S.A., southwards along coastal plain and contiguous foothills of the Sierra Madre Occidental in northwestern México, to southcentral Nayarit. In Nayarit, most collecting sites situated in the coastal plain that dominates the northwestern sector of the state, but also at intermediate elevations (1000–1900 m) along the upper drainage of the Río Grande de Santiago (Fig. 18).

Apart from the unresolved status of *jacksoni* (see below), collection records, as reported here and by Hoffmeister (1986), likely delimit the full geographic extent of *S. arizonae.* In our museum searches to redefine the distribution of *S. mascotensis* in western México, we have not encountered examples of *S. arizonae* to the south of the localities now documented from Nayarit. To the northwest—in Sinaloa, Durango, and Sonora—places where the species has been collected lie on coastal plain and lower Pacific-facing slopes of the Sierra Madre Occidental. Along eastern slopes of that mountain axis and onto adjoining plateaus, one finds populations of *S. hispidus* proper, corresponding to the race *S. h. berlandieri* (Baker 1956, Baker & Greer 1962, Anderson 1972, Severinghaus & Hoffmeister 1978, Matson & Baker 1986).

The presence of *S. arizonae* at moderate elevations in eastern Nayarit (Mesa del Nayar, 1300 m; Ocota Airstrip, 1900 m) appears anomalous in light of the usual occurrence of the species in coastal plain of the westcentral region (Fig. 18). Both karyotypic and morphological data, however, confirm the specific assignment of these outlier populations. Carleton et al. (1982) had noted similar disjunct distributional records among certain Nayarit *Peromyscus* and speculated that riparian vegetation along major rivers, like the Río Grande de Santiago and Río Huayanamota, may provide dispersal corridors to the state's interior. Matson (1982) offered a similar explanation for certain tropical rodent taxa that reach the canyon region of southwestern Zacatecas.

Remarks.—Nayarit samples of this large-bodied *Sigmodon* most closely resemble Bailey's (1902) *S. hispidus major,* described from nearby Sinaloa. Zimmerman's (1970) argument for the taxon's synonymy with Mearn's (1890) *S. arizonae* is persuasive, and our observations and results support his conclusion. While the discriminant scores of the holotypes of *arizonae* and *plenus* fall outside the limits of craniodental variation obtained for the Nayarit series (Fig. 17), a posteriori classification casts the morphological affinity of the Arizonan taxa with them and *major,* not with representatives of *S. hispidus* or *S. mascotensis* (Table 6). Further, some allowance must be duly given for geographic variation, and Zimmerman (1970) had previously remarked that the Sinaloan and Nayarit samples averaged slightly larger than those from Arizona, a distinction reflected in his cluster analysis. Verification of a diploid count of 22 for animals from the type locality of *arizonae,* where specimens have not been collected since 1932 according to Hoffmeister (1986), would help to cement the usage of this name; to date, reported karyotypes represent the taxa *cienegae, major,* and *plenus* (Zimmerman 1970, this study).

The invocation of geographic variation less easily explains the unexpected assignment of the type of *S. hispidus jacksoni* to Nayarit *S. mascotensis* (Table 6). Zimmerman (1970) arranged *jacksoni,* also named from Arizona, as another junior synonym of *S. arizonae,* but Hoffmeister (1986) later

Table 7.—Measurements (mm) of type specimens of taxa currently associated with *Sigmodon arizonae.*

	arizonae	*major*	*plenus*	*jacksoni*
Sex	M	M	M	M
Age	A	O	A	J
TOTL	320.0	365.0	316.0	249.0
LT	116.0	156.0	147.0	108.0
LHF	36.0	40.5	36.5	33.0
ONL	40.2	40.4	37.1	31.1
ZB	22.1	23.5	21.7	18.1
IOB	5.5	5.3	5.5	4.9
BBC	14.6	16.0	14.4	14.2
BOC	8.1	8.0	8.2	7.4
DBC	11.7	12.8	12.3	11.1
DTR	4.5	5.7	3.6	3.2
LR	13.6	14.0	12.0	10.0
BR	8.2	8.6	7.4	6.7
PPL	14.0	14.7	13.4	10.0
LBP	7.5	7.5	7.2	6.2
BBP	8.2	8.7	8.5	6.7
LIF	8.6	8.8	8.7	6.3
LD	11.3	11.4	11.1	8.5
BZP	4.4	4.6	4.6	3.3
LZS	4.7	6.2	5.5	4.2
LAB	6.4	6.5	6.6	5.8
LM1–3	6.62	6.96	6.54	6.35
WM1	2.36	2.35	2.22	2.05
DI	2.12	2.53	2.03	1.59
DM	7.4	7.7	7.0	6.1

drew attention to the problematic characteristics of the type, a juvenile and so far the only known specimen. We can only echo Hoffmeister's reservations while assuring that the specimen is not an individual of *S. mascotensis.* It was statistically associated with that species as the best multivariate choice among the taxonomic alternatives offered in our discriminant function analysis and given the weight accorded certain pivotal variables, especially LAB and LM1-3. With regard to both, the molar row and bulla of *jacksoni* are small compared with other holotypes and with the Nayarit series of *S. arizonae* (Table 7, Appendix). Nor does the individual's immature age sufficiently explain the erroneous numerical classification—length of molar row, at least, is age invariant. And we reiterate that inclusion of juveniles in preliminary morphometric comparisons, whether principal component or discriminant function analyses, did not obscure taxonomic separation among Nayarit species and *S. hispidus.* The conformation of the zygomatic spine in *jacksoni* more closely resembles the condition typical of *S. hispidus* than that of *S. arizonae.* We doubtfully retain Goldman's (1928) *jacksoni* in the synonymy of *S. arizonae* for want of more convincing evidence of its specific relationships and status.

