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The taxonomic status of the Yucatán brown brocket, *Mazama pandora* (Mammalia: Cervidae)

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Abstract.—The Yucatán brown brocket deer, described as *Mazama pandora*, is now treated as a subspecies of either the common brown brocket *Mazama gouazoubira*, or of the red brocket *M. americana*. Analysis of brocket deer from México and Central and South America, reveals that the Yucatán brown brocket is sympatric with the red brocket in México and, while similar to *M. gouazoubira*, warrants recognition as a separate species.

Merriam (1901) described a brown brocket from the Yucatán Peninsula as *Mazama pandora*. Allen (1915) retained *M. pandora* as a species and aligned it with the brown brocket group. Gaumer (1917) treated *M. pandora* as a synonym of *Cariacus rufinus* (Bourcier & Pucheran 1852), variously considered either a red or a brown brocket. Tate (1939:226), believing that red brockets (his Division A [large brockets]) occurred only in South America, allied *M. pandora* with his Division B (small brockets) in which he included both "red" and "brown" species. Goldman & Moore (1945) listed *pandora* as a subspecies of the Mexican red brocket *M. sartorii* Saussure, 1860 (=*M. americana*), a taxon Tate (1939) had questionably equated with *M. tema* Rafinesque, 1817, (=*M. americana*) and included in his Division B group. Hershkovitz (1951) listed *pandora* as a subspecies of the common South American brown brocket *M. gouazoubira* (Fischer 1814). Miller & Kellogg (1955) and Hall & Kelson (1959) followed Hershkovitz's allocation and used the name combination *M. gouazoubira pandora*. Later, Hershkovitz (1966: 743, footnote) changed his mind and, having decided that the Yucatán brown brocket was a color variant of the red brocket, said it "should be known as *Mazama americana pandora*." Genoways & Jones (1975) agreed, as did Hall (1981), Ramírez P. et al. (1986), and Grubb (1993). Czernay (1987) and Bisbal (1991), however, disagreed and treated *pandora* as an disjunct subspecies of *M. gouazoubira*.

As currently understood (Grubb 1993), *Mazama* is represented in México by a single species, the red brocket *M. americana* (Erxleben 1777), found in the states of Campeche, Quintana Roo, Yucatán, Chiapas, Oaxaca, Veracruz, Tamaulipas, and San Luis Potosí (Hall 1981, Ramírez P. et al. 1986, Grubb 1993). Hall (1981) recognized three subspecies in México: *M. a. pandora* in the northern Yucatán Peninsula, *M. a. cerasina* Hollister, 1914, in easternmost Chiapas (but did not cite a record), and *M. a. temama* Kerr, 1792, elsewhere in the country. *Mazama americana* also occurs southward through Central and South America to Argentina (Cabrera 1961, Eisenberg 1989, Emmons & Feer 1990, Redford & Eisenberg 1992). The only other brocket currently known north of South America is *M. guoazoubira permira* Kellogg, 1946, a brown brocket endemic to Isla

San José, one of the Islas Perlas in the Gulf of Panamá. *Mazama gouazoubira* is widespread in South America.

Recent field work on the Yucatán Peninsula (Fig. 1) has confirmed Czernay's (1987) and Bisbal's (1991) conclusion that both a red and a brown species of *Mazama* occur in México. Our analysis of specimens shows *pandora* (Fig. 2) to be a brown brocket that warrants recognition as a species distinct from *M. gouazoubira*.

Materials and Methods

We examined 74 specimens of *Mazama* from México, Central America, Colombia, and Venezuela (Fig. 1). Specimens are deposited in three collections in México and four in the United States: Universidad Veracruzana (UV), Xalapa; Instituto de Biología (IBUNAM), Distrito Federal; Instituto Nacional de Investigaciones sobre Recursos Bióticos (INIREB), El Colegio de la Frontera Sur, San Cristobal de las Casas, Chiapas; American Museum of Natural History (AMNH), New York; Field Museum of Natural History (FMNH), Chicago, Illinois; Florida Museum of Natural History (UF), University of Florida, Gainesville; and National Museum of Natural History (USNM), Washington, D.C. The samples include the type specimens of *M. pandora* Merriam, 1901, and *M.* [*gouazoubira*] *permira* Kellogg, 1946.

We recorded body measurements (from label information) and 8 qualitative characters of the pelage and cranium, along with 14 cranial dimensions in females and 23 in males (Tables 1 & 2) as follows:

Qualitative characters.—1) color pattern (brown versus red); 2) insertion of antlers (parallel or U-shaped versus divergent or V-shaped); 3) condition of unworn antlers (fluted along total length versus either heavily rugose or ridged at the base, but otherwise relatively smooth); 4) shape of zygomatic arch in lateral view above glenoid fossa (elevated posteriorly versus broadly rounded); 5) nasals domed versus straight in lateral profile; 6) shape of premaxillae (tapering anteriorly versus broad anteriorly); 7) shape of posterior margin of palate (mesopterygoid fossa U-shaped versus V-shaped); 8) presence and length of sulcus associated with supraorbital foramen.

Measurements.—External: Total length, tail, hind foot, ear, and mass (weight). Cranial (Table 2): Condylobasal length (CBL); condylo-premolar length (CPL); zygomatic breadth (ZB); maxillary toothrow (from anterior alveolar margin of first premolar to posterior alveolar margin of last molar; MAX); breadth of braincase (BBC); postorbital constriction (POC); breadth of rostrum (width across rostrum at most vertical juncture of maxilla-premaxilla suture; BR); length of auditory bulla (LAB); width of auditory bulla (WAB); distance from posterior margin of orbit to posterior base of pedicel (DOP); maximum diameter of pedicel (DP); distance between pedicels (DPP); length of antlers (including pedicel; LA). We recorded other measurements including condylo-incisive length of mandible, condylo-premolar length of mandible, angular-coronoid height, height of pedicel, maximum diameter of antler above burr, maximum distance between antlers above burr, minimum distance between antlers above burr, distance between antlers points, as well as dimensions of premolars. However, we do not report them in this analysis because of their overall lack of diagnostic value within the focus of this report. We also do not compare the direction of nape hairs and the degree of tuft development on the forehead because too few skins of *pandora* were available to make these comparisons meaningful.

We segregated our sample into four groups: 1) 34 specimens from México, Central America, and Colombia having a red coat, V-shaped mesopterygoid fossa, and comparatively short, parallel antlers; 2) 7 *M. guoazoubira permira* from Isla San José, Gulf of Panamá; 3) 8 *M. gouazoubira* ssp. from Colombia and Venezuela; and 4)

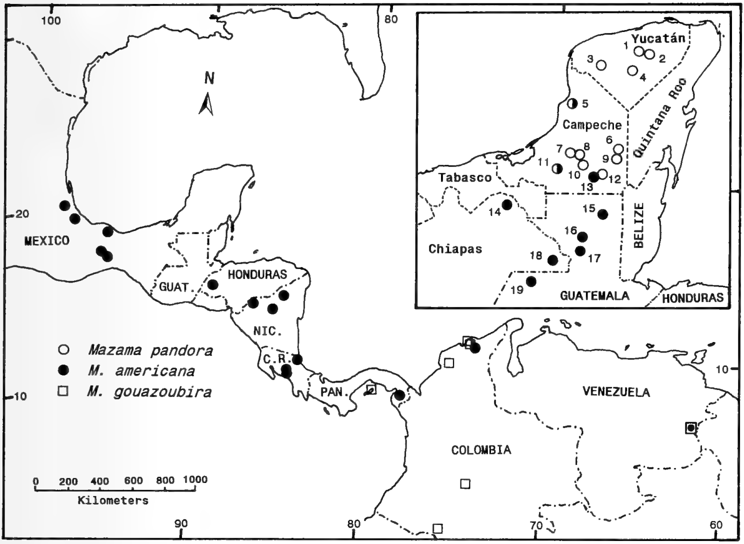

Fig. 1. Map of localities represented by specimens of *Mazama* spp. reported on here. Localities listed under Specimens Examined identified in sequence for each country (and for each State in México) from north to south, west to east. Numbered localities on inset of the Yucatán Peninsula and adjacent Guatemala and Chiapas, México as follows: Mexico, Yucatán—1) Tunkás, 2) Dzitás, 3) 10 km SE of Muna, 4) Tixcacaltuyub; Campeche—5) Pokiazum [=Pocyaxum], 6) Ejido El Refugio, 7) Apazote, 8) 5 km W of Antigua Central Chiclera La Esperanza, 9) Ejido Nuevo Becal, 10) La Tuxpeña, 11) Central Chiclera Villahermosa, 12) 73 km SSW of Xpujil, 13) Calakmul; Chiapas—14) Palenque; Guatemala—15) Petén, Tikal, 16) Petén, La Libertad region, 17) Petén, Sayaxche; Mexico, Chiapas—18) Ejido López Mateos; Guatemala—19) Huehuetenango, Barrillas.

Table 1.—Comparison of selected qualitative characters of populations of *Mazama* spp. from México, Central America, Colombia, and Venezuela. See Materials and Methods for abbreviations and descriptions of character states; CA = Central America; SA = South America (Colombia and Venezuela).

Character	*M. pandora*	*M. americana* México	*M. americana* CA	*M. americana* SA	*M. gouazoubira* Panamá	*M. gouazoubira* SA
Color	gray-brown	red	red	red	gray-brown	gray-brown
Antlers						
insertion	divergent	parallel	parallel	parallel	parallel	parallel
unworn	fluted	rugose	rugose	rugose	ridged	ridged
ZA elevation	narrow arch	broad arch	broad arch	broad arch	broad arch	broad arch
Nasal profile	humped	straight	straight	straight	straight	straight
Premaxillae	broad	tapering	tapering	tapering	tapering	tapering
Palatal margin	10-U/1-V	V-shaped	12-V/2-U	V-shaped	V-shaped	V-shaped
SO sulcus	≥20 mm	≤20 mm	≤20 mm	variable	≤5 mm	≥20 mm

Fig. 2. Adult male *Mazama pandora* with moderately-worn antlers. Photographs by Oscar Moctezuma.

Table 2.—Selected measurements of population samples of *Mazama* spp. from México, Central America, Colombia, and Venezuela. See Materials and Methods for abbreviations and descriptions of measurements; CA&Col = Central America and Colombia; Col&Ven = Colombia and Venezuela; Ven = Venezuela. Sexes are combined except for postorbital constriction. Values are given as range over mean followed by sample size in parentheses.

		M. americana			*M. gouazoubira*	
Measurement	*M. pandora*	México	CA&Col	Ven[a]	Panamá	Col&Ven
CBL	161.3–177.0 169.5 (8)	162.0–171.0 166.9 (4)	156.8–180.0 171.3 (10)	208.9–209.5 209.2 (2)	156.2–171.2 165.3 (3)	159.0–176.0 166.6 (8)
CPL	114.4–127.0 120.5 (8)	109.0–121.2 114.7 (10)	106.0–120.6 115.3 (11)	142.4–143.9 143.2 (2)	110.0–118.9 115.0 (5)	109.5–119.0 112.9 (8)
ZB	70.9–84.5[b] 77.7 (13)	73.6–86.5 79.8 (13)	73.0–90.8 79.6 (13)	90.9–97.2 94.1 (2)	68.8–74.6 71.5 (4)	69.8–80.0 73.7 (8)
MAX	49.9–51.9 50.6 (6)	48.0–54.3 50.9 (6)		59.6–61.0 60.3 (2)	50.5	49.0
BBC	53.7–59.1 55.7 (14)	52.5–59.9 56.1 (13)	51.6–61.2 56.4 (14)	61.5–62.2 61.9 (2)	47.7–51.0 49.9 (5)	49.8–56.6 53.2 (8)
POC–♂♂	59.1–70.2[b] 67.1 (7)	46.5–61.2 49.3 (14)	46.6–55.5 50.3 (7)	52.1–59.3 55.7 (2)	43.8–47.5 45.8 (3)	44.5–56.7 48.4 (4)
POC–♀♀	47.6–52.6 49.6 (8)	46.7–49.2 48.2 (3)	46.1–54.5 49.2 (7)		43.8–44.5 44.2 (2)	45.0–50.0 47.2 (4)
BR	18.2–26.6 22.3 (12)	18.7–24.4 21.6 (10)	20.0–28.0 22.9 (14)	26.5–28.5 27.5 (2)	19.8–25.2 22.1 (4)	19.0–26.2 21.6 (8)
LAB	23.6–26.6 25.1 (6)	20.0–23.4 21.3 (5)	20.3	23.8–26.6 25.2 (2)	17.6–19.4 18.7 (3)	21.3
WAB	10.4–12.4 11.6 (6)	8.7–10.3 9.4 (5)	9.5	8.6–10.9 9.8 (2)	8.1–9.1 8.6 (3)	10.1
DOP	34.9–41.6[b] 38.5 (5)	33.4–47.1 37.9 (5)		47.7–49.5 48.6 (2)	33.8	43.4
DP	19.7–22.3 21.1 (6)	11.4–19.7 14.0 (7)		15.3–20.8 18.1 (2)	6.7	12.6
DPP	39.6–46.0 43.2 (7)	26.4–40.7 32.0 (7)		35.7–43.0 39.4 (2)		31.2
LA	112.4–142.0 126.6 (6)	50.4–91.1 70.5 (10)	81.1–96.0 86.4 (3)	106.4–129.8 118.1 (2)	50.5–69.0 59.8 (2)	54.7–71.3 63.0 (2)

[a] Two large males (USNM 374880, 374883) identified as *M. americana shelia.*

[b] Sample includes one subadult male.

20 specimens from México having either a brown to grayish-brown coat, U-shaped mesopterygoid fossa, domed nasals, or long, divergent antlers (because most specimens were incomplete, specimens were assigned to this group on the basis of one or more of these features). Some specimens representing both groups 1 and 4 were from sympatric populations on the Yucatán Peninsula. Complete measurements are available for only a few specimens in each group because most specimens are incomplete; several are only skulls (some fragmented), and a few consist of only frontals with antlers.

In addition to these four samples we added two extremely large male red brockets from eastern Venezuela identified as *M. americana shelia* (see measurements in Table 2). These specimens provided additional means to compare and contrast the size of the auditory bullae and the size and length of antlers and pedicels between *pandora*, *americana*, and *gouazoubira*.

Results and Discussion

Brockets in the first group clearly represent *M. americana* as the taxon is known today. All skins are reddish ventrally and uniformly bright reddish dorsally. Skulls have a narrow, tapering rostrum (premaxillae); small (usually less than 20 mm in length) to obsolete sulci associated with supraorbital foramina (Fig. 3A); straight nasals (in lateral profile; Fig. 4A); narrow postorbital constriction; dorsal margin of squamosal root of zygoma broadly arched above glenoid fossa (in lateral profile; Fig. 5A); and predominately V-shaped mesopterygoid fossa (U-shaped in only 2 of 32 specimens with complete palates). In males, the pedicels are short and slender; antlers are either parallel or convergent and, in the unworn condition, moderately to extremely rugose at the base (Fig. 6A).