Ecological notes.—Localities where specimens of *S. arizonae* were captured in Nayarit generally fall within the Arid Upper Tropical Subzone (sensu Goldman 1951). The dominant vegetation at these sites was characterized by field personnel as savanna-woodlands, deciduous tropical forest, palm forest, or mangrove swamp. For localities where microhabitat origin can be reasonably determined, however, individual *Sigmodon* were consistently trapped in open grassy and herbaceous settings, usually in the presence of ample water—whether in the form of rivers and their floodplains, lakes and ponds, or drainage sloughs through agricultural fields and pastures. As noted above, *S. arizonae* taken near San Pedro Lagunillas inhabited a dense stand of water hyacinth bordering the small lake, some of the traps placed on floating mats of the plant. At Ocota Airstrip in southeastern Nayarit (1900 m), surrounded by pine and oak forest, *S. arizonae* were trapped only in grassy patches at the bottom of a nearby arroyo with standing pools of water. Near La Concha, the single specimen of *S. arizonae* was swimming in the shallow Río Canas and caught by hand, after diving straight to the bottom to escape the first attempt at capture.

In view of its presence on coastal plain and along river valleys into Nayarit's interior, *S. arizonae* was collected with a wide variety of rodent species: *Sciurus aureogaster, S. colliaei, Spermophilus annulatus, S. variegatus, Pappogeomys bulleri, Thomomys umbrinus, Chaetodipus pernix, Liomys irroratus, L. pictus, Baiomys tay-*

lori, Hodomys alleni, Neotoma mexicana, Oryzomys palustris, Peromyscus boylii, P. maniculatus, P. melanophrys, P. pectoralis, P. simulus, P. spicilegus, and *Reithrodontomys fulvescens.* It was documented with *S. alleni* in southern coastal plain (Chacala, San Blas) and with *S. mascotensis* in the southern ridge and valley country (2 mi E San Pedro Lagunillas).

Specimens examined.—Durango: Chacala (USNM 96735–96742). Nayarit: Acaponeta (USNM 91398, 91399); near La Concha, Río Canas, Nayarit-Sinaloa state line (USNM 509978); 1 mi S Cuautla (USNM 509980, 510765); Mesa del Nayar, 4500 ft (USNM 511700); Ocota Airstrip (USNM 523944–523951, 524385); Playa Colorado, 15 km S Santa Cruz (USNM 553988–553995, 554152, 554153); 4 mi E Playa Los Corchos (USNM 553996, 554158); San Blas (USNM 89214); 2 mi E San Pedro Lagunillas, east side of lake (USNM 509999, 510003, 510012, 510013, 510017–510019, 510028–510033, 510035–510037, 510039, 510040, 510042–510045, 510047, 510764, 510765, 510768, 510769, 510771, 510775, 510777, 510780–510783, 510785, 510788, 510791); 6 km S Santa Cruz (USNM 553987, 554151); 1.4 mi N (by rd) Tacote (USNM 509979, 510764); Tepic (USNM 88237). Sinaloa: Ahomé (USNM 131541–131543); Culiacan (USNM 96741); Escuinapa (AMNH 24072–24078, 24080–24084, 24086–24094, 24096–24103, 24105–24117, 24484–24486, 24488, 24490–24492, 24494–24497, 24777, 24778, 24476–24478, 24480–24483, 24889–24891, 25887; FMNH 20098); Microondas La Muralla (USNM 524486, 524487); Pinos Gordo (UMMZ 75265); Plomosas (USNM 91401); Rosario (AMNH 13755; USNM 91400); Sierra de Choix, 50 mi NE Choix (USNM 96270–96275). Sonora: Alamos (USNM 96276–96278); Bacerac (USNM 250901); Nogales (USNM 2213); Magdalena (USNM 17806/24743–17808/24745); 23 km S Nogales (USNM 251032); Oputo (USNM 250902–250903).

Sigmodon mascotensis Allen

Sigmodon mascotensis Allen, 1897b:54 (type locality—México, Jalisco, Mineral San Sebastian, near Mascota, 3300 ft; holotype—AMNH 8321/6655).—Bailey, 1902:108 (reallocated as a subspecies of *S. hispidus*).—Zimmerman, 1970:435 (reinstatement as species).—Hall, 1981: 740 (arrangement as nominate subspecies).

Sigmodon colimae Allen, 1897b:55 (type locality—México, Colima, plains of Colima; holotype—AMNH 2648/2318).—Bailey, 1902:108 (synonymy with *S. hispidus mascotensis*).—Allen, 1906:209 (reinstatement as subspecies of *S. hispidus*).—Zimmerman, 1970:446 (synonymy with *S. mascotensis*).—Hall, 1981: 741 (full synonymy with *S. m. mascotensis*).

Sigmodon hispidus tonalensis Bailey, 1902: 109 (type locality—México, Chiapas, Tonalá; holotype—USNM 75144).

Sigmodon hispidus inexoratus Elliot, 1903: 144 (type locality—México, Jalisco, Ocotlan; holotype FMNH 8651).—Hall, 1981:740 (reallocation as a subspecies of *S. mascotensis*).

Sigmodon hispiduas [sic] *atratus* Hall, 1949:149 (type locality—México, Michoacan, 6.5 mi W Zamora, 5950 ft; holotype—MVZ 100628).—Russell, 1952: 82 (synonymy with *S. hispidus inexoratus* Elliot).—Hall, 1981:740 (full synonymy with *S. mascotensis inexoratus*).

Sigmodon hispidus obvelatus Russell, 1952: 81 (type locality—México, Morelos, 5 mi S Alpuyeca, 3700 ft; holotype—TCWC 4921).

Sigmodon hispidus ischyrus Goodwin, 1956:8 (type locality—México, Oaxaca, Yautepec District, Santo Domingo Chontecomatlán, "El Arco" gorge of Río Grande, 2600 ft; holotype—AMNH 171600).—Zimmerman, 1970:446 (synonymy with *S. mascotensis*).—Hall, 1981:740 (retention as a subspecies of *S. mascotensis*).

Distribution.—Coastal plain, interior basins, and west- and south-facing slopes of western México, from southern Nayarit and southwestern Zacatecas to southern Oaxaca and extreme southwestern Chiapas; occurring at low to intermediate elevations (sea level to 2100 m), most localites of specimens examined falling between 500 and 1500 m; and absent from the highlands of the Transverse Volcanic Range, Sierra Madre del Sur, and northern Oaxaca (Fig. 16). In Nayarit, limited to the southeastern quadrant of the state, mostly in tablelands and low mountains but also collected at low elevation in the valley of the Río Grande de Santiago (Fig. 18).

The range of *S. mascotensis* closely approaches that of the *S. hispidus* complex in three regions where sympatry may be eventually recorded. Two involve relatively arid interior valleys, the Tequisquiapan Valley, in southern Queretaro and western Hidalgo, and the Tehuacán Valley, in western Puebla. The third includes the warm lowlands of the Isthmus of Tehuantepec in western Chiapas and southeastern Oaxaca, where, as perceptively observed by Goodwin (1969:199), "*Sigmodon h. mascotensis* does not intergrade with the smaller short-tailed cotton rats of the *hispidus* group [i.e., *toltecus* and *saturatus*] that are prevalent on the Gulf drainage." The basis of his conviction can be readily grasped when perusing the AMNH series from the Tehuantepec district.

Remarks.—In hindsight, the specific affinity of forms now gathered under synonymy of *S. mascotensis* was predictable from the early descriptions themselves. Thus, Bailey (1902:109) characterized *tonalensis,* his new subspecies of *S. hispidus,* as "Similar to *mascotensis* but larger and slightly browner," and further allowed that "This is merely a large form of *mascotensis,* from which there is no sharp geographic separation." In similar manner, the recurring focus of contrast in the differential diagnosis of the other synonyms has been Allen's (1897b) *S. mascotensis* (Elliot 1903, Hall 1949, Russell 1952, Goodwin 1956), including his own *S. colimae,* which he described in the same publication. With regard to the separation of the latter from *S. mascotensis,* Allen (1897b:55) acknowledged that "I am unable to recognize any distinctive cranial features." Specific recognition, as for many other forms described in the late 1800s, rested upon subtle differences in pelage color or size and those posited from actually few specimens (Allen had available four individuals each of his new species *mascotensis* and *colimae*).

Our examinations of types, referred specimens of original type series, and other museum holdings confirm the morphological homogeneity and probable genetic closeness among those populations now arranged under *S. mascotensis.* Allen's (1897b) type of *S. mascotensis* (AMNH 8321/6655) was consistently associated phenetically with our Nayarit samples (Figs. 2 and 17, Table 6), as were the four other holotypes seen and measured (*colimae, tonalensis, inexoratus,* and *ischyrus*—Table 6). Pelage color and texture of the latter four, as well as their cranial features, match the general color pattern and morphology of *S. mascotensis.* We did not examine the type of Hall's (1949) *atratus* (MVZ 100628), though Russell's (1952) merger of the Michoacan taxon into full synonymy with *S. hispidus inexoratus,* accepted by Hall & Kelson (1959) and maintained by Hall (1981) as *S. mascotensis inexoratus,* conveys much about the specimen's inseparability from *S. mascotensis.* Hall's own illustration (1949:150, plate IX) of the type specimen strongly suggests an example of *S. mascotensis,* including possession of the oblong paraptertygoid fenestrae; his single referred specimen, from Zamora (USNM 120268), is undoubtedly an example of the species. Nor did we personally study the holotype of Russell's (1952) *obvelatus* (TCWC 4921); however, all other specimens from his original series (TCWC 4920, 4922, 4923) exhibit the characteristic

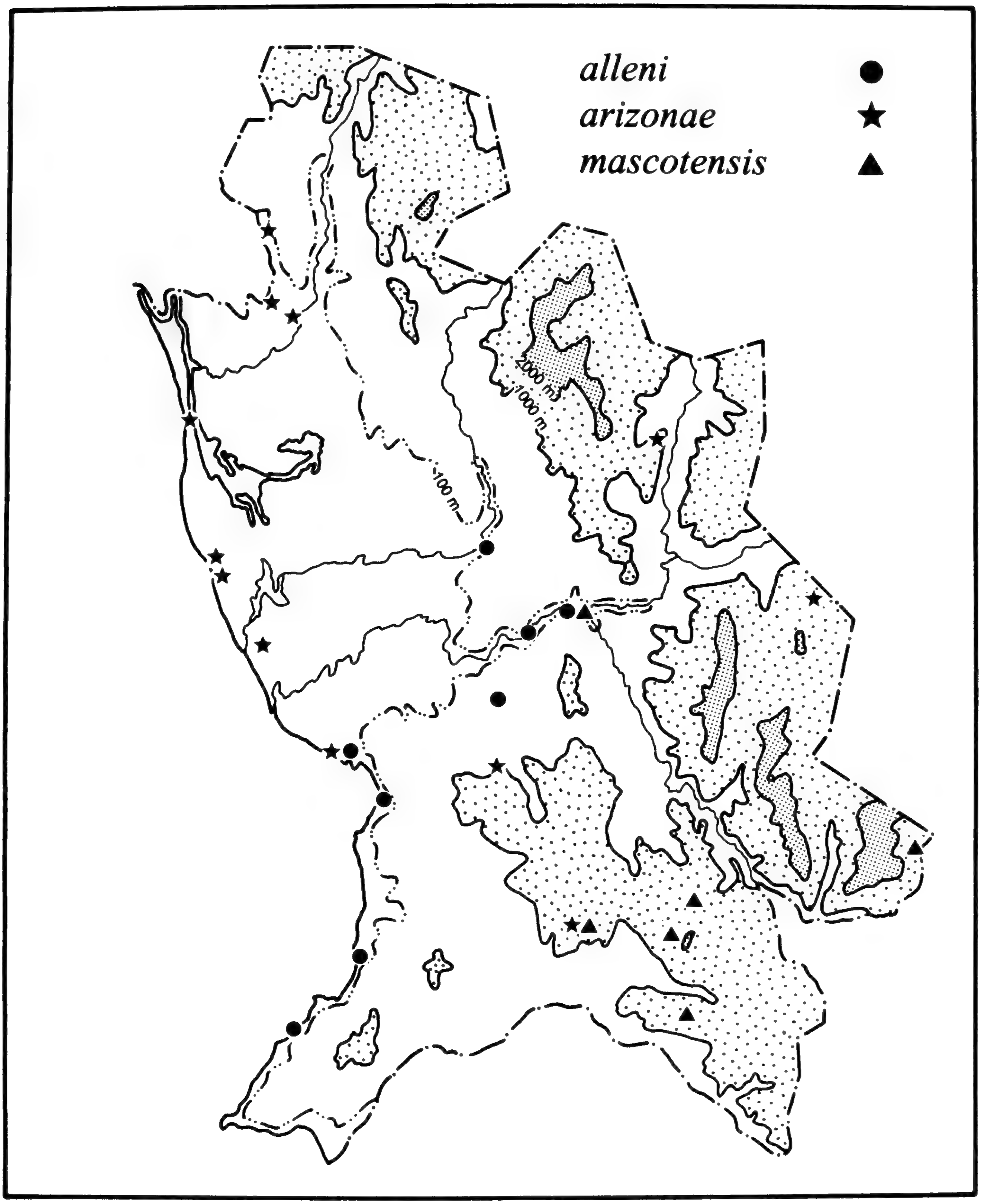


Fig. 18. Distribution of three species of *Sigmodon* in Nayarit, México, based on collections reported herein (dashed-dotted line = 100 m contour; light stipple = elevations between 1000 and 2000 m; dense stipple = elevations above 2000 m).

morphology of *S. mascotensis,* as do others in the USNM collections from Morelos.