The second group comprises only *Mazama gouazoubira permira*. These are small deer having a grayish-brown coat, minute or absent supraorbital foramina and associated sulci, straight nasals (in lateral profile), narrow postorbital constriction, squamosal root of zygoma broadly arched above glenoid fossa (in lateral profile), and a V-shaped mesopterygoid fossa. Males have short, slender pedicels and short, straight, parallel antlers.

Group three consists of small to medium-sized Colombian and Venezuelan *M. gouazoubira*, which have a grayish-brown coat, narrow postorbital constriction, predominately V-shaped mesopterygoid fossa, straight to slightly and evenly convex nasals (in lateral profile; Fig. 4C), and broadly arched (in lateral profile; Fig. 5C) squamosal root of zygoma above glenoid fossa. Males have slender pedicels and short to long, straight antlers that are ridged at the base in the unworn condition. Both sexes have supraorbital foramina and associated sulci of variable size, but usually greater than 20 mm in length.

The fourth group consists only of brown brockets from the Yucatán Peninsula and represent the taxon described by Merriam (1901) as *M. pandora*. These deer are characterized by brown to gray-brown dorsal pelage and paler to whitish venters (Fig. 2); comparatively-broad, spatulate premaxillae; broad postorbital constriction, especially in males (Table 2); posterior half of nasals conspicuously humped in lateral profile (Fig. 4B); large supraorbital foramina usually opening into prominent, long grooves (sulci usually longer than 20 mm, Table 2; Fig. 3B); posterior margin of palate predominantly U-shaped in outline (V-shaped in only 1 of 11 specimens where condition could be assessed); and dorsal margin of squamosal root of zygoma narrowly arched above glenoid fossa (Fig. 5B). Males have massive pedicels (Figs. 3B & 4B) and long, divergent, and usually curved antlers that may converge at the tips. The frontal region is broad in *M. pandora*, especially in males (Fig. 3B; compare values for postorbital constriction in Table 2). Bivariate diagrams (Fig. 7) of postorbital constriction plotted against breadth of braincase illustrate sexual dimorphism in this dimensions in *M. pandora*. Although these measurements of a subadult male (IBUNAM 38345) fall between the clusters of adult females and males, the postorbital constriction is clearly larger than that of the largest female in our sample. In contrast, the diagrams (Fig. 7) for *M. americana* and *M. gouazoubira* show no evidence of differences between the sexes in postorbital constriction.

Mazama pandora is larger than sympatric *M. americana*, and has a larger patch of longer dark stiff hairs on the forehead (Fig. 2). Males have heavier antlers that are fluted along almost the entire length in the unworn condition (Fig. 6B). The flutes in unworn antlers are separated by thin, sharp ridges; "deeply plicated or furrowed longitudinally" was how Merriam (1901:106) described them. The furrowed appearance is not always evident in heavily worn antlers.

Merriam (1901) described *M. pandora* as a "grayish or drab brown" brocket deer based on a male (holotype) from Tunkás, Yucatán, and a female from Apazote, Campeche. His description was accurate and emphasized the characteristics of color, width of forehead, configuration of zygo-

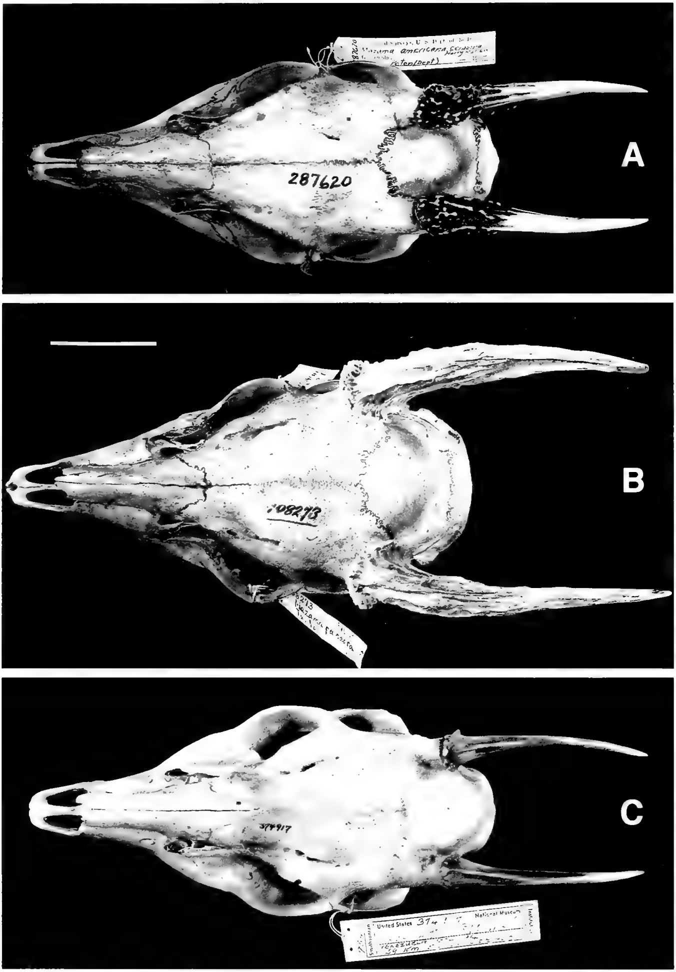

Fig. 3. Dorsal views of skulls of *Mazama*. A, *M. americana* (USNM 287620) from Petén, Guatemala; B, *M. pandora* (USNM 108273, holotype) from Yucatán, México; C, *M. gouazoubira* (USNM 374917) from Bolívar, Venezuela. Horizontal bar equals 40 millimeters.

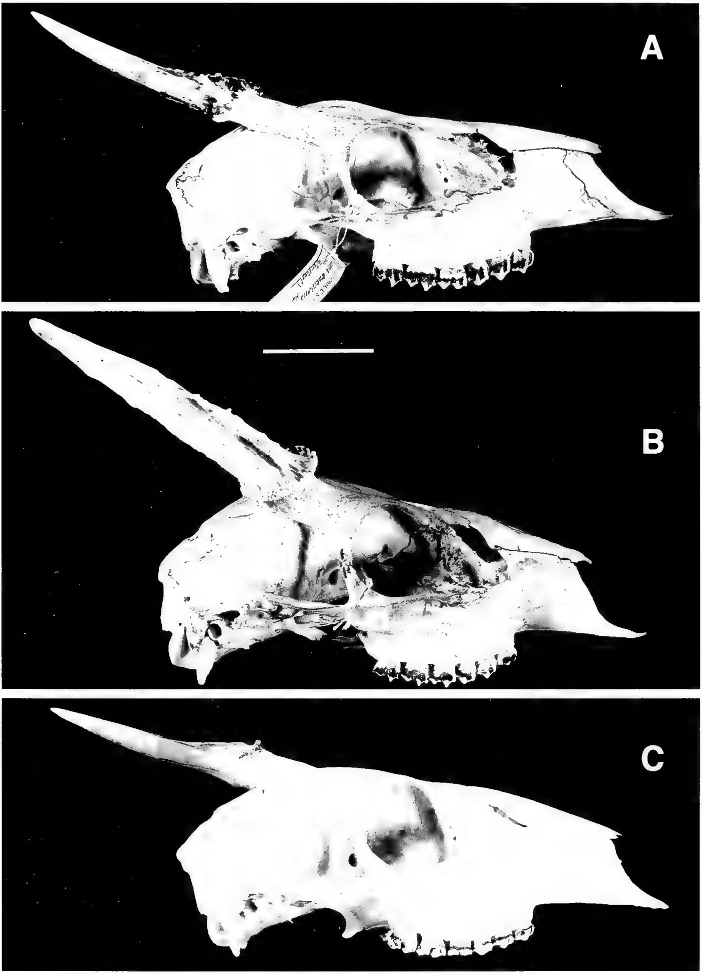

Fig. 4. Lateral views of skulls of *Mazama*. A, *M. americana* (USNM 287620) from Petén, Guatemala; B, *M. pandora* (USNM 108273, holotype) from Yucatán, México; C, *M. gouazoubira* (USNM 374917) from Bolívar, Venezuela. Horizontal bar equals 40 millimeters.

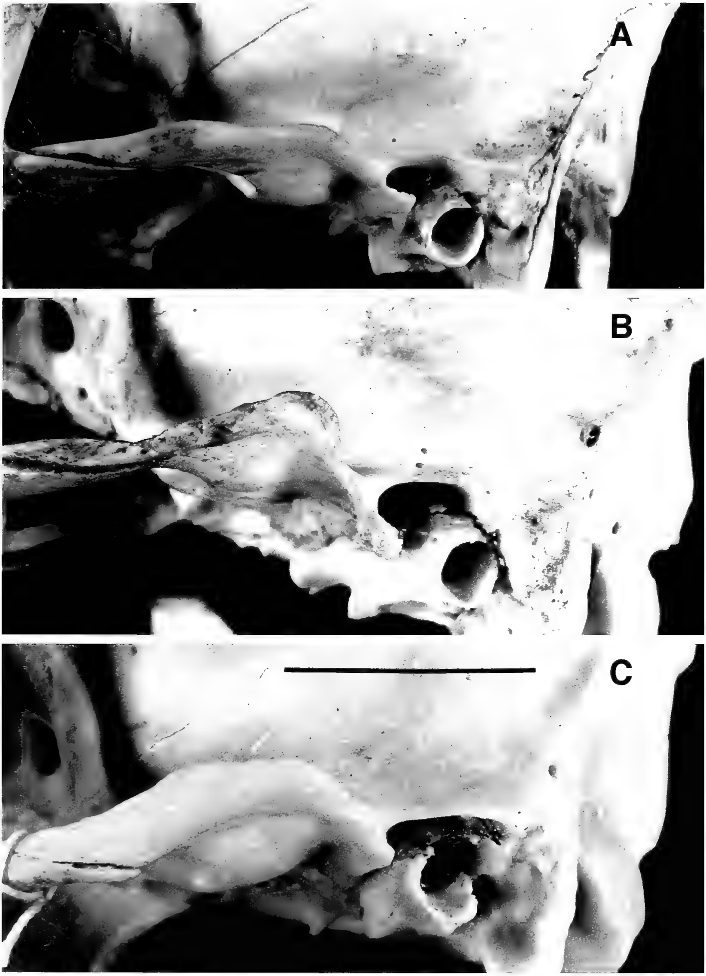

Fig. 5. Lateral view of squamosal region of skull of *Mazama* spp. showing the configuration of the zygomatic arch above the glenoid fossa. A, *M. americana* (USNM 287620) from Petén, Guatemala; B, *M. pandora* (USNM 108273, holotype) from Yucatán, México; C, *M. gouazoubira* (USNM 374917) from Bolívar, Venezuela. Horizontal bar equals 20 millimeters.

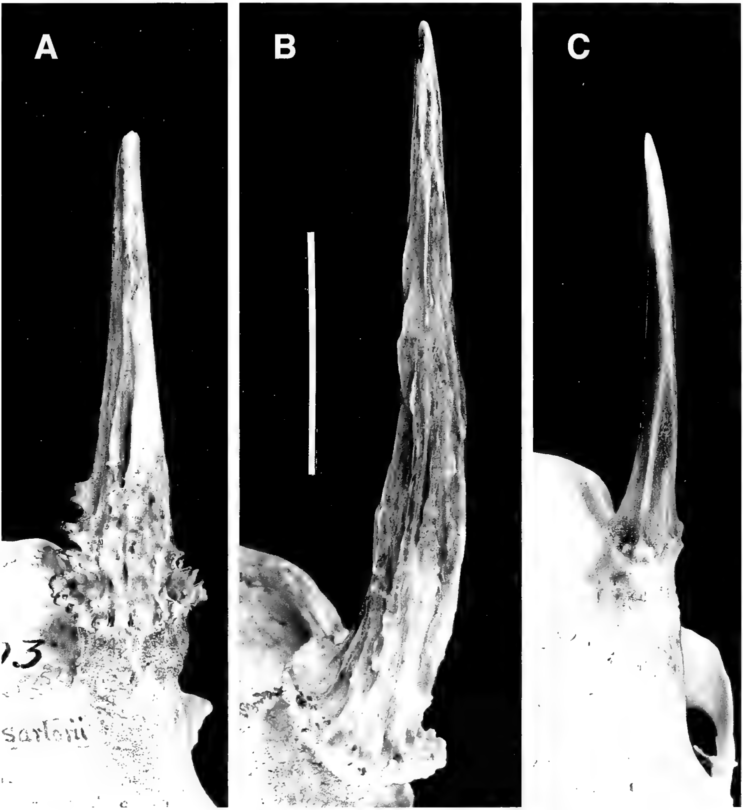

Fig. 6. Antlers of *Mazama* spp. A, Unworn antler of *M. americana* (USNM 6203) from Veracruz, México; B, unworn antler of *M. pandora* (USNM 108278, holotype) from Yucatán, México; C, moderately worn antler of *M. gouazoubira* (USNM 374917) from Bolívar, Venezuela. Vertical bar equals 40 millimeters.

matic arch above glenoid fossa, and the size and appearance of the antlers that we also found useful for distinguishing between *pandora* and other brocket deer. Merriam contrasted his new species with *M. sartorii* (=*M. americana*) and pointed out a number of cranial and dental features to distinguish the two, in addition to those cranial features we have mentioned here. Merriam (1901) provided external measurements of the male holotype; to which we add external measurements (in mm) of another male, IBUNAM 38343 from Campeche: Total length 1120, tail 75, hind foot 262, ear 110; weight 21 kg.

Czernay (1987) and Bisbal (1991) are the only workers since 1959 who have treated *M. pandora* as a brown brocket (*M. goua-*

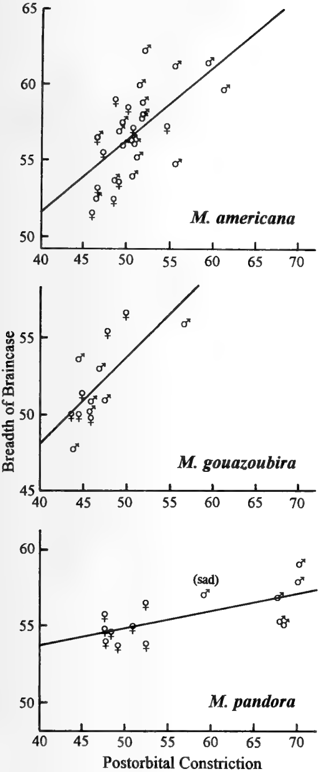

Fig. 7. Bivariate diagrams of postorbital constriction plotted against breadth of braincase in *Mazama americana*, *M. gouazoubira*, and *M. pandora*. The male (IBUNAM 38345) between the clusters of males and females in the plot for *M. pandora* is a subadult (sad).

zoubira pandora). The major similarity between *M. pandora* and *M. gouazoubira* is coat color. All other modern workers have treated *pandora* as a subspecies of *americana* following Hershkovitz (1966:743, footnote) who said, "The Yucatán Peninsula brocket is a red brocket and should be known as *Mazama americana pandora*. Its generally brownish color (but not its color pattern), backwardly directed nuchal hairs, and small size misled authors, including myself, into regarding *pandora* as a race of the brown brocket, *Mazama gouazoubira*." Hershkovitz rationalized the grayish brown coat color by claiming that brown color variants are found throughout the range of the red brocket.