In accepting the name changes proposed by Zimmerman (1970), Hall (1981) retained most junior epithets as subspecies of *S. mascotensis,* a nomenclatural formality unsubstantiated by fresh analyses of intraspecific variation. Our qualitative appraisal

Table 8.—Measurements (mm) of type specimens of taxa considered as synonyms of *Sigmodon mascotensis.*

	mascotensis	*colimae*	*tonalensis*	*inexoratus*	*ischyrus*
Sex	F	M	M	M	M
Age	A	A	O	A	A
TOTL			350.0	310	
LT			166.0	146	145.5
LHF			41.0	36	34.5
ONL	34.7	36.0	38.9	37.1	37.4
ZB	19.5	19.9	22.0	20.5	21.3
IOB	5.2	5.1	5.8	5.0	5.2
BBC	13.5	13.9	14.9	14.3	14.3
BOC	7.4	8.2	8.1	7.7	7.7
DBC	11.5	11.3	12.5	10.9	11.7
DTR	4.2	3.7	4.4	3.9	4.4
LR	12.1	12.0	13.7	12.2	13.4
BR	6.4	6.8	7.8	7.4	7.9
PPL	12.4	12.7	14.0	13.9	14.0
LBP	6.1	6.6	6.3	7.4	6.5
BBP	7.5	8.0	8.3	7.9	8.2
LIF	8.7	7.8	9.7	7.9	8.4
LD	10.0	9.6	11.4	10.7	10.8
BZP	4.0	4.2	4.8	4.4	4.0
LZS	4.7	5.1	5.2	5.8	5.1
LAB	5.4	6.0	5.9	5.6	5.9
LM1–3	6.12	6.61	6.23	6.32	6.13
WM1	2.18	2.20	2.09	2.24	2.10
DI	1.97	2.12	2.21	2.14	2.19
DM	6.2	6.3	7.3	6.7	6.7

of some 500+ museum specimens, collected across the range of *S. mascotensis* as now defined, suggests that such future analyses should devote attention to populations from eastern Oaxaca and contiguous Chiapas. Even allowing for the advanced age of the type specimen of Bailey's (1902) *tonalensis* (Table 8), the populations it represents—for example, those from Tehuantepec and Guiengola, Oaxaca—are impressive for their size, which approximates the dimensions attained by adult *S. arizonae.* In addition, these large Oaxacan animals typically possess a more corrugated palate and pronounced mesopterygoid spine, again more like examples of *S. arizonae* and less like most *S. mascotensis.* Still, in inflation of the bullae, size of the foramen ovale, frequency of parapterygoid fenestrae, and pelage features, these series fit best with *S. mascotensis.*

Apart from the enigmatic combination of traits found in these southern populations, samples of *S. mascotensis* from the northern and middle parts of its range appear uniform and display the kinds of minor interlocality variation attributable to differences in age composition, molting stage, and collecting season. Further, no chromosomal variation is thus far known for populations distributed over this region, from Nayarit to western Oaxaca (Zimmerman 1970, this report). To our knowledge, chromosomes of named forms from eastern Oaxaca (*ischyrus*) or western Chiapas (*tonalensis*) have yet to be examined.

Ecological notes.—*Sigmodon mascotensis* was common in the southern part of Nayarit, where most collecting sites represent the Arid Lower Tropical Subzone (Goldman 1951). The region is topographically diverse with low mountains and tablelands dissected by river valleys and steeply eroded arroyos. Ridges are covered with tropical deciduous forest that grades into oak and pine-oak woodland associations at the upper elevations; meandering streams and valley bottoms, rocky outcrops and old lava flows afford ample terrain for open grass and brush stands and mixed savanna-scrublands. Where verifiable, specimens of *S. mascotensis* originated from the latter habitats, as well as from around agricultural fields bordered with rank brush. At Estanzuela, traplines that produced *S. mascotensis* ran through grassland and broken pine-oak woods and along a streambank covered with ferns. South of Ahuacatlan, examples of *S. mascotensis* were captured in tall grasses interspersed among rocks, bare soil, and scattered oaks and cactus.

In addition to *Sigmodon alleni* and *S. arizonae, S. mascotensis* was documented sympatrically with *Sciurus aureogaster, S. colliaei, Spermophilus variegatus, Pappogeomys bulleri, Liomys irroratus, L. pictus, Baiomys taylori, Neotoma mexicana, Oryzomys melanotis, O. palustris, Peromyscus maniculatus, P. melanophrys, P. pectoralis, P. spicilegus,* and *Reithrodontomys fulvescens.* The locality of sympatry with *S. alleni,* Arroyo de Jiguite near its confluence with the Río Grande de Santiago (100 m), is situated in a lowland region where a number of intermediate- to high-elevation *Peromyscus* species were unexpectedly found to occur (Carleton et al. 1982).