Mazama pandora and *M. americana* are sympatric in humid forest habitats at the base of the Yucatán Peninsula. While *M. americana* appears to be restricted to humid tropical forests, the Yucatán brown brocket also occupies more open and drier deciduous and thorn forest habitats of the northern Yucatán Peninsula. The Mayan Indians of the Yucatán Peninsula have long recognized the presence of a brown brocket distinct from the red species, as has the Club Safari International (A. Rivera, pers comm), and Mexican government officials who oversee hunting activity (J. M. Reyes, pers comm.).

Little is known about the biology of *M. pandora* other than what can be inferred by its distribution in arid habitats of the Yucatán Peninsula. The larger auditory bulla of *M. pandora* (contrast B with A & C in Fig. 8) may be correlated with the greater sound-carrying characteristics of more open habitats. Because sound frequencies carry farther in savannas and open-forest formations, *M. pandora* may have greater reliance on its hearing capability than is characteristic of *M. americana*, whose denser forest habitat of larger trees effectively dampens long-distance sound travel, especially during the warmer daytime.

Remarks.—Grubb (1993) used the spelling "*gouazoupira*," which is the original spelling used by Fischer (1814). Fischer described two brockets, *Cervus gouazoupira* and *Cervus gouazoupita* based, respectively, on the Guarani vernaculars Guazú-birá and Guazú-pitá used by Azara (1802) for Paraguayan brown and red brocket deer. Hershkovitz (1951), likely having assumed that Fischer's "*Gouazoupira*" was a lapsus

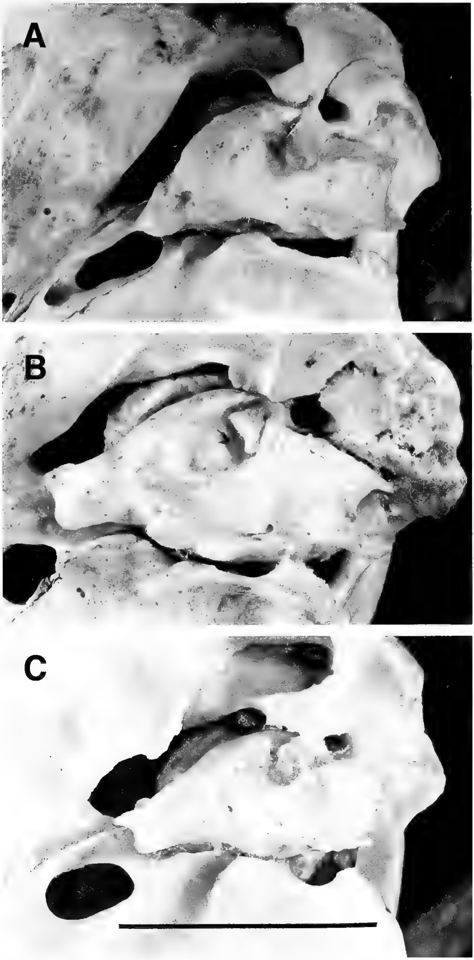

Fig. 8. Auditory bullae of *Mazama* spp. A, Right bulla of *M. americana* (USNM 287620) from Petén, Guatemala; B, left bulla (print made from reversed negative) of *M. pandora* (USNM 108273, holotype) from Yucatán, México; C, right bulla of *M. gouazoubira* (USNM 374917) from Bolívar, Venezuela. Horizontal bar equals 20 millimeters.

for *gouazoubira*, changed the spelling to *gouazoubira*, technically an unjustified emendation. With the exception of Grubb (1993), *gouazoubira* is the commonly-used spelling. A. L. Gardner (see BZN, 1996) has petitioned the International Commission on Zoological Nomenclature to validate Hershkovitz's (1951) emendation of the name. Therefore, the spelling *gouazoubira* is used in this report.

Specimens Examined

Localities for the following specimens plotted on map in Fig. 1 in the order listed below for each State in México, and for each country elsewhere. The geographic sequence is from north to south, west to east.

Mazama americana (36).—Mexico (19): Puebla, near La Aurora Mining Camp [plotted point in Fig. 1 is approximate] (AMNH 100193 ♂); Veracruz, Mirador (USNM 6007 ♂, 6201 ♂, 6202 ♂, 6203 ♂), Mirador Pilapa (UV 372 ♂, not plotted), Municipio Mecayapan, Ejido Santa Martha (UV 129 ♂, 131 ♂); Campeche, Pokiazum [=Pocyaxum] IBUNAM 26395 ♂), Central Chiclera Villahermosa (IBUNAM 38352 ♂, 38353 ♂), Municipio Champotón, Zona Arqueológica de Calakmul (IBUNAM 37333 ♂); Oaxaca, Juchitán-Sarabia (AMNH 185273 ♂, 185274 ♀), San Miguel Chimalapa (IBUNAM 26392 ♂), locality unknown (AMNH 207449 ♀); Chiapas, Palenque (USNM 100418 ♀), Municipio Ocosingo, Ejido López Mateos, Río Lacantun (INIREB ♂), locality unknown (uncataloged UV ♂ from Zoológico Regional Miguel Alvarez del Toro, Tuxtla Gutierrez). Guatemala (5): Petén, Tikal (UF 6788 ♀), La Libertad region (USNM 287620 ♂), Sayaxche (UF 6795 ♂); Huehuetenango, Barrillas (AMNH 75137 ♂, 75138 ♀). Honduras (1): Lempira, Pucca [=Cerro Puca] (AMNH 130032 ♀). Nicaragua (4): Zelaya, Peña Blanca [=Peñas Blancas] (AMNH 29826 ♀); Madriz, San Juan [=San Juan Telpaneca, fide Allen, 1910] (USNM 29451 ♀); Matagalpa, Lavala [=Savala, see Allen 1915 for spelling; Jones & Genoways 1970 for location] (AMNH 28427 ♀, 28432 ♂). Costa Rica (3): Limón, Tortuguero (UF 13825 ♂); San José, Sabanillas de Pirris (FMNH 35173 ♂); Puntarenas, Pozo Azul (AMNH 19209 ♂). Panamá (1): Darién, El Reál (AMNH 37616 ♂). Colombia (1): Magdalena, Mamanacanaca (USNM 282137 ♀). Venezuela (2): Bolívar, 59 km SE of El Dorado (USNM 374880 ♂, 374883 ♂)

Mazama gouazoubira permira (7).—Panamá (5): Panamá, Isla San José (AMNH 144472 ♂, 144473 ♀; USNM 277144 ♂—holotype, 277145 ♂, 277146 ♀, 277147 ♂, 277148 ♀).

Mazama gouazoubira spp. (8).—Colombia (7): Magdalena, Guairaca [=Ensenada de Gayraca] (FMNH 13168 ♂), Bonda (FMNH 18800 ♀); Bolívar, San Juan Nepomuceno (FMNH 68804 ♀); Meta, La Macarena, Río Guapaya (FMNH 87868 ♀, 87869 ♂, 87870 ♂); Putamayo, Río Mecaya (FMNH 70559 ♀). Venezuela (1): Bolívar, 59 km SE of El Dorado (USNM 374917 ♂).

Mazama pandora (20).—México (20): Yucatán, Tunkás (USNM 108273 ♂—holotype), Dzitás (USNM 269164 ♀), 10 km SE of Muna (IBUNAM 1625 ♀), Municipio Sotuta, Tixcacaltuyub, 100 km SE of Mérida (IBUNAM 38349 ♂, 38350 ♂, 38351 ♀); Campeche, Pokiazum [=Pocyaxum] (IBUNAM 26393 ♂, 26394 ♂), Municipio Hopelchén, Ejido El Refugio, 35 km NNE of Xpujil (IBUNAM 36707 ♂), Apazote (USNM 108287 ♀), Municipio Champotón, 5 km W of Antigua Central Chiclera La Esperanza (IBUNAM 26624 ♂, 26625 ♀, Municipio Hopelchén, Ejido Nuevo Becal (INIREB 9 ♂), La Tuxpeña (USNM 181263 ♀), Central Chiclera Villahermosa (IBUNAM 38343 ♂, 38344 ♀, 38345 ♂, 38346 ♀), 73 km SSW of Xpujil (IBUNAM 38347 ♂, 38348 ♂).

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Two new species of ergasilid copepods parasitic on fishes cultured in brackish water in Taiwan

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Abstract.—*Ergasilus lobus* and *Diergasilus kasaharai* are described based on the specimens obtained from the gill filaments of the moribund fishes cultured in brackish water in southern part of Taiwan. The former species was obtained from Malabar reef-cod (*Epinephelus malabaricus*) and the latter, from milkfish (*Chanos chanos*) and Borneo mullet (*Liza macrolepis*). A key to the 22 species of *Ergasilus* occurring on the coastal, brackish water fishes of the world is provided.

Copepods of the family Ergasilidae are generally known as parasites of freshwater fishes throughout the world. Nevertheless, some of them are found on estuarine and/or coastal fishes. According to Ho (1991), in the course of copepod evolution, poecilostome copepods represented by the Ergasilidae succeeded only once in invading freshwaters, and those ergasilids occurring on coastal, brackish water fishes are a group of poecilostomes secondarily adapted for marine existence.

Several species of ergasilids are known to cause disease in finfish cultured in brackish waters (Nigrelli 1950, Nakajima & Egusa 1973, Paperna 1975, Wijeyaratne & Gunawardene 1988, Leong & Wong 1988, Hogans 1989). In this paper, two species of ergasilids are reported from the fishes cultured in brackish water in the southern part of Taiwan, a species of *Ergasilus* and a species of *Diergasilus*.

On 2 October 1992, a moribund Malabar reef-cod (*Epinephelus malabaricus*) was brought to the Laboratory of Fish Disease at the Chiayi Institute of Technology for examination. The fish came from a culture pond located in Chi-ku Village of Tainan County. A close examination showed that its gill filaments were infected with *Ergasilus* sp. (Fig. 1A) or contained many "vacuoles" (Fig. 1B). Since no other abnormalities were detected, the death of the fish was suspected to be caused by the infection of the ergasilid copepod. Later, on 23 June 1993, a mass mortality occurred in another culture pond in the same village where about 9000 juvenile Malabar reef-cods (imported from Thailand) were cultured. For 15 days, about three to four hundred dead fish were removed daily from the pond. Examination of the dead fish revealed the same condition, carrying *Ergasilus* sp. and with many "vacuoles" in the gill filaments, as observed in October 1992 from another pond. A subsequent histological examination of the "vacuoles" in the gill filaments showed no trace of microbes or protozoan parasites; "vacuoles" may have formed by the host's reaction to the hooking and/or penetration of the ergasilid's antenna.

On 23 December 1993, a mass mortality occurred in a culture pond in Chi-ku Village where about 20,000 milkfish (*Chanos chanos*) were cultured. In the beginning, about 10 fish died daily, but after a week more than 100 fish died in a day. Examination of the moribund fishes revealed that

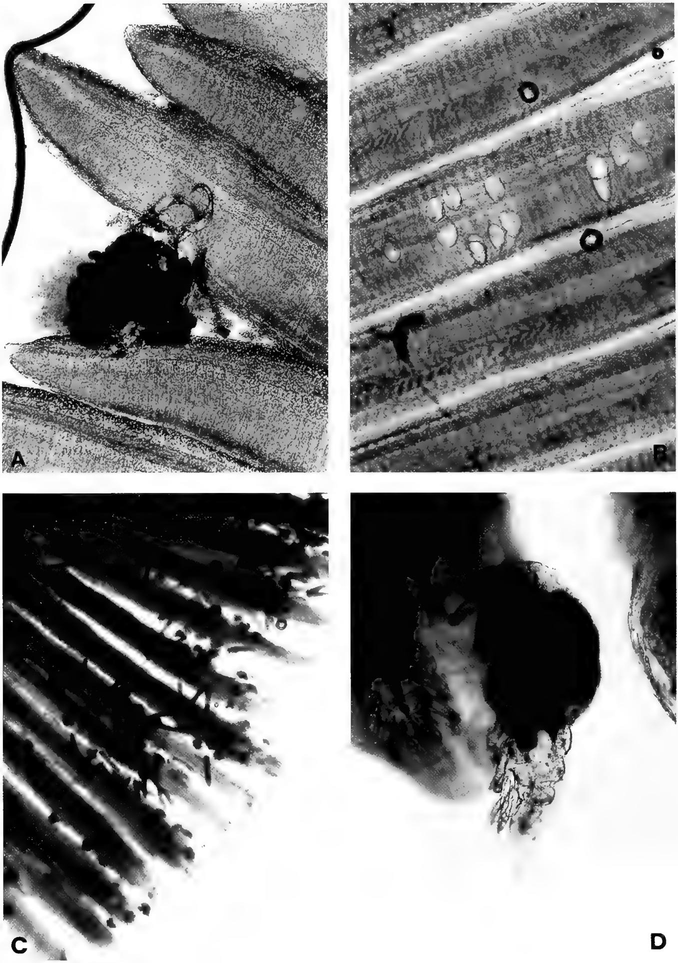

Fig. 1. Gill filaments of diseased fishes. A. from *Epinephelus malabaricus* showing attachment of *Ergasilus lobus*; B. from *E. malabaricus* showing the "vacuoles"; C. from *Liza macrolepis* showing a heavy infestation with *Diergasilus kasaharai*; D. from *L. macrolepis* showing attachment of *D. kasaharai*.

death was caused by the parasitism of a species of ergasilid copepod belonging to *Diergasilus*. More than 130 copepods could be removed from the gill filaments of an infected fish. In October 1994, the same parasite was found on Borneo mullet (*Liza macrolepis*) cultured together with tilapia (*Oreochromis* sp.) in a pond in Hu-Nei Village in Kaoshiung County. Two to three hundred mullets per day died for about a week. The moribund mullets, swimming at the edge of the pond, were found to carry between 500 to 1000 copepods on their gill filaments (see Fig. 1C); these filiments showed inflamation, necrosis and were coated with excessive amount of mucus. Undoubtedly, the death of the mullets were due to the heavy parasitism of *Diergasilus* sp. (Fig. 1D).

About 160 species of poecilostome copepods are currently classified in 26 genera of the family Ergasilidae (Malta 1993, 1994; Amado et al. 1995). Of these 26 ergasilid genera, *Ergasilus* is the largest with about three-quarters of the known ergasilid species. Identification of the species of *Ergasilus* has been a problem for many biologists who are not familiar with this group of parasitic copepods.

In as much as the culture of marine finfish in the coastal area in brackish water is becoming more and more popular in many parts of the world, identification of those potential fish disease causing ergasilids is becoming more and more indispensable. In addition to describing the above-mentioned species of *Ergasilus* and *Diergasilus* a key to the species of *Ergasilus* which may occur on coastal, brackish water fishes is also provided as a quick identification method for these pathogens.

Materials and Methods

Moribund fishes obtained from fishermen were examined under the dissection microscope for abnormalities and the presence of parasites. Upon the discovery of parasitic copepods, photographs were taken with the parasites in situ, after which the parasites were removed from the host and preserved in 70% ethyl alcohol. Microscopical examination of the ergasilid copepods was based on specimens fixed and preserved in ethyl alcohol and which were cleared in 85% lactic acid for a couple of hours before taking measurements and making dissections. All drawings were made with the aid of a camera lucida. All measurements were taken from the longest, widest and deepest parts of the body and are given in mm unless mentioned otherwise.

Descriptions

Ergasilus lobus, new species
(Figs. 2–3)

Material examined.—10 ovigerous females recovered from gill filaments of a moribund Malabar reef-cod, *Epinephelus malabaricus* (Bloch et Schneider), cultured in Chi-ku Village in Tainan County in Taiwan on 23 Jun 1993. Holotype (USNM 278225) and 2 paratypes (USNM 278226) have been deposited in the Division of Crustacea, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Female.—Body 0.55 (0.53–0.57) long and 0.30 (0.27–0.32) wide, with greatly inflated cephalothorax (including first pediger) and relatively short and small metasome and urosome (Fig. 2A, B). Genital double somite distinctly wider than long (Fig. 2C) and armed on ventral surface with a row of fine spinules across mid-region and another row on posterior margin. Spinules on other parts of urosome as shown in Fig. 2D. Caudal ramus (Fig. 2C, D) slightly longer than wide, tipped with 1 long and 3 short setae. Egg sac (Fig. 2A) distinctly longer than body, about 0.64 in length and 0.16 in width.

Antennule (Fig. 3A) 6-segmented, armature of 3, 12, 4, 4, 2 and 7 elements. Antenna (Fig. 3B) strongly curved, without sensilla or seta; 1st segment wider than long, second segment slightly longer than

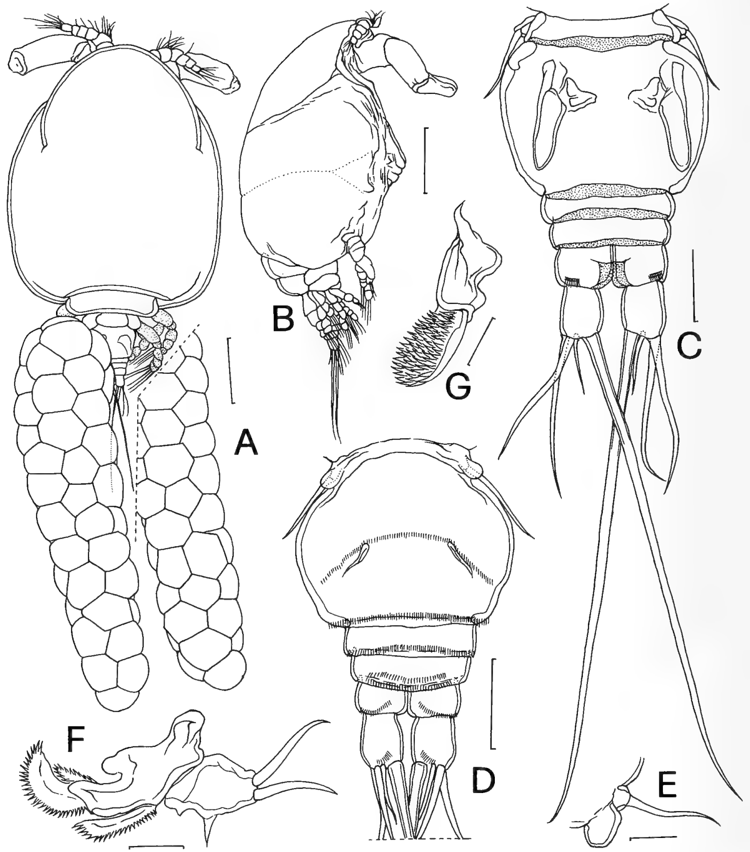

Fig. 2. *Ergasilus lobus*, new species, female: A. habitus, dorsal; B. habitus, lateral; C. urosome, ventral; E. leg 5; F. mandible and maxillule; G. maxilla. Scale bars: 0.1 mm in A, B; 0.03 mm in C, D; 0.01 mm in E, F, G.

third segment, and terminal claw distinctly shorter than third segment. Mandible (Fig. 2F) a serrated, falciform blade bearing a spinulose process on anterior margin and another uniserrated process on posterior margin. Maxillule (Fig. 2F) with 2 long and 1 short setae. Maxilla 2-segmented; proximal segment large and unarmed, distal segment (Fig. 2G) small and spinulose. Legs 1–4 (Fig. 3C–E) biramous, with formula of spines and setae as follows:

P1	Coxa 0-0	Basis 1-0	Exopod	I-0; 0–1; II, 1, 4
			Endopod	0-1; 0–1; II, 4

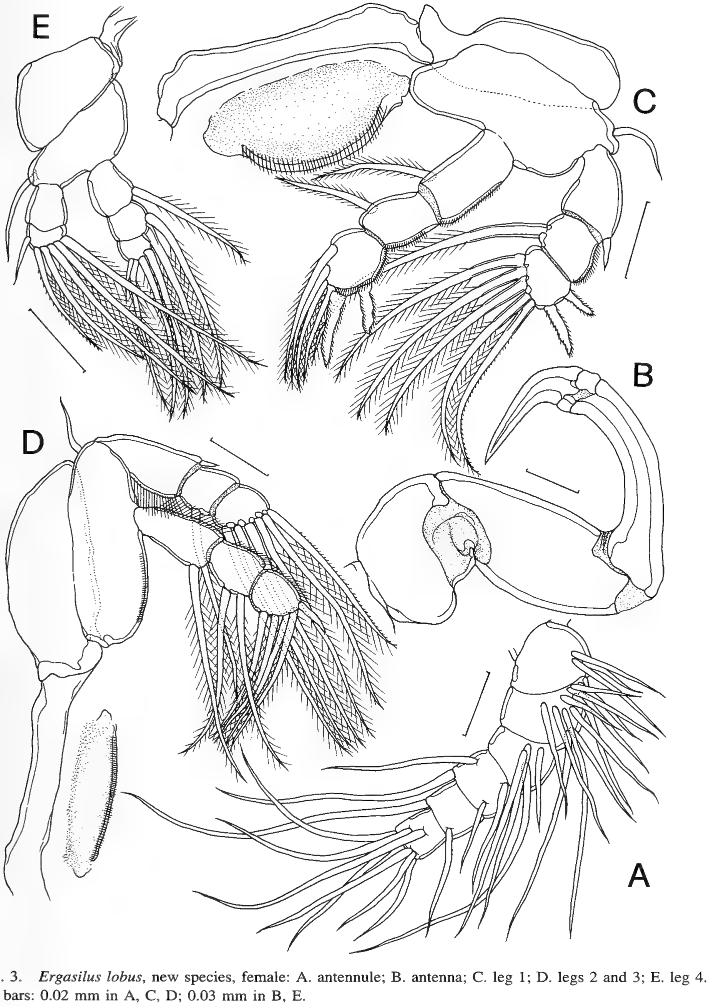

Fig. 3. *Ergasilus lobus*, new species, female: A. antennule; B. antenna; C. leg 1; D. legs 2 and 3; E. leg 4. Scale bars: 0.02 mm in A, C, D; 0.03 mm in B, E.

P2, P3	Coxa 0-0	Basis 1-0	Exopod	I-0; 0–1; 1, 5
			Endopod	0-1; 0–2; I, 4
P4	Coxa 0-0	Basis 1-0	Exopod	0-0; I, 1, 4
			Endopod	0-1; 0–2; I, 3

Intercoxal bar with prominent posteroventral plate in leg 1 (Fig. 3C) less developed in legs 2 and 3 (Fig. 3D) and absent in leg 4. Leg 5 (Fig. 2C, D, E) much reduced, represented by a small knob tipped with a seta; a small protuberance located ventral to leg 5 (Figs. 2D, E).

Etymology.—The species name *lobus* in Latin means "a protuberance". It is here used as a noun in apposition and refers to the small rounded projection located ventral to the extremely reduced leg 5.

Remarks.—Currently, about 120 species of *Ergasilus* are known. However, only ten of them are characterized by a greatly inflated cephalothorax which is more than twice the length of the rest of the body. These ten species are: *E. argulus* Cressey, 1970; *E. auritus* Markewitsch 1940; *E. centrachidarum* Wright, 1882; *E. luciopercum* Henderson, 1926; *E. manicatus* Wilson, 1911; *E. myctarothes* Wilson, 1913; *E. orientalis* Yamaguti, 1939; *E. parvitergum* Ho, Jayarajan & Radhakrishnan, 1992; *E. plecoglossi* Yamaguti, 1939; and *E. rotundicorpus* Jones & Hine, 1983. The new species can be easily distinguished from these similar species, except for *E. argulus*, *E. myctarothes*, and *E. parvitergum*, by the absence of an inflated, cuticular, outer membrane between the first and second segments of the antenna.

According to Cressey & Collette's (1970) description, *E. argulus* differs from the new species in having two setules on the inner margin of the second segment of the antenna, a 2-segmented endopod on leg 1, and seven elements on the terminal segment of the exopod on legs 2 and 3. Based on Wilson's (1913) description, *E. myctarothes* is distinguishable from the new species by the fine structure of the antenna; its shaft bears a small, subterminal, inner protuberance and the claw is armed with two small teeth on inner margin near the center; besides, the armatures on legs 1 to 4 also show differences.

The new species is most similar to *E. parvitergum* known from India (Ho et al. 1992). The similarities are seen not only in the general appearance of the body, but also in the reduction of the tergum of the fourth pediger and leg 5. Nevertheless, *E. parvitergum* can be distinguished from the new species in lacking a lobe on leg 5 and having an outer spine on the second exopod segment of leg 1 and the first exopod segment of leg 4.

Diergasilus kasaharai Do, 1981
(Figs. 4–6)

Material Examined.—Numerous ovigerous females and young females recovered from gill filaments of milkfish (*Chanos chanos*) cultured in Chiku Village in Tainan County, Taiwan on 23 Dec 1993 and Borneo mullets (*Liza macrolepis*) cultured in Hu-Nei Village in Kaoshiung County, Taiwan in Oct 1994. Two lots of specimens (USNM 278227 and 278228) have been deposited in the Division of Crustacea, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Female.—Body 0.59 (0.51–0.68) long, 0.30 (0.23–0.44) wide, and 0.27 (0.16–0.33) thick, with greatly inflated cephalothorax (Fig. 4A, B). Cephalothorax (including first pediger) distinctly wider than long and truncated anteriorly. Metasomal somites abruptly narrowed from cephalothorax and decreasing in size posteriorly (Fig. 4A). Genital double somite wider than long, bearing a hyaline lateral spine in egg-sac attachment area (Fig. 4C). Spinulation on ventral surface of urosome as shown in Fig. 4C. Caudal ramus (Fig. 4C) about as wide as long and tipped with 1 long and 3 short setae. Egg sac (Fig. 4A, B) shorter than body, 0.51 (0.45–0.62) long and 0.11 (0.11–0.13) wide (based on 20 individuals).

Antennule (Fig. 4D) 5-segmented, ar-

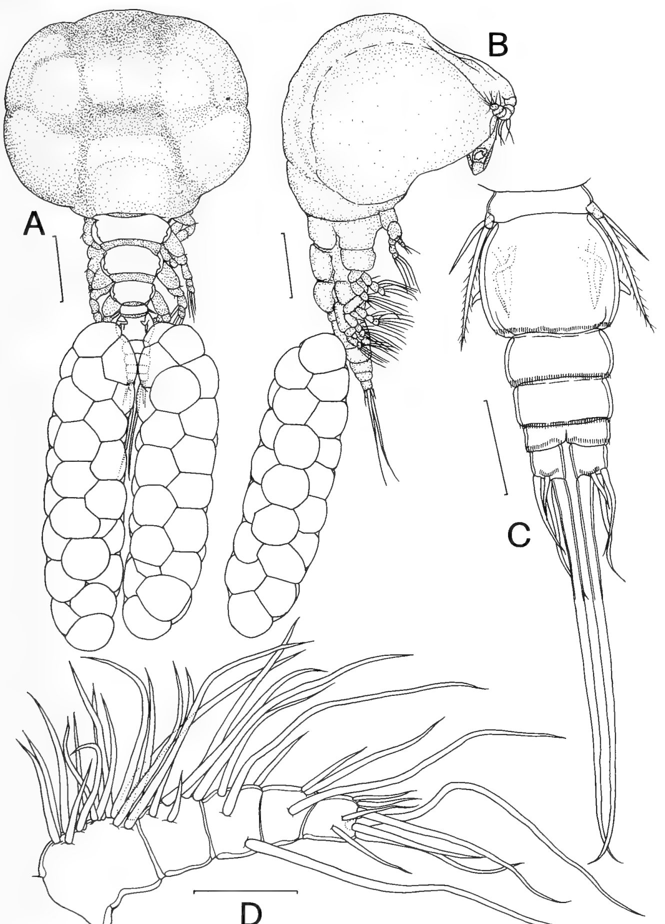

Fig. 4. *Diergasilus kasaharai*, female: A. habitus, dorsal; B. habitus, lateral; C. urosome, ventral; D. antennule. Scale bars: 0.1 mm in A, B; 0.04 mm in C; 0.03 mm in D.