Specimens examined.—Chiapas: Cintalapa, Cinco Cerros (AMNH 148825–148828); Cintalapa, 555 m (UMMZ 92476, 94033–94035, 96306); Tonalá (AMNH 167430, 167431); mountains near Tonalá (USNM 75144, 76089). Colima: Armería, sea level–200 ft (USNM 33323/45351–33332/45360, 34185); Colima, 1700 ft (USNM 33333/45361–33341/45369); plains of Colima (AMNH 2646/2319, 2647/2129, 2648/2318, 2649); 3 mi SE Colima (UMMZ 100693, 100694). Guerrero: 0.5 mi W Acahuizotla, 3000 ft (UMMZ 109205); Acapulco, near sea level (USNM 70764); Agua del Obispo, 2900 ft (UMMZ 108558); Chilpancingo, 4800 ft (FMNH 47550, 47552, 47554–47557, 48466, 51947–51949; UMMZ 81461–81470, 84015, 84016, 89262, 104977–104991; USNM 70300, 70760–70763); Cuapongo (FMNH 47553); El Limón (126530, 126531); Iguala, 750 m (UMMZ 92597, 93455–93462); near Ometepec, 200 ft (USNM 71575, 71576); Tlalixtaquilla, 4200 ft (USNM 70234). Jalisco: Ameca, 4000 ft (USNM 82247); 6 mi W Ameca, 4300 ft (UMMZ 95495–95499); 7 mi W Ameca, 4000 ft (UMMZ 95500); Atenquique (AMNH 26322–26324); Atemajac, 4500 ft (USNM 34146/46223); 4 mi NE Autlán, 3000 ft (UMMZ 95501–95507, 96268); Estancia (AMNH 25289, 25346, 25350, 25357, 25358, 25364–25366); Huejuquilla, 5400 ft (USNM 90810); Lagos, 6150 ft (USNM 78969, 80348); Las Canoas (AMNH 26317–26321, 26551–26557); Mascota, Mineral San Sebastián, 3300 ft (AMNH 8321/6655, 8322/6656); 0.5 mi W Mazamitla (UMMZ 100695, 100696, 100698); Ocotlán, 5000 ft (FMNH 8651–8653, 8656–8658, 8660–8662, 8664–8666; USNM 120153–120159); Ojo de Agua, near Amatlán (AMNH 25360); Rancho Palo Amarillo, near Amatlán (AMNH 25353–25356); Arroyo de Plantanar (AMNH 25348, 25349, 25361); 2 mi N Resolana, 1500 ft (UMMZ 95510–95512); Río Santa María (AMNH 25347, 25359); Tuxpan (AMNH 26293, 26294); Zacoalco, 3000 ft (USNM 34143/46220–34145/46222); Zapotlán, 4000 ft (USNM 3359/45624, 33590/45625). Michoacan: Hacienda El Molino (USNM 20440/35670); La Huacana (USNM 126522–126529); La Salada (USNM 126520, 126521); 9.6 mi S Lombardía, 1400 ft (UMMZ 110562, 110563); Los Reyes (USNM 125933–125935); Queréndaro, 5800 ft (USNM 50201); 12 mi S Tzitzio, road to Huetamo, 1050 m (UMMZ 92214); Zamora (USNM 120268). Morelos: 5 mi S Alpuyeca, 3500 ft (TCWC 4921, 4922); Cuernavaca, 5000 ft (USNM 51164, 51165); 2 km S Jonacatepec, 4500 ft (TCWC 4920); Puente de

Ixtla (USNM 126938–126940); Yautepec, 4100 ft (USNM 51166–51169); 6 mi W Yautepec, 6000 ft (TCWC 4923). Nayarit: 8 mi S (by rd) Ahuacatlán (USNM 523952–523955); Amatlán (AMNH 25345, 25351, 25352); Arroyo de Jiguite, Río Santiago, 100 m (USNM 523956–523977, 523979–523981, 523983–523986, 524386–524392); 1.8 mi NW (by rd) Coapan, 4650 ft (USNM 511701); Estanzuela (USNM 510051–510058, 510793–510799); Rancho Sapotito, 3500 ft (USNM 511702–511706, 511756); 1 mi SW San José del Conde, 3000 ft (UMMZ 95492–95494); 2 mi E San Pedro Lagunillas, east side of lake (USNM 509982–509998, 510000–510002, 510004–510011, 510014–510016, 510020–510027, 510034, 510038, 510041, 510046, 510048–510050, 510766, 510767, 510770, 510772–510774, 510776, 510778, 510779, 510784, 510786, 510787, 510789, 510790, 510792); 2 mi N Santa Isabel, 3800 ft (UMMZ 95490, 95491). Oaxaca: Agua Blanca, 4000 ft (AMNH 145823); Buena Vista (AMNH 145252); Cerro Calderona, 3000 ft (AMNH 147696); Cuicatlán, 640 m (UMMZ 96801); Escuranos (AMNH 143950); Guiengola, 3600 ft (AMNH 142522, 142523, 142530–142533, 143432, 143951, 147697–147712); Huajuapam, 5500 ft (USNM 70233, 70235, 70236); Huilotepec (AMNH 143430); Jalapa (AMNH 171618, 171619, 175188–175191); Juchitán (AMNH 175193–175197); La Reforma (AMNH 175192; FMNH 14100, 14102); 5 km N Las Cuevas (AMNH 142524–142527); Limón (AMNH 186920); Miahuatlán (UMMZ 94032); Mixtequilla (AMNH 175186); Morro Mazatlán (AMNH 167432, 171607, 171654); Nizanda (AMNH 175253); Oaxaca, 5000 ft (USNM 68230, 68652–68654); Cerro Palma de Oro (AMNH 147717); Cerro Pozo Río (AMNH 142529, 148816, 148817); Puerto Angel, 100–300 ft (USNM 71577–71581); Reforma, 50 m and 100 m (UMMZ 96805, 96806); Rincón Bamba (AMNH 148819–148823); Sacatepec (AMNH 189288); San Antonio (AMNH 143425–143427, 143477); San Dionisio, Buena Vista (AMNH 145992–145997); San Pedro Jilotepec (AMNH 145249, 149922, 149923); Santa Lucía (AMNH 144572); Santiago Lachiguiri (AMNH 145832–145835); Santo Domingo, 900 ft (AMNH 3096/2415; USNM 73316–73318); Cerro Sombrerito (AMNH 145831); Tamazulapam, 7000 ft (USNM 70231, 70232); Tapanatepec (AMNH 177093–177100, 177980); Tehuantepec, 150 ft (AMNH 142535, 147713, 147714, 148824, 171608–171617, 171620, 171621, 171655–171658, 175184, 175185, 175187; USNM 9672/9508, 9673/9509, 9671/9510, 11907, 13071, 13072, 73315); 50 mi N Tehuantepec (AMNH 174811); Teotitlán, 950 m (UMMZ 89263, 89264, 91602); Tequisistlán (AMNH 143420–143424); Cerro de Tigre (AMNH 142534, 147716); Zanatepec (FMNH 14101). Puebla: Tehuacán (UMMZ 89250–89260, 89323; USNM 9385/8667); 2 mi W Tehuacán, 5200 ft (UMMZ 103188); Tepanco (UMMZ 89261). Queretaro: Cadereyta, 2100 m (UMMZ 93737); Tequisquiapam (USNM 78427). Zacatecas: 6 km S Apozol, 1170 m (MSU 27240); 16 km SSE Monte Escobedo, 2010 m (MSU 27241–27247); 5 km NE San Juan Capistrano, near Las Tablas, 1330 m (MSU 23645); 18 km N San Juan Capistrano, near Las Tablas, 1100 m (MSU 27234–27239); 2 mi N Santa Rosa, 3850 ft (MSU 11668, 12475); Valparaíso, 6200 ft and 6500 ft (USNM 92008–92010).