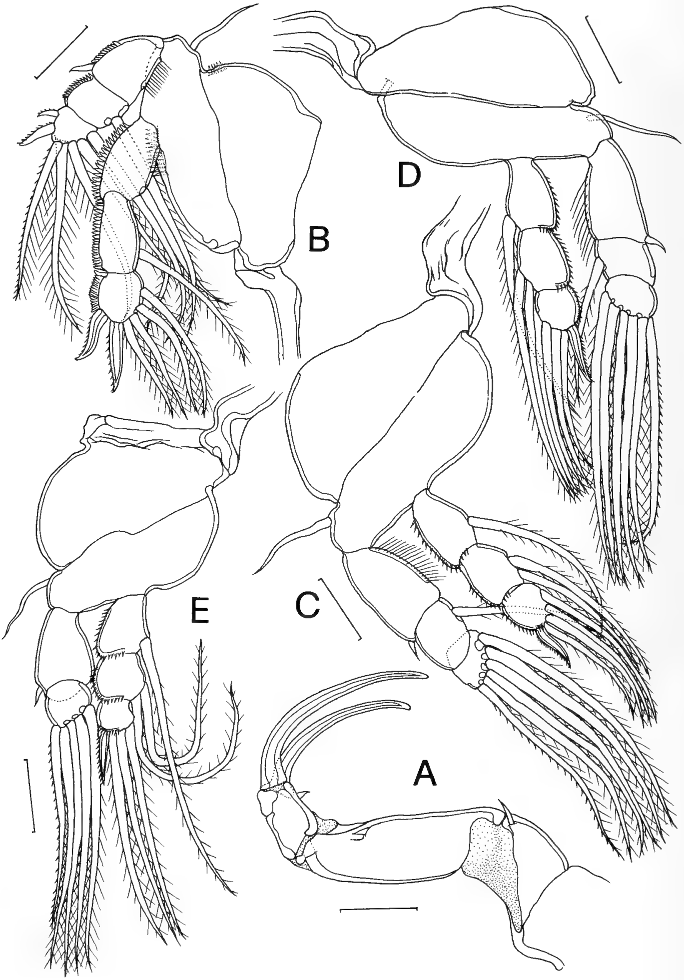

Fig. 5. *Diergasilus kasaharai*, female: A. antenna; B. leg 1; C. leg 2; D. leg 3; E. leg 4. Scale bars: 0.03 mm in A; 0.02 mm in B, C, D, E.

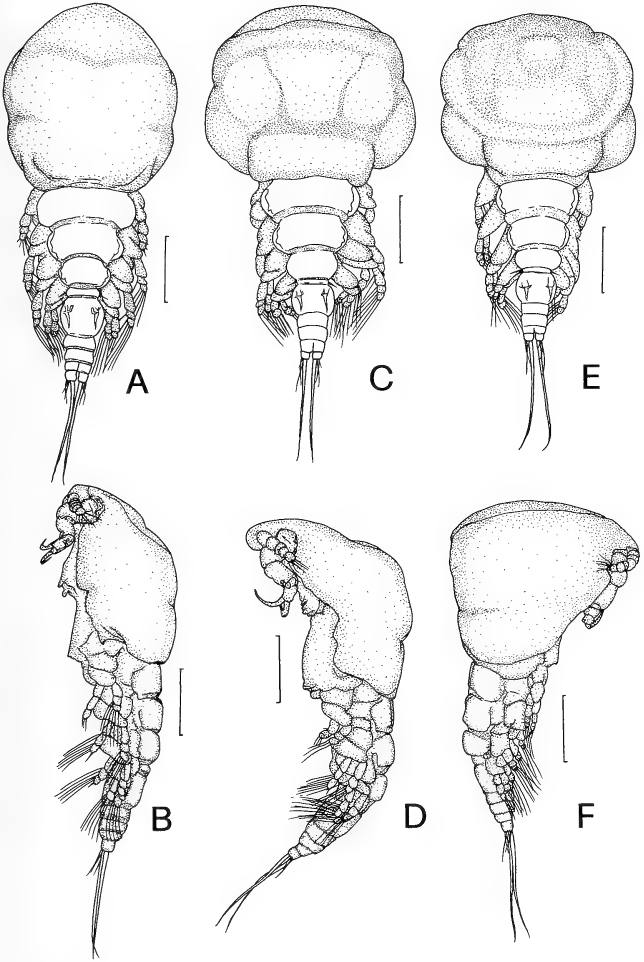

Fig. 6. *Diergasilus kasaharai*, habitus of females showing various state of inflation in cephalothorax: A. dorsal; B. same individual, lateral; C. dorsal; D. same individual, lateral; E. dorsal; F. same individual, lateral. Scale bars: 0.1 mm in all drawings.

mature of 15, 5, 4, 3 and 8 elements. Antenna (Fig. 5A) 3-segmented and tipped with 2 long, unequal claws; each segment bearing a small distal, inner seta; and second segment largest, longer than first and third segments combined. Mandible, maxillule, and maxilla as in the above species. Legs 1–4 (Fig. 5B–E) biramous, with formula of spines and setae as follows:

P1	Coxa 0-0	Basis 1-0	Exopod	I-0; 0–1; II, 1, 4
			Endopod	0-1; 0–1; II, 4
P2, P3	Coxa 0-0	Basis 1-0	Exopod	I-0; 0–1; 6
			Endopod	0-1; 0–2; I, 3
P4	Coxa 0-0	Basis 1-0	Exopod	I-0; 1, 4
			Endopod	0-1; 0–2; I, 3

Lateral margins of all endopods with a row of spinules, except for leg 1 with a row of teeth. First two exopodal segments of leg 1 with row of teeth on lateral margin. Leg 5 (Fig. 4C) much reduced, represented by a basal seta and a small papilla tipped with a long pinnate seta.

Remarks.—This is the second report of *Diergasilus kasaharai*. The first report was made by Do (1981) from the striped mullet (*Mugil cephalus*) caught in Kojima Bay, Okayama, Japan. The specimens from Taiwan bear close resemblance with those found in Japan in the structure of all appendages and differs from it only in the shape of the cephalothorax. In those specimens from Taiwan, the inflated cephalothorax is truncated at the front end (Fig. 4A, B), but in those from Japan, it is bluntly pointed as in a typical ergasilid copepod (Do 1981).

After a close examination of more than 100 individuals, it became clear that the shape and size of the cephalothorax of the specimens from Taiwan change as the parasite approaches the ovigerous state. It swells into a globose, lobular structure with a truncated anterior surface (Fig. 6A–C). And, even in the least inflated individuals (Fig. 6A, B), the cephalothorax is still distinguishable from those reported from Japan; it is not as pointed and globular as illustrated by Do (1981). However, with the lack of information about the maturity related changes in the cephalothorax of the Japanese specimens, we shall refrain from considering the above-mentioned differences as a species distinction between the specimens from Japan and Taiwan.

Key to *Ergasilus* Found on Coastal Fishes

There are more than 120 nominal species of *Ergasilus*. Most of them were either not well described by their discoverer, or have not been seen again since the original report. Further, their type specimens are either inaccessible or no longer extant. Consequently, it is difficult, if not impossible, to construct a key for quick identification of the members of this important genus of parasites. Fortunately, only about one-fifth of the members of *Ergasilus* are parasitic on the coastal, brackish water fishes and they are relatively better known; thus, attempt to construct a key to the species of *Ergasilus* in coastal waters is feasible.

Based on the reports of Wilson (1913), Brian (1927), Markewitsch (1933, 1940), Bere (1936), Yamaguti (1939), Redkar et al. (1952), Cressey & Collette (1970), Roubal (1981), Byrnes (1986), Kabata (1986, 1988, 1992), Leong & Wong (1988), Wijeyaratne & Gunawardene (1988), Ho et al. (1992), and the present work, 25 species of *Ergasilus* are currently known to occur on fishes of coastal, brackish waters. However, *Ergasilus ponticus* Markewitsch 1940 and *Ergasilus wilsoni* Markewitsch 1933 are excluded from the following key due to the lack of complete species information. Both of them were poorly described originally and have not been adequately redescribed.

Ergasilus funduli Krøyer 1863 was once considered to be a junior synonym of *Ergasilus manicatus* Wilson 1911 (Roberts 1970, Margolis & Arthur 1979). However, according to Kabata's (1986) re-examination of the type specimens (deposited in the Zoological Museum, University of Copenhagen), the structure of the antenna of *E. funduli* clearly indicated that it is a different species. Nevertheless, details of the leg armature of *E. funduli* are still unknown, and it is not included in the following key.

While many of the 22 species appearing in the following key are known from a single location, some of them are widely distributed, for instance, *Ergasilus orientalis* Yamaguti has been reported from Japan (Yamaguti 1939), Australia and Brazil (Cressey & Collette 1970) and *Ergasilus lizae* Krøyer is know from the Gulf of Mexico (Bere 1936), Pacific coast of North America (Hanan 1976, Kabata 1988), Australia (Kabata 1992), and the Mediterranean Sea (Ben Hassine 1983, Ben Hassine & Raibaut 1981). When a key is available for general use, more of these coastal *Ergasilus* species will show a pattern of much wider distribution than it is known now.

Appendages of small, difficult to dissect species of *Ergasilus* reported in the early part of this century were not well described; these appendages are the key characteristics to the species identification. In some cases, like Fraser's (1920) description on *Ergasilus turgidus*, there are discrepancies on the armature of appendages between the text and the illustrations. Thus, in construction of the following key, the characteristics of less ambiguity were employed and, in the case of conflict between the text and the illustration, the feature appeared in the illustration was adopted.

An interesting feature about the Ergasilidae is that only the adult female is parasitic. As in a typical free-living copepod, all members of this family pass through their naupliar and copepodid stages in a free-living mode of life; after molting into the adult and mating, the male dies and only the female seeks fish host to enter into a parasitic mode of life. Thus, the following key is intended only for the adult female.

1a. Cephalothorax greatly inflated, at least twice longer than remaining body length (metasome + urosome) 2
b. Cephalothorax may or may not be inflated, if inflated less than twice length of remaining body (metasome + urosome) 8
2a. Antenna with an inflated membrane between first and second segment. .. 3
b. Antenna without such membrane ... 6
3a. Antenna with a balloon-like cuticular inflation at base of third segment of antenna .... *manicatus* Wilson, 1911
b. Antenna without such inflation 4
4a. Claw and shaft (third segment) of antenna with protuberance on inner margin .... *auritus* Markevich, 1940
b. Claw and shaft of antenna without such protuberance 5
5a. Cephalothorax twice longer than wide; ventral surface of caudal ramus with two rows of minute spines .... *orientalis* Yamaguti, 1939
b. Cephalothorax about 1.5 times longer than wide; ventral surface of caudal ramus without spinules .... *rotundicorpus* Jones & Hine, 1983
6a. Second segment of leg 1 exopod and first segment of leg 4 exopod with outer spine 7
b. Same segment on same leg ramus without outer spine .. *lobus*, new species
7a. Terminal segment of endopod on legs 2 and 3 with six setae .... *myctarothes* Wilson, 1913
b. Same segment on same leg rami with one spine and four setae .... *parvitergum* Ho, Jayarajan, & Radhakrishnan 1992
8a. Middle segment of leg 2 endopod with one inner seta 9
b. Middle segment of leg 2 endopod with two inner setae 12
9a. Middle segment of leg 3 endopod with one inner seta *intermedius* Kabata, 1992
b. Middle segment of leg 3 endopod with two inner setae. 10
10a. Middle segment of leg 1 exopod without inner seta ...... *monodi* Brian, 1927
b. Middle segment of leg 1 exopod with one inner seta 11
11a. Antenna with an inflated membrane between first and second segments, its claw and shaft (third segment) bearing protuberance on inner margin .... *turgidus* Fraser, 1920

b. Antenna without such inflated membrane or protuberance .... *polynemi* Redkar, Rangnekar & Murti, 1951

12a. Antenna with an inflated membrane between first and second segments, its claw bearing two protuberances on inner margin ...... *labracis* Krøyer, 1864

b. Antenna without such inflated membrane or protuberance 13

13a. Armature on terminal segment of leg 1 endopod II, 4 14

b. Armature on same segment of same leg I, 5 .... *mugilis* Vogt, 1877

c. Armature on same segment of same leg I, 4 .... *longipalpus* Wilson, 1913

14a. Armature on terminal segment of exopod on legs 2 and 3 I, 6 15

b. Armature on same segment of same leg rami 6 17

15a. Middle segment of leg 1 exopod without outer spine 16

b. Same segment of same leg with outer spine .... *ceylonensis* Fernando & Hanek, 1973

16a. Antennule 6-segmented; eggs in egg sac multiseriate ... *ogawai* Kabata, 1992

b. Antennule 5-segmented; eggs in egg sac uniseriate .... *uniseriatus* Ho, Jarayajan & Radhakrishnan, 1992

17a. Terminal segment of endopod on legs 2 and 3 armed with one short and four long setae 18

b. Same segment of same leg rami with five long setae .... *borneoensis* Yamaguti, 1954

18a. Antennule 5-segmented 19

b. Antennule 6-segmented 20

19a. Caudal ramus long, ratio of length to width greater than 2; leg 1 intercoxal plate heavily armed with coarse spinules ...... *spinilaminatus* Kabata, 1992

b. Caudal ramus short, ratio of length to width less than 1.5; leg 1 intercoxal plate without coarse spinules .... *rostralis* Ho, Jarayajan & Radhakrishnan, 1992

20a. Intercoxal plate of leg 1 with coarse denticles on posterior margin; protopods of legs 1–4 bearing patches of spinules ..... *australiensis* Roubal, 1981

b. Intercoxal plate of leg 1 without denticles; protopods of legs 1–4 without patches of spinules .. *lizae* Krøyer, 1863

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Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 5. Probable hybrid origin of *Amazilia distans* Wetmore & Phelps

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Abstract.—*Amazilia distans* Wetmore & Phelps, 1956, is believed to be a hybrid between *Hylocharis cyanus* and *Amazilia fimbriata*. The hybrid, collected in Estado Táchira, Venezuela, exhibits a blended mosaic of plumage characters of the parental species. External measurements of the hybrid fall between the character means of the parental species which overlap in size.

The unique holotype of *Amazilia distans* Wetmore & Phelps, 1956 was collected by Ramón Urbano at "El Salao" (300 m) near Burgua, Estado Táchira, Venezuela, on 17 July 1954. Originally deposited in the Colección Ornitológica Phelps (No. 60790), Caracas, the type was cataloged on 9 October 1956, in the National Museum of Natural History (USNM 461695), Smithsonian Institution. Collar et al.'s (1992) report of a second specimen in the Colección Phelps was based on a misreading of the Phelps card catalog (fide M. Lentino, N. Collar). References treat *A. distans* as a valid species (e.g., Morony et al. 1975, Meyer de Schauensee & Phelps 1978, Hilty & Brown 1986, Sibley & Monroe 1990, Collar et al. 1992). Analyses reported here suggest that it represents a hybrid between *Hylocharis cyanus* and *Amazilia fimbriata*. I provide a detailed hybrid diagnosis employing the methods and assumptions outlined in Graves (1990) and Graves & Zusi (1990).