Sigmodon alleni Bailey

Sigmodon alleni Bailey, 1902:112 (type locality—México, Jalisco, San Sebastian, Mascota; holotype—USNM 88227).

Sigmodon vulcani Allen, 1906:247 (type locality—México, Jalisco, Volcán de Fuego, 3050 m; holotype—AMNH 26310).

Sigmodon guerrerensis Nelson & Goldman, 1933:196 (type locality—México, Guerrero, Omilteme, 8000 ft; holotype—USNM 126936).

Sigmodon planifrons Nelson & Goldman, 1933:197 (type locality—México, Oaxaca, Juquila, 5000 ft; holotype—USNM 71918).

Sigmodon planifrons minor Goodwin, 1955:1 (type locality—México, Oaxaca, District of Tehuantepec, 12 km NE Tenango, Santa Lucía, 4000 ft; holotype—AMNH 143429).

Sigmodon macdougalli Goodwin, 1955:3 (type locality—México, Oaxaca, 12 km S Yautepec, Santo Tomás Teipán, 7000 ft; holotype—AMNH 149122).

Sigmodon macrodon Goodwin, 1955:4 (type locality–México, Oaxaca, District of Tehuantepec, 20 km W Mixtequilla, Cerro San Pedro; 3600 ft; holotype—AMNH 142536).

Sigmodon planifrons setzeri Goodwin, 1959:447 (replacement name for *S. planifrons minor* Goodwin, 1955, preoccupied by *S. minor* Gidley, 1922).

Distribution.—Pacific coastal lowlands and contiguous slopes of western cordilleras, from southern Sinaloa to central Oaxaca (see Baker 1969, Shump & Baker 1978). In Nayarit, at low elevations (sea level to 760 m) in the southwestern quadrant of the state, the deepest interior records found along the lower valleys of the Río San Pedro and the Río Grande de Santiago (Fig. 18).

The geographic range of *S. alleni,* as presently understood, is partly congruent with the revised distribution of *S. mascotensis.* Individuals of the former, however, apparently prefer more mesic habitats, which may explain the species' occurrence farther north into Sinaloa and at higher elevations, up to 3050 m and into pine-oak vegetation (Baker 1969), as well as its absence from the upper drainage of the Río Balsas and Lago de Chapala, dryer interior basins where *S. mascotensis* is found. Nevertheless, the geographic range of *S. alleni* deserves further documentation, as we have encountered many instances of specimens mistakenly intermixed with *S. mascotensis* in museum collections.

Remarks.—In his description of *S. alleni,* Bailey (1902) recorded the co-occurrence of his new species with *mascotensis* at San Sebastián, Jalisco, and with *major* (now = *S. arizonae*) at San Blas, Nayarit. Based on these records of overlap, Bailey diagnosed *alleni* as a species and relegated all other members of his *hispidus* group to subspecies of the latter. While explaining his choice of patronym, he continued (1902: 113), "It [*S. alleni*] is the species Dr. Allen had in mind in writing his description of *mascotensis* from which he intended to separate the Colima form, but as the two specimens of the species here named *alleni* were not fully adult he unfortunately selected as his type another specimen that proves to be the same as the form to which on the following page he gave the name *colimae.*" Allen (1906) continued to recognize *colimae* as distinct from *mascotensis,* but we concur with Bailey's taxonomic judgement regarding both the synonymy of *colimae* under *mascotensis* and their specific distinction from *S. alleni.* The possibility of confusion is understandable, as we noted above under the morphometric results, particularly when separating isolated skulls of *S. alleni* from those of *S. mascotensis.*

The junior synonyms that have accrued to Bailey's *S. alleni,* following Baker (1969) and Shump & Baker (1978), require substantiation. To us, their arrangement as a single species seems improbable. Although they exhibit the reddish brown dorsum and softer fur typical of *alleni* sensu lato, the types of *planifrons* and *planifrons setzeri* are strikingly diminutive in all dimensions of the skin and skull—particularly as reflected in the narrow incisors, delicate molar rows, constricted interorbit, tiny otic capsules, and shorter tail—compared with *alleni*-like taxa also described from Oaxaca (*macdougalli* and *macrodon*) or with typical *alleni* from farther north (including *vulcani* and *guerrerensis*). The divergent treatment of *planifrons* by Goodwin (1969), who retained it as a species, and Baker (1969), who relegated it to a subspecies of *S. alleni* (along with *macdougalli* and *macrodon* in full synonymy) warrants reconciliation. It is noteworthy that Goodwin (1969) had identified both *planifrons* and *macdougalli* from Santa Lucia, Oaxaca, the type locality of his (1955, 1959) *planifrons setzeri.* Renewed study of the Oaxacan forms will prove critical to much-needed revision of the *S. alleni* complex.

Ecological notes.—Other rodents captured at localities with *Sigmodon alleni* include *Sciurus colliaei, Spermophilus annulatus, Thomomys umbrinus, Liomys pictus, Baiomys taylori, Hodomys alleni, Neotoma mexicana, Oryzomys melanotis, O. palustris, Osgoodomys banderanus, Peromyscus maniculatus, P. melanophrys, P. pectoralis, P. simulus,* and *P. spicilegus.* Records of sympatry with other *Sigmodon* appear to fall where coastal plain meets southern foothills, with *S. arizonae* at San Blas and with *S. mascotensis* at Arroyo de Jiguite.