Materials and Methods

The holotype of *Amazilia distans* was sexed as male (testes drawn on original label). The unstriated maxillary ramphotheca (see Ortiz-Crespo 1972) and brilliant plumage of the specimen indicate that it is an adult in definitive plumage (Figs. 1, 2). The unique appearance of *A. distans* cannot be attributed to mutation or developmental variation of any known taxon. Nor does it seem to represent a morphologically distinctive or geographically isolated population of another species of *Amazilia*. Consequently, *A. distans* appears either to be a valid species or a hybrid. As hybrids have no standing in zoological nomenclature, the burden of proof lies with the taxonomist to reject conclusively the hybrid origin of *A. distans* before bestowing species status on it. I was unable to reject the hypothesis of hybridity.

Hybridization between species from different subfamilies, Phaethornithinae and Trochilinae, is unknown (Graves 1990). Assuming a hybrid origin for *A. distans*, the pool of potential parental species (=geographic pool) can be limited to the species of trochiline hummingbirds ($n = 23$; see Appendix 1) that occur regularly below 1000 m elevation in the region immediately south and east of the Andes in Estado Táchira and Estado Apure, Venezuela (Phelps & Phelps 1958, Meyer de Schauensee & Phelps 1978, Hilty & Brown 1986). I compared *A. distans* directly with specimens of all hummingbird species in the collections of the National Museum of Natural History, Smithsonian Institution, paying particular attention to those listed in Appendix 1. Notes, photographs, and videotape of the holotype were compared with the extensive

Table 1.—Ranges and means (± one standard deviation) of measurements (mm) of representative specimens (adult male) of *Hylocharis cyanus, Amazilia fimbriata,* and the hybrid, *Hylocharis cyanus* × *Amazilia fimbriata* (= *Amazilia distans* Wetmore & Phelps, 1956; USNM 461695).

	cyanus (n = 12[a])	*fimbriata* (n = 16[b])	Hybrid
Wing chord	47.1–53.0	52.4–56.5	51.0
	49.8 ± 1.5	54.7 ± 1.4	
Bill length	14.8–18.5	17.3–22.0	18.6
	16.9 ± 1.1	19.8 ± 1.3	
Rectrix 1	24.1–27.4	26.2–30.1	26.6
	25.9 ± 1.2	28.8 ± 1.0	
Rectrix 5	25.1–28.1	27.7–32.5	27.4
	26.7 ± 1.0	30.6 ± 1.4	

[a] Colombia (n = 5), Venezuela (n = 4), Guyana (n = 3).

[b] Colombia (n = 8), Venezuela (n = 8).

series of *Amazilia* and *Hylocharis* in the American Museum of Natural History, New York.

Color descriptions were made under Examolites (MacBeth). 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 central and outermost rectrices) were taken with digital calipers and rounded to the nearest 0.1 mm (Table 1). Measurements and least squares regression lines were projected on bivariate plots to illustrate size differences (Wilkinson 1989).

The hybrid diagnosis was approached in a hierarchical manner. The presumed parental species of *A. distans* were hypothesized through the comparative analysis of plumage pattern and color, feather shape, and bill color. As a second step, the restrictive hypothesis was tested with the quantitative analysis of size and external proportions. Concordance of results is regarded as strong support for the hypothesis (Graves 1990, 1993a, 1993b, 1996a; Graves & Zusi 1990). Atavism or hybrid luxuriance has not been demonstrated in hybrid hummingbirds (Banks & Johnson 1961, Graves 1990). For brevity, *A. distans* will be referred to as a hybrid in the remainder of this paper.

Results and Discussion

Several characters of the hybrid permit its parental species to be identified: (a) bill red tipped with black in life; (b) base of bill conspicuously swollen, nasal flanges unfeathered and exposed; (c) crown glittering bluish-green; (d) throat glittering bluish-green, chin and upper throat streaked with white; (e) indistinct white pectoral spot; (f) abdomen gray along midline; and (g) rectrices black, innermost and outermost about the same length (Appendix 2; Fig. 1, 2; Table 1). None of the potential parental species considered one at a time exhibits this suite of character states in definitive or subdefinitive plumage.

The red bill of the hybrid appears to be the most useful character for initially narrowing the field of potential parental species. Adult males of several species in Appendix 1 have pink or red mandibular (lower jaw) ramphothecae (*Lophornis delattrei, L. stictolophus, Chrysuronia oenone, Hylocharis cyanus, Amazilia versicolor, A. fimbriata,* and *A. viridigaster*), and some specimens of *A. fimbriata* have pinkish-brown maxillary ramphothecae (upper jaw). However, bright red maxillary ramphothecae are found in only three species, *L. delattrei, L. stictolophus,* and *Hylocharis cyanus. Lophornis* can be eliminated as possible parents of *A. distans* because they possess elongated rufous crests and predominately rufous rectrices, which would almost certainly be expressed in a hybrid. *Hylocharis cyanus* is thus identified as the parental contributor of the red maxillary ramphotheca of the hybrid.

Identifying the second parental species is most easily accomplished by focusing on the plumage characters of the hybrid that are lacking in *Hylocharis cyanus*. Plumage of the head, chin, throat and upper breast of *H. cyanus* is glittering purple. The inheritance of iridescence in hybrid hum-

Fig. 1. Lateral and ventral views of male *Amazilia fimbriata* (top), *Hylocharis cyanus* (bottom), and their putative hybrid, *A. distans* Wetmore & Phelps (USNM 461695).

Fig. 2. Lateral view of head and bill of the type of *Amazilia distans* Wetmore & Phelps (USNM 461695).

mingbirds is poorly understood (Graves 1990, Graves & Zusi 1990). In this case, however, I assume that hybridization between two purple-crowned species would not result in offspring with a bluish-green crown. The glittering bluish-green crown and throat of the hybrid suggest that the second parental species has iridescent green plumage in these areas, ruling out *Klais guimeti* (purple chin and upper throat) as a parental species. In another example, the rectrices of *Chrysuronia oenone* are shining coppery-gold on both dorsal and ventral surfaces, whereas the rectrices of the hybrid are black, similar to those of *H. cyanus* (bluish-black). Hybridization of *C. oenone* and *H. cyanus* would likely produce offspring with bronze-colored or dark brown rectrices that are significantly paler, less melanized, than those of the hybrid. In a similar fashion, *Campylopterus falcatus* (chestnut rectrices, thickened primary rachises), *Colibri thalassinus* and *C. coruscans* (purple auricular tufts, banded rectrices), *Chlorostilbon poortmani* (shining golden-green tail), *Chlorestes notatus* (brilliant bluish-green plumage from breast to undertail coverts), *Chalybura buffonii* (lengthened silky-white undertail coverts), *Heliomaster longirostris* (tail spots, brilliant magenta gorget), *Thalurania furcata* (purple lower breast, deeply forked tail), *Heliodoxa leadbeateri* (violet crown patch), *Sternoclyta cyanopectus* (violet breast patch, white-tipped rectrices, heavy curved bill), *Coeligena coeligena* (brown plumage), *Ocreatus underwoodii* (racket-tipped rectrices, tibial "puffs"), *Aglaiocercus kingi* (greatly elongated rectrices with metallic bluish-green dorsal surfaces), and *Chaetocercus jourdanii* (rufous shafts of rectrices, rose throat), can be removed from the list of potential parental species because they exhibit plumage characters not expressed in the hybrid. By the process of elimination, the second parental species appears to be one of three species of *Amazilia* that are sympatric with *Hylocharis cyanus* in Táchira, Venezuela (Appendix 1).

Wetmore & Phelps (1956:4) noted that the type of *A. distans* had the general appearance of *Amazilia fimbriata*, differing from that species "in the glittering blue foreneck and upper breast, and in possess-

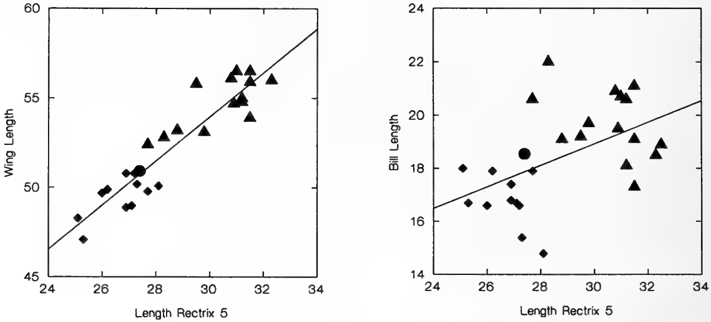

Fig. 3. Bivariate plots of selected measurements (see Table 1) of male *Hylocharis cyanus* (diamonds), *Amazilia fimbriata* (triangles), and their putative hybrid (filled circle), *A. distans* Wetmore & Phelps (USNM 461695). Least squares regression lines are illustrated for comparison.

ing a crown spot differing in color from the rest of the head . . . . the appearance of the specimen is so distinct from that of other species of the genus [*Amazilia*] that we have no hesitance in describing it as representing a new species." I concur with Wetmore and Phelps that *A. fimbriata* bears more than a fleeting resemblance to *Amazilia distans* in plumage pattern. In fact, the hybrid is nearly intermediate in appearance between *Hylocharis cyanus* and *Amazilia fimbriata.* Significantly, the hybrid lacks plumage traits that characterize *A. versicolor* (e.g., dark subterminal band on the outermost rectrices) and *A. viridigaster* (e.g., brown or buff undertail coverts). In conclusion, evidence gleaned from bill and plumage characters suggest that *A. distans* represents a hybrid of *Hylocharis cyanus* and *Amazilia fimbriata.*

External measurements.—Measurements of avian hybrids fall within the mensural ranges exhibited by their parental species as a consequence of a polygenic mode of inheritance (see Buckley 1982). External measurements of adult male *Hylocharis cyanus* and *Amazilia fimbriata* overlap and the difference in character means (larger species divided by smaller) is modest: wing chord (9.8%) bill length (17.2%); rectrix 1 (11.2%); and rectrix 5 (14.6%). Consistent with the hypothesis derived from plumage color and pattern, measurements of the hybrid fall between the character means of the parental species (Table 1, Fig. 3). Had the hybrid's measurements fallen outside the range of those of *Hylocharis cyanus* and *Amazilia fimbriata,* this particular hybrid hypothesis would have been rejected.

In summary, both plumage and morphological data are consistent with the hypothesis that *Amazilia distans* represents a hybrid between *Hylocharis cyanus* and *Amazilia fimbriata.* These species overlap extensively in Amazonia. For taxonomic purposes the *Amazilia distans* Wetmore & Phelps is available only for the purpose of homonymy.

Berlioz (1929) described a supposed hybrid specimen, *Hylocharis cyanus* × *Amazilia fimbriata,* prepared in the "Bahia" style and presumably collected in Brazil. Unfortunately, he failed to report the specimen's registration number or in what museum the specimen was deposited. Later, he (Berlioz 1951:287 equivocated in his identification, suggesting that the specimen might represent *Hylocharis pyropygia* (Salvin & Godman 1881), poorly-known and somewhat doubtful species from Bahia, Brazil (see Sibley & Monroe 1990):

> "D'ailleurs, faute de connaître alors des *Hyl. pyropygia* authentiques, j'avais primitivement décrit ce spécimen . . . comme étant probablement un hybride: *Agyrtrina* [*Amazilia*] *fimbriata nigricauda* X *Hylocharis cyanus*. Sans rejeter définitivement cette hypothèse, très justifiable par l'apparence de l'Oiseau, il me semble pourtant plausible, maintenant que l'identification, comme espèce distincte, d'*Hyl. pyropygia* s'est affirmée par l'existence de plusieurs spécimens identiques, de considérer dubitativement cet Oiseau comme référable aussi à cette dernière espèce."

To further complicate matters, Berlioz (1938) had proposed in earlier paper that *Hylocharis pyropygia* was actually a hybrid between *Chlorostilbon aureoventris* and *Hylocharis cyanus*. In any case, there appears to be no previous verified examples of the hybrid combination reported here (*Hylocharis cyanus* × *Amazilia fimbriata*).

Sight records.—Sight records of "*Amazilia distans*" in northwestern Venezuela and adjacent Colombia (see Hilty & Brown 1986, Collar et al. 1992) are problematic, and, to my knowledge, none is supported by diagnostic photographs. Although these sightings may refer to *Hylocharis* × *Amazilia* hybrids, they more likely represent the manifestation of imaginations fertilized by the possibility of observing a narrowly distributed endemic. Identification of hummingbird hybrids under field conditions is virtually impossible (Graves 1996b).

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Appendix 1

Species of hummingbirds that occur regularly below 1000 m elevation in southwestern Estado Táchira and extreme western Estado Apure, Venezuela: *Campylopterus falcatus*, *Colibri thalassinus*, *C. coruscans*, *Klais guimeti*, *Lophornis delattrei*, *L. stictolophus*, *Chlorestes notatus*, *Chlorostilbon mellisugus*, *C. poortmani*, *Thalurania furcata*, *Hylocharis cyanus*, *Chrysuronia oenone*, *Amazilia versicolor*, *A. fimbriata*, *A. viridigaster*, *Chalybura buffonii*, *Heliodoxa leadbeateri*, *Sternoclyta cyanopectus*, *Coeligena coeligena*, *Ocreatus underwoodii*, *Aglaiocercus kingi*, *Heliomaster longirostris*, *Chaetocercus jourdanii*.

Appendix 2

General comparative description of definitive plumages of male *Hylocharis cyanus*, *Amazilia fimbriata*, and the hybrid, *H. cyanus* × *A. fimbriata* (=*Amazilia distans* Wetmore & Phelps, 1956; USNM 461695). 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 forecrown and crown (to a line drawn across the crown at the rear of the orbits) of *cyanus* are glittering purple, bordered posteriorly by dark bluish-green on the hindcrown. The hindneck, upper back, and scapulars are dark green, gradually turning to bronzy green and then coppery on the lower back and rump, respectively; the upper-tail coverts are purplish black. In *fimbriata* the dorsal plumage (capital and spinal tracts) is primarily dark green, with bronze reflections on the crown and upper-tail coverts. The dorsum of the hybrid is intermediate in appearance between *cyanus* and *fimbriata*, but more closely resembling the latter species. The forecrown is glittering greenish-blue and the upper-tail coverts are dark bronzy green.