Specimens examined.—Nayarit: Arroyo de Jiguite, Río Santiago, 100 m (USNM 523935, 523978, 523982, 523987, 523988); 4 km S Aticama (USNM 524479, 524480); Chacala (USNM 523934); 1.2 mi S (by rd) El Casco, Río Chilte, 480 ft (USNM 511697–511699); 3.5 mi E (by rd) El Venado (USNM 509981); 1 km S La Villita (524478); 1 mi S Lo de Marcos, sea level (USNM 523936–523943); San Blas (USNM 89212, 89213); 3.5 mi E San Blas, 100 ft (UMMZ 100680, 100681).

Sigmodon hispidus

Sigmodon berlandieri Baird, 1855:333 (type locality—México, Coahuila, Río Nasas; holotype—USNM 566/1687).

Sigmodon borucae Allen, 1897a:40 (type locality—Costa Rica, Puntarenas, Boruca; holotype—AMNH 11761/10045).

Sigmodon hispidus eremicus Mearns, 1897: 4 (type locality—México, Sonora, Cienega Well, 30 mi S monument no. 204, Mexican boundary line; holotype—USNM 60319).

Sigmodon hispidus saturatus Bailey, 1902: 111 (type locality—México, Tabasco, Teapa; holotype—USNM 99998).

Sigmodon hispidus microdon Bailey, 1902: 111 (type locality—México, Yucatán, Puerto Morelos; holotype—USNM 108467).

Sigmodon borucae chiriquensis Allen, 1904:68 (type locality—Panamá, Chiriquí, Boqueron; holotype—AMNH 18789).

Sigmodon hispidus griseus Allen, 1908:657 (type locality—Nicaragua, Chontales, coastal lowlands; holotype—AMNH 28497).

Sigmodon hispidus confinis Goldman, 1918:21 (type locality—United States, Arizona, Graham County, Safford, 2900 ft; holotype—USNM 204241).

Sigmodon zanjonensis Goodwin, 1932:1 (type locality—Guatemala, Zanjon, 9000 ft; holotype—AMNH 69277).

Sigmodon hispidus villae Goodwin, 1958:2 (type locality—México, Chiapas, 5 mi E Teopisca, 6000 ft; holotype—AMNH 174799).

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Appendix.—Descriptive statistics for selected cranial and external variables and OTUs of *Sigmodon.*

Species	OTU	*n*	Mean	Range	*SD*
		Total length			
S. alleni	OTU 1	14	245.8	221.0–278.0	16.3
S. arizonae	OTU 3	15	305.5	247.0–363.0	33.6
S. mascotensis	OTU 5	20	278.1	242.0–313.0	20.1
	OTU 6	32	257.0	220.0–305.0	21.4
S. hispidus	OTU 9	44	250.8	220.0–282.0	18.4
		Tail length			
S. alleni	OTU 1	14	110.2	91.0–130.0	10.7
S. arizonae	OTU 3	15	124.4	101.0–145.0	13.6
S. mascotensis	OTU 5	20	132.3	110.0–156.0	12.3
	OTU 6	32	112.3	96.0–141.0	10.5
S. hispidus	OTU 9	44	99.1	81.0–115.0	8.6
		Hindfoot length			
S. alleni	OTU 1	17	30.2	27.0–32.0	1.4
S. arizonae	OTU 3	19	38.5	34.0–43.0	2.3
S. mascotensis	OTU 5	21	34.1	31.0–38.0	1.9
	OTU 6	33	35.0	31.0–38.0	1.7
S. hispidus	OTU 9	47	33.3	31.0–36.0	1.3
		Mass (Weight)			
S. alleni	OTU 1	17	72.1	49.0–106.0	15.9
S. arizonae	OTU 3	19	150.3	83.0–300.0	54.8
S. mascotensis	OTU 5	21	99.6	63.0–148.0	22.6
	OTU 6	33	77.4	51.0–122.0	17.8
S. hispidus	OTU 9	15	89.8	68.0–144.0	18.3
		Occipitonasal length			
S. alleni	OTU 1	17	32.1	27.9–36.0	2.2
S. arizonae	OTU 3	21	35.2	27.4–40.4	3.5
S. mascotensis	OTU 5	27	32.8	29.8–37.0	1.9
	OTU 6	40	31.6	27.5–35.3	1.7
S. hispidus	OTU 9	50	34.6	30.2–37.7	1.8
		Zygomatic breadth			
S. alleni	OTU 1	20	17.8	15.8–19.8	1.0
S. arizonae	OTU 3	25	20.9	17.4–23.8	1.6
S. mascotensis	OTU 5	27	18.7	17.0–20.7	1.0
	OTU 6	45	18.3	15.6–20.7	1.0
S. hispidus	OTU 9	53	19.3	16.3–21.1	1.0
		Interorbital breadth			
S. alleni	OTU 1	19	5.0	4.6–5.6	0.1
S. arizonae	OTU 3	25	5.1	4.5–5.6	0.3
S. mascotensis	OTU 5	27	4.9	4.5–5.5	0.3
	OTU 6	45	5.0	4.6–5.4	0.2
S. hispidus	OTU 9	53	5.1	4.4–5.7	0.2
		Breadth of braincase			
S. alleni	OTU 1	19	13.7	12.9–14.3	0.4
S. arizonae	OTU 3	21	14.9	13.9–16.3	0.6
S. mascotensis	OTU 5	27	14.0	13.1–14.7	0.4
	OTU 6	43	13.9	12.6–14.6	0.4
S. hispidus	OTU 9	53	14.4	13.3–15.4	0.5

Appendix.—Continued.

Species	OTU	*n*	Mean	Range	*SD*
Breadth of occipital condyles					
S. alleni	OTU 1	20	7.3	6.7–7.8	0.3
S. arizonae	OTU 3	20	8.1	6.9–8.8	0.5
S. mascotensis	OTU 5	27	7.4	6.9–8.0	0.3
	OTU 6	41	7.5	6.9–8.2	0.3
S. hispidus	OTU 9	52	7.5	6.1–8.0	0.3
Depth of braincase					
S. alleni	OTU 1	19	10.2	9.3–11.3	0.5
S. arizonae	OTU 3	19	11.7	9.9–12.9	0.9
S. mascotensis	OTU 5	27	11.3	10.8–12.2	0.3
	OTU 6	41	10.8	8.9–11.7	0.5
S. hispidus	OTU 9	52	10.7	9.8–11.6	0.4
Distance between temporal ridges					
S. alleni	OTU 1	20	3.3	2.7–3.9	0.3
S. arizonae	OTU 3	24	4.4	3.3–5.0	0.4
S. mascotensis	OTU 5	27	4.0	3.3–4.8	0.4
	OTU 6	45	3.7	2.5–4.4	0.4
S. hispidus	OTU 9	53	3.2	2.5–4.1	0.3
Length of rostrum					
S. alleni	OTU 1	17	10.7	9.1–12.5	1.0
S. arizonae	OTU 3	25	11.6	8.3–13.7	1.3
S. mascotensis	OTU 5	27	10.6	9.0–12.7	0.9
	OTU 6	43	10.3	8.1–11.7	0.7
S. hispidus	OTU 9	50	11.6	9.8–13.0	0.8
Breadth of rostrum					
S. alleni	OTU 1	20	6.5	5.5–7.5	0.5
S. arizonae	OTU 3	24	7.0	5.4–8.9	0.8
S. mascotensis	OTU 5	27	6.4	5.5–7.4	0.5
	OTU 6	45	6.3	5.3–7.2	0.4
S. hispidus	OTU 9	53	6.7	5.7–7.8	0.5
Postpalatal length					
S. alleni	OTU 1	19	11.2	9.3–12.8	0.9
S. arizonae	OTU 3	20	12.8	9.6–15.5	1.6
S. mascotensis	OTU 5	27	11.5	10.0–13.2	0.8
	OTU 6	41	10.9	9.2–12.7	0.7
S. hispidus	OTU 9	52	12.1	5.6–7.3	0.4
Length of bony palate					
S. alleni	OTU 1	20	6.1	5.4–7.1	0.5
S. arizonae	OTU 3	25	6.6	5.3–8.0	0.5
S. mascotensis	OTU 5	27	6.1	5.2–6.9	0.4
	OTU 6	45	6.1	5.1–6.8	0.4
S. hispidus	OTU 9	53	6.6	5.6–7.3	0.4
Breadth of bony palate					
S. alleni	OTU 1	20	7.2	6.7–8.1	0.4
S. arizonae	OTU 3	25	8.1	6.7–9.2	0.5
S. mascotensis	OTU 5	27	7.2	6.7–8.0	0.4
	OTU 6	45	7.4	6.8–8.0	0.3
S. hispidus	OTU 9	53	7.7	6.7–8.5	0.3

Appendix.—Continued.

Species	OTU	*n*	Mean	Range	*SD*
		Length of incisive foramen			
S. alleni	OTU 1	20	6.7	5.8–7.6	0.5
S. arizonae	OTU 3	25	8.0	6.2–9.7	0.9
S. mascotensis	OTU 5	27	6.9	5.9–8.2	0.6
	OTU 6	45	6.7	5.5–7.8	0.5
S. hispidus	OTU 9	53	7.8	6.2–9.0	0.6
		Length of diastema			
S. alleni	OTU 1	20	8.6	7.2–10.2	0.8
S. arizonae	OTU 3	25	9.8	7.3–12.1	1.3
S. mascotensis	OTU 5	27	8.7	7.6–10.3	0.7
	OTU 6	45	8.3	6.3–9.7	0.7
S. hispidus	OTU 9	53	9.5	7.7–11.2	0.8
		Breadth of zygomatic plate			
S. alleni	OTU 1	20	3.6	3.0–4.1	0.3
S. arizonae	OTU 3	25	4.1	3.1–5.1	0.5
S. mascotensis	OTU 5	27	3.6	2.8–4.5	0.4
	OTU 6	45	3.7	3.0–4.6	0.3
S. hispidus	OTU 9	53	3.9	2.6–4.8	0.4
		Length of zygomatic spine			
S. alleni	OTU 1	20	3.8	3.1–4.4	0.4
S. arizonae	OTU 3	25	5.0	3.6–5.9	0.7
S. mascotensis	OTU 5	27	4.3	3.3–4.9	0.4
	OTU 6	46	4.4	3.2–5.5	0.5
S. hispidus	OTU 9	53	4.5	3.2–5.5	0.5
		Length of auditory bulla			
S. alleni	OTU 1	20	5.1	4.6–5.6	0.3
S. arizonae	OTU 3	24	6.1	5.3–6.8	0.3
S. mascotensis	OTU 5	27	5.3	4.9–5.8	0.2
	OTU 6	43	5.3	4.7–5.8	0.2
S. hispidus	OTU 9	53	6.3	5.7–7.0	0.3
		Length of maxillary toothrow			
S. alleni	OTU 1	20	5.70	5.36–6.13	0.19
S. arizonae	OTU 3	25	6.82	6.30–7.39	0.25
S. mascotensis	OTU 5	27	5.95	5.59–6.78	0.26
	OTU 6	46	6.23	5.80–6.63	0.23
S. hispidus	OTU 9	53	6.39	6.00–6.81	0.18
		Width of upper first molar			
S. alleni	OTU 1	20	1.90	1.76–2.03	0.08
S. arizonae	OTU 3	25	2.29	2.12–2.47	0.09
S. mascotensis	OTU 5	27	2.01	1.84–2.26	0.09
	OTU 6	46	2.09	1.94–2.34	0.08
S. hispidus	OTU 9	53	2.15	1.91–2.32	0.08
		Depth of upper incisor			
S. alleni	OTU 1	20	1.81	1.47–2.12	0.09
S. arizonae	OTU 3	25	2.01	1.53–2.37	0.22
S. mascotensis	OTU 5	27	1.81	1.52–2.07	0.08
	OTU 6	46	1.85	1.47–2.17	0.15
S. hispidus	OTU 9	53	1.99	1.52–2.22	0.16
		Depth of mandible			
S. alleni	OTU 1	20	5.8	5.1–6.6	0.4
S. arizonae	OTU 3	25	6.6	5.2–7.6	0.6
S. mascotensis	OTU 5	27	5.9	5.3–6.7	0.4
	OTU 6	46	5.8	4.7–6.7	0.4
S. hispidus	OTU 9	53	6.4	5.4–7.2	0.4

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