The sides of the head, throat, and upper breast of *cyanus* are deep glittering purple; exposed white feather bases on the chin impart a spotted or mottled appearance. Feathers of the lower breast, sides, and flanks are dark brownish-gray tipped with a dark green disc; greenish feather tips are less apparent near the midline. Vent feathers are white and the under-tail coverts are dull brownish-black (blue reflections in bright light). Feathers of the chin, throat, and upper breast of *fimbriata* have glittering green discs (when viewed head-on); feathers are white basally, narrowly fringed with white. White feather margins and a few completely white feathers form an indistinct spot near the center of the lower breast. The belly, sides, and flanks are green with an indistinct grayish-white stripe along the midline. Vent feathers are white; under-tail coverts are dark gray (with greenish reflections) moderately margined with white or pale grayish-white. The venter of the hybrid more closely resembles that of *fimbriata*. Feather discs of the chin, throat, and upper breast are bluish-green, a few are distinctly purple. Traces of the white pectoral spot of *fimbriata* are present (one completely white feather); under tail coverts are dark slate gray margined with dull white.

The tail of *cyanus* is bluish-black. In *fimbriata*, the outer rectrices (2–5) are dull bluish-black; the outer margins of rectrices 2–4 are glossed with dark green. The central rectrices (1) are dark green, becoming dull bluish-black distally. The tail of the hybrid is similar in color to that of *cyanus*, but the outer margins of rectrices 2–4 are faintly glossed with bronzy-green; the basal two-thirds of the central rectrices (1) are glossed with bronzy-green.

The maxillary ramphotheca is red, tipped with black in *cyanus*, and moderately to heavily melanized (pinkish-brown to black in life) in *fimbriata*. Ramphotheca of the hybrid exhibits an intermediate amount of melanin; the specimen tag notes that the bill was red with a black tip in life.

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A new species of the catfish genus *Glanapteryx* (Siluriformes: Trichomycteridae)

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Abstract.—A new species of the glanapterygine trichomycterid genus *Glanapteryx* is described from the upper Rio Negro in Brazil, State of Amazonas. The new species, currently represented by a single specimen, is the only fish so far known to occur in the remote "Morro dos Seis Lagos" lake complex, a region with high levels of natural radioactivity. *Glanapteryx niobium*, new species, is distinguished from its only congener, *G. anguilla*, by a white collar immediately posterior to head, the dark pigmentation on the ventral surface of the head, the longer pectoral-fin remnant, the lanceolate caudal fin, and the narrow union of branchial membranes to the isthmus.

Resumo.—Uma nova espécie do gênero *Glanapteryx* (Trichomycteridae, Glanapteryginae) é descrita do alto Rio Negro, Estado do Amazonas, Brazil. A nova espécie, atualmente conhecida por um único exemplar, é o único peixe encontrado até o momento no remoto complexo de lagos chamado Morro dos Seis Lagos, uma região com altos níveis de radioatividade natural. *Glanapteryx niobium*, espécie nova, distingue-se da única outra espécie do gênero, *G. anguilla*, pelo colar branco logo após a cabeça, a pigmentação escura na face ventral da cabeça, o maior comprimento da nadadeira peitoral, a forma lanceolada da nadadeira caudal e a união estreita das membranas branquiais ao istmo.

The remarkable catfish genus *Glanapteryx* was established by Myers (1927) to include a single eel-like species, *G. anguilla*, from the upper Rio Negro in Brazil. The species was subsequently illustrated in Myers (1944), along with descriptions of other members of the subfamily Glanapteryginae, which was established in the same paper. *Glanapteryx anguilla* was redescribed by de Pinna (1989) on the basis of additional material mostly from the rio Negro in Brazil. That publication also included osteological data which formed the basis for a phylogenetic diagnosis of the genus and species, and a hypothesis of phylogenetic relationships among glanapterygines. The occurrence of *G. anguilla* in the Orinoco basin was suggested by de Pinna (1989) and later confirmed by Nico & de Pinna (1996).

Glanapteryx has to date been restricted to its type species, and although representatives of the genus are now being collected regularly, nothing is known of their biology. The present paper reports on a distinctive second species of the genus. The new species is remarkable mainly in its occurrence in a remote region in the Amazon called Morro dos Seis Lagos (meaning "hill of the six lakes"), a large and poorly-known complex of relatively high-elevation lakes in the upper Rio Negro. The region is known for its high level of natural radioactivity. The new *Glanapteryx* seems to be the only fish species occurring in these lakes.

Material and methods.—All measurements are straight-line, taken according to the protocol described in de Pinna (1989).

Abbreviations are: CAS (California Academy of Sciences, San Francisco); INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus); MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo); ex (number of specimens); C&S (material cleared and stained); SL (standard length); HL (head length); an (anus); pf (pelvic fin); and up (urogenital papilla).

Comparative glanapterygine material examined-*Glanapteryx anguilla*: CAS 56048 (holotype), MZUSP 36530 (21 ex, 2 C&S); *Listrura nematopteryx*: MZUSP 36974 (holotype), MZUSP 36975 (12 paratypes), MZUSP uncat. (5ex C&S); *Listrura camposi*: MZUSP uncat. (1ex); *Pygidianops eigenmanni*: CAS 11121 (2 paratypes, 1 C&S); *Pygidianops* sp.: INPA 8080 (3ex); *Typhlobelus ternetzi*: CAS 56201 (2 paratypes, 1C&S); *Typhlobelus sp*: INPA 12929 (10 ex, 2 C&S). Comparative material of other trichomycterids is listed in de Pinna (1992).

Glanapteryx niobium, new species
Fig. 1

Holotype.—INPA 12421, 55.3 mm SL; Brazil, State of Amazonas, Pico da Neblina National Park, Morro dos Seis Lagos (approx. 0°17′N, 66°41′W), Lago Esperança. Collected by Ulysses C. Barbosa and Victor Py-Daniel, 11 Sep 1990.

Diagnosis.—Distinguished from its only congener, *G. anguilla*, by the following characteristics: 1—presence of a well-defined wide white collar-like band shortly posterior to head (Fig. 1; coloration uniform in *G. anguilla*); 2—ventral part of head darkly-pigmented (Fig. 1B; dark pigmentation on ventral surface of head scarce or absent in *G. anguilla*); 3—caudal fin lanceolate, its middle portion projecting beyond rest of fin (Fig. 2; caudal fin round in *G. anguilla*); 4—branchial membranes narrowly united to isthmus (membranes more broadly united to isthmus in *G. anguilla*); 5—pectoral fin long (40% of HL), and of even width, not narrowing towards tip (Fig. 3; fin 9–25% of HL and narrowing gradually to tip in *G. anguilla*). Characters 1 to 3 are considered autapomorphic for the species (see Discussion).

Description.—Morphometric data are provided in Table 1. Holotype preserved in strongly contorted position, SL and proportions thereof may be inexact. Overall form of body similar to that of *G. anguilla* (see de Pinna, 1989, fig. 1). Body eel-like, head continuous with trunk. Body round in cross section for most of its length, gradually more compressed posterior to anal opening. Caudal peduncle gently tapering to caudal fin. Dorsal and ventral profiles of body nearly straight. Anterior portion of caudal peduncle slightly deeper than remainder of body. Dorsal and ventral profiles of caudal peduncle converging gradually to caudal fin.

Head small (HL approx. 7% of SL), less deep than body, its dorsal surface flat. Branchial membranes narrowly united to isthmus, gill openings wide, not constricted. Eyes very small but well formed, with distinct lenses and covered by thin transparent integument. Eyes located on nearly vertical surface of head, facing almost laterally. Posterior nares slightly anterior to eyes, very close to mesial margin of eyeball, but separated from it by narrow strip of integument (eye and naris not adpressed as in *G. anguilla*). Anterior nares opening located on short tube of integument, continuous posterolaterally with nasal barbel. Three large sensory pores situated serially on dorsolateral surface of head and anterior portion of trunk. Posterior pore located slightly posterior to vertical through origin of pectoral fin. Middle pore dorsal to uppermost point of branchial membrane. Anterior pore smallest and positioned dorsal and slightly anterior to middle pore. Mouth subterminal, upper jaw slightly longer than lower, corners not markedly externded posteriorly. Lips poorly differentiated, continuous with remainder of head and with covering of sensory papillae comparable to those over rest of head. All barbels large and robust,

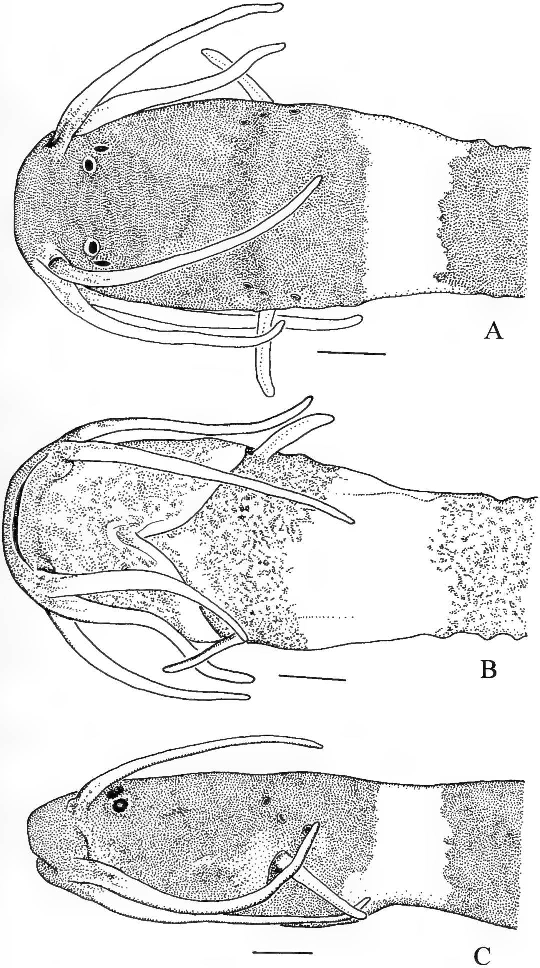

Fig. 1. *Glanapteryx niobium*, holotype, INPA 12421. Views of head. A—dorsal; B—ventral; C—lateral. Scale bars = 1 mm.

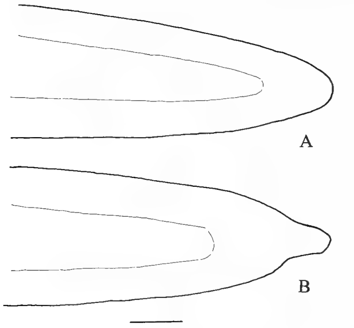

Fig. 2. Caudal fin and part of caudal peduncle. A—*Glanapteryx anguilla*, MZUSP 36530; B—*G. niobium*, holotype, INPA 12421. Scale bar = 1 mm.

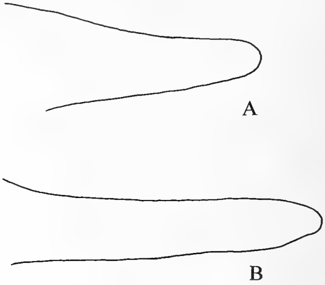

Fig. 3. Profile of pectoral fin. A—*Glanapteryx anguilla*, MZUSP 36530; B—*G. niobium*, holotype, INPA 12421.

with visible internal cores and similar to each other in general aspect. Maxillary and rictal barbels asymmetric in single known specimen. Right maxillary barbel reaching tip of extended pectoral fin, left barbel reaching only to midlength of same fin. Right rictal barbel extending slightly posterior to pectoral-fin base, barbel on left reaching beyond fin tip. Maxillary barbel longer than rictal on right, situation reversed on left side. Nasal barbels both extending to anterior margin of white collar.

Pectoral fin vestigial, reduced to small flap on side of body, originating immediately posterior to dorsal-most point of branchial membrane. Width of pectoral fin nearly even from base to tip, about as wide as rictal barbel at base, its tip round. Three pectoral-fin rays present, but visible only with strong transmitted light, apparently unbranched and unsegmented. First ray longer and thicker than other two, extending to tip of fin, third ray shortest. Pelvic fin vestigial, reduced to two roughly triangular flaps anterior to anal opening (Fig. 4). Dorsal, anal, and adipose fins absent. Caudal fin small and inconspicuous, continuous with remainder of caudal peduncle and body, lanceolate in shape, with middle rays longest. Caudal-fin rays 2 + 2 (i.e., only two branched rays). Branched rays with incipient segmentation proximally. Procurrent caudal-fin rays numerous, at least 25 dorsally and ventrally. Exact number difficult to determine in alcoholic specimen.

Pigmentation in preservative.—Overall coloration uniform dark tan, lighter on ventral half of head and body. Wide white area (about 0.5 HL) located on body shortly posterior to head, forming well-defined collar encircling whole circumference of body. Collar formed by abrupt disappearance of dark chromatophores distributed on rest of

Table 1.—Morphometric data for holotype of *Glanapteryx niobium*, INPA 12421 (in mm or as proportion of SL, TL, or HL, as indicated in parentheses).

head length	4.0 (mm)
head width	0.75 (HL)
head depth	0.52 (HL)
mouth width	0.48 (HL)
interorbital	0.41 (HL)
eye diameter	0.06 (HL)
anterior internarial width	0.33 (HL)
posterior internarial width	0.24 (HL)
collar width (lateral view)	0.40 (HL)
pectoral-fin length	0.40 (HL)
standard length	55.3 (mm)
total length	1.05 (SL)
preanal length	0.65 (TL)
body depth	0.05 (TL)
caudal peduncle length	0.28 (TL)
caudal peduncle depth (max.)	0.05 (TL)

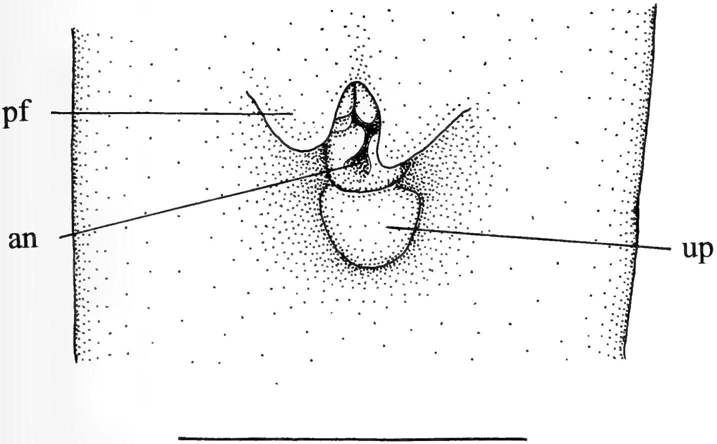

Fig. 4. Pelvic fins and surrounding structures in *Glanapteryx niobium*, holotype, INPA 12421, ventral view. Scale bar = 1 mm.

body. Caudal peduncle with more fragmented covering of dark pigmentation. Ventral surface of body, except for collar, with uniform scattering of dark chromatophores, less dense than on dorsal surface but still conspicuous. Head with slightly denser covering of dark chromatophores than those on body. Ventral surface of head and anterior portion of trunk with dense covering of melanophores, only slightly sparser than on dorsal surface. Cephalic sensory-canal pores with narrow white rim. All barbels with fields of dark chromatophores at base, abruptly fading shortly distal to that point. Narrow white ring around eyes, widest at posteroventral margin. Distal portion of branchial membranes lacking melanophores. Pectoral fin almost totally white, only few dark chromatophores located near base. Base of caudal fin with same pigmentation as caudal peduncle, its distal portion white. Distal portion of procurrent-ray dorsal and ventral areas without dark chromatophores. Pelvic fin remnant lacking dark pigmentation.

Etymology.—The specific epithet, *niobium*, a noun in apposition, refers to niobium, the chemical element chiefly responsible for the high background radiation of the Morro dos Seis Lagos, the known fish fauna of which is so far limited to the new *Glanapteryx* species.

Discussion.—Although as yet represented by a single specimen, there is little doubt that *G. niobium* is distinct from *G. anguilla*. The latter is currently known by tens of specimens, a sample which allows a satisfactory estimate of the degree of intraspecific variation expected for the genus (cf. de Pinna 1989). The differential characters displayed by *G. niobium*, summarized in the diagnosis above, have not been seen in any examined specimen of *G. anguilla*.

The new species is readily distinguishable from its only congener mainly by the white collar formed by a well-defined area lacking dark chromatophores. This area forms a white ring around the whole circumference of the body, and is striking against the dark pigmentation of the remainder of the fish. In *G. anguilla*, the dark pigmentation is even along the whole length of the body, with no fading in the collar region. The white collar of *G. niobium* is unique among the Trichomycteridae, and can be considered autapomorphic for the species. The lack of pigmentation in the collar region is particularly striking because the remainder of the body and head surface in *G. niobium* is more heavily pigmented than in *G. anguilla*, which contributes to a marked contrast. The white collar is evident even in ventral aspect, because in *G. niobium* the ventral surface of the head and anterior portion of the abdomen is more heavily pigmented than what is usual in other glanapterygines and trichomycterids in general. The heavy dark pigmentation on the ventral side of *G. niobium* is itself autapomorphic.

The lanceolate shape of the caudal-fin in *G. niobium* is also unique to that species among trichomycterids. The caudal fin in the family is commonly round, furcate or emarginated, and the unique lanceolate shape in *G. niobium* is considered an autapomorphy for the species. The peculiar caudal shape is a result of the prolongation of the five middle caudal-fin rays, which are far longer than the others.

The pectoral-fin length readily distinguishes *G. niobium* and *G. anguilla*. In *G. anguilla* the length of the fin is at most 25% of HL, never reaching 40% of HL as seen in *G. niobium*. This characteristic, however, is not autapomorphic, because the relative length of the fin varies widely in glanapterygines, making a polarity assessment of the condition in *G. niobium* uncertain. The same uncertainty applies to the shape of the fin, another character that apparently distinguishes the two species but which cannot unabiguously be determined as autapomorphic for either.

An additional difference that may be observed between the holotype of *G. niobium* and most specimens of *G. anguilla* is the number of sensory pores on the posterior part of head (3 versus 4, respectively). These pores trace the highly reduced laterosensory canal system of glanapterygines. The two anterior pores are openings of the postotic canal (running through pterotic, see Arratia & Huaquin 1995) and the two posterior ones represent the lateral-line canal (running through supracleithrum and ending shortly posterior to it). The posterior branch of the lateral line in some specimens splits further and opens into a tiny additional posterior pore (not considered in the discussion below). On the basis of topographical correspondence, the pore lost in *G. niobium* seems to be the last one (posterior lateral-line pore) present in four-pored *G. anguilla*. However, the number of pores is intraspecifically variable in *G. anguilla*. While most specimens examined of the species indeed have four pores (cf. fig. 2C in de Pinna 1989), a few specimens have only three pores, like in the only known specimen of *G. niobium*. Therefore, the difference in sensory-pore number cannot be used to separate the two *Glanapteryx* species confidently. The infraorbital canal in *G. anguilla* (incomplete as in all other trichomycterids except Trichogeninae and Copionodontinae) is bifurcated distally, and opens through two minute pores posterior to the eye (cf. de Pinna 1989, fig. 5A). These pores could not be located in *G. niobium*, but they are also invisible externally in some specimens of *G. anguilla*, and cannot be confirmed as absent in *G. niobium* until more specimens are available for anatomical studies.

Not all characters diagnostic for *Glanapteryx* given by de Pinna (1989: 363) can be checked in *G. niobium*, which is known only from the holotype. Of the eight characters proposed by de Pinna, numbers 2 (triangle-shaped premaxilla), 3 (simplified pelvic bone, when present), and 5 (pronounced interdigitations between frontals, sphenotics and supraoccipital in fully-grown individuals) are internal traits presently unobservable in the new species. *Glanapteryx niobium*, however, demonstrates all of the remaining characters.

Those are (numbering of de Pinna 1989): 1—absence of the anal fin; 4—reduced, diphycercal caudal fin; 6-eighty-eight or eighty-nine vertebrae (not directly observed in *G. niobium*, but likely in view of its body elongated to a degree similar to that of *G. anguilla*); 7—posterior naris mesial to eye, adjoined to mesial margin of eyeball; 8—combination of three-rayed and short pectoral fin. Not all of those characters are unambiguous evidence of monophyly. The anal fin is also lacking in some recently discovered, as of yet undescribed glanapterygine species, seemingly more closely related to genera other than *Glanapteryx*. The same applies to the diphycercal and reduced caudal fin. Character 8 is a combination character, and although appropriate for identification, does not hold as evidence for monophyly (*Pygidianops* has a short but one-rayed pectoral fin, while *Listrura camposi* has a three-rayed but long fin).

Remaining characters seem to provide relatively reliable but still circumstantial evidence of relationships. The position of the posterior nares is indeed unique, but other glanapterygines (*Pygidianops* and *Typhlobelus*) have eyes greatly reduced or lost, making a comprehensive comparison impossible. Still, allocation of *G. niobium* to the genus *Glanapteryx* is the best course of action based on the combination of all the evidence above.

Some internal characters illustrated and described by de Pinna (1989) seem unique to *G. anguilla* among the trichomycterids so far examined, although not yet explicitly proposed as synapomorphic. These are the posteriorly tripartite palatine; the enlarged head of the vomer; the anterior canal-bearing part of the sphenotic separated from the frontal; and the cartilage plug on the posterolateral margin of the premaxilla. All those characteristics are probably either autapomorphies for *G. anguilla* or synapomorphies for *Glanapteryx*. Their exact level of generality will have to await examination of the internal anatomy of *G. niobium*.

Habitat notes.—*Glanapteryx niobium* is the only fish species known to date from the Morro dos Seis Lagos lake complex. The collecting effort in the area intensively sampled various microhabitats with different fishing gear. Still, only the single specimen of *G. niobium* was found in the Lago Esperança (a second specimen of seemingly the same species was captured in that lake, but was subsequently lost). Similar collecting efforts were undertaken in all the other five lakes, but failed to secure any fish.

The Morro dos Seis Lagos is located inside the Yanomami indigenous preserve, itself part of the Pico da Neblina National Park. It is located approximately 60 km northeast of São Gabriel da Cachoeira. The Morro dos Seis Lagos is an isolated round outcrop 6 km in diameter, about 40 km away from the nearest elevated areas (Serra do Padre, to the north). It is covered by thick laterite crust, reddish brown in color. Morro dos Seis Lagos includes six major lakes at an altitude of 300 m, plus a number of smaller water bodies. Those are the only true lakes in the Brazilian Amazon, and are permanently isolated from other water courses. The lake beds were a consequence of the collapse of underlying rocky blocks.

The level of radiation in the region is extremely high, because of the concentration of radioactive minerals naturally in the soil, mainly niobium, thorium and cerium. Radiation detectors worn by expedition members in the field recorded daily radiation exposures equivalent to the maximum considered tolerable for a whole week according to international standards. In several places the measured emission was well over 25 milliroentgens. One of the creeks around the lake, Igarapé Ya-Mirim, is so radioactive as to cause itching in bathers after repeated exposure, and is called "itching creek" by indians, who avoid settling in the region. There is also a thermal spring in the area.

The spot where *G. niobium* was collected with a hand seine was about 1 m deep, and had a thick layer of leaf litter on the bottom, amidst which the fish was hiding. The water was transparent, green at distance, still, and acidic (pH 4.0). The invertebrate fauna was reported as rich by the collectors.

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I thank Victor Py-Daniel and Ulysses Barbosa for collecting and bringing to my attention the single known specimen of *G. niobium*. Py-Daniel also provided the habitat data. The expedition to Morro dos Seis Lagos was part of the First Brazilian Multidisciplinary Expedition to Pico da Neblina, organized and funded by INPA in 1990. A visit to Manaus during which I was able to examine the INPA ichthyological collections was sponsored by the Graduate Program in Entomology of that institution, through José A. Rafael. I am also grateful to Cristina Cox-Fernandes, Paulo Petry, Efrem Ferreira, and Labish N. Chao for their help during my visit. The manuscript benefitted from reviews by Richard Vari and Scott Schaefer. Research funding is provided by CNPq and FAPESP.

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A new species of *Nannosquilla* (Crustacea: Stomatopoda: Nannosquillidae) from the eastern Pacific and new records of species of *Neogonodactylus* (Gonodactylidae) from the Pacific coast of Mexico

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Abstract.—A large series of specimens of stomatopods was collected from intertidal and shallow subtidal habitats along the Pacific coast of Mexico. A new species of *Nannosquilla* Manning is described from the southeastern part of the Baja California Peninsula, and new records are provided for species of *Neogonodactylus* Manning, including the first record for Mexico of *N. lalibertadensis* (Schmitt), previously known from Ecuador and Panama.

A total of 50 species and 22 genera of stomatopod crustaceans are known from the eastern Pacific. They belong to three of five currently recognized superfamilies of Stomatopoda: Gonodactyloidea, Lysiosquilloidea and Squilloidea (see Hendrickx & Salgado-Barragán 1991). Among these, 29 species are known from the Pacific coast of Mexico, eight species belong to the genus *Neogonodactylus* Manning, and seven to the genus *Nannosquilla* Manning.

Species of the family Nannosquillidae and Gonodactylidae have been somewhat rarely reported in literature dealing with the eastern Pacific. This is mostly due to three factors: with a few exceptions, they are of small size, they often are burrowing species or live among coral or rubble and they generally feature a depth range too shallow to be sampled by research vessels, yet often too deep to be visited by non-scuba divers.

Recent collection of specimens of crustaceans in intertidal and shallow subtidal habitats along the Pacific coast of Mexico yielded some interesting specimens of stomatopods, including an undescribed species of *Nannosquilla*. Additional material deposited in the crustacean collection of UNAM at Mazatlán and belonging to the recently described genus *Neogonodactylus* Manning (Manning 1995: 80) allows us to report an additional species for the Pacific coast of Mexico and add records for two otherwise scarcely cited species.

Abreviations and acronyms used are: coll., collector; TL, total length (in millimeters); EMU, Estación Mazatlán UNAM, Invertebrates Reference Collection; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C.; UABCS, Invertebrates Collection, Departamento de Biología, Universidad Autónoma de Baja California Sur. Latitude and longitude were obtained in the field with a ICOM global positioning system (GPS).

Family Nannosquillidae Manning, 1980

Nannosquilla raymanningi, new species

Figs. 1–3

Material examined.—Holotype, 1 female (TL 22.2 mm), Ensenada Grande, Isla Partida, Baja California Sur, Mexico (24°33′N, 110°24′W), 17 Aug 1994, 13.7 m, sandy bottom, scuba diving, collected by hand using quinaldina (coll. C. Sánchez Ortiz) (EMU-4620); paratypes 1 male (TL 20.3 mm) and 1 female (TL 22 mm), same locality (EMU-4621); paratypes 1 male (TL 20.7 mm) and 1 female (TL 23.6 mm), same locality (USNM 285512); paratypes 2 females (TL 20.3 and 21.0 mm), same lo-

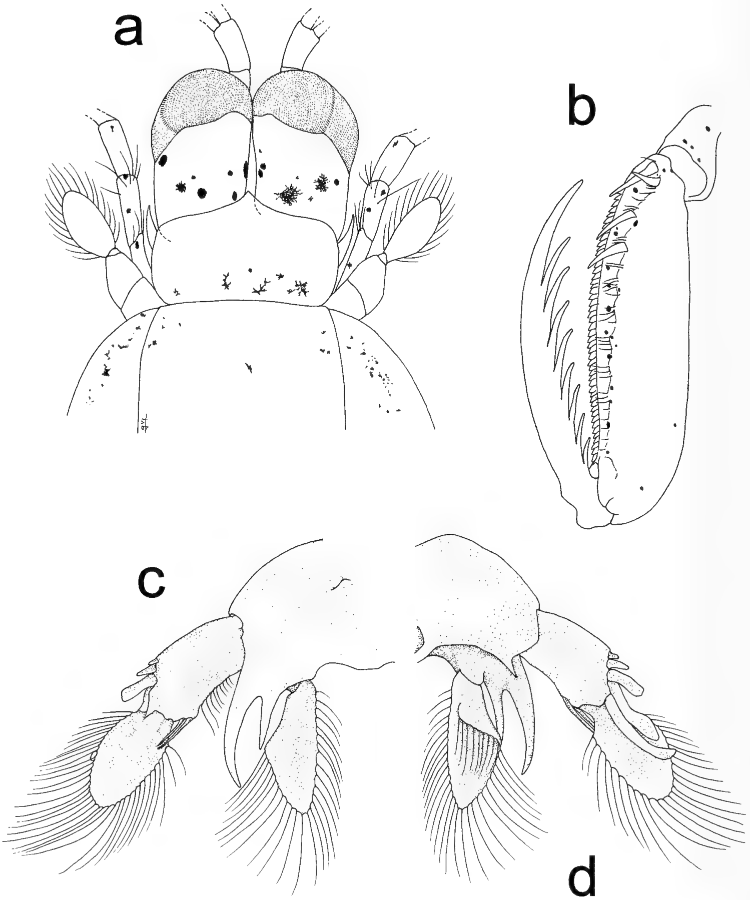

Fig. 1. *Nannosquilla raymanningi*, new species, female holotype. a, anterior part of body; b, right raptorial claw, inner face; c, right uropod, ventral view; d, right uropod, dorsal view (EMU-4620).

cality (EMU-4622); 1 male (TL 20.3 mm) and 1 female (TL 22.8 mm) (UABCS).

Description.—Eye small, short, not overreaching antennular peduncle. Cornea subglobular, not bilobed, set obliquely on stalk and slightly expanded laterally. Ocular scales fused at base and most of length, but distinctly separated in distal portion; apex acute or rounded. Upper antennular flagellum with 11 free articles; lower longer, with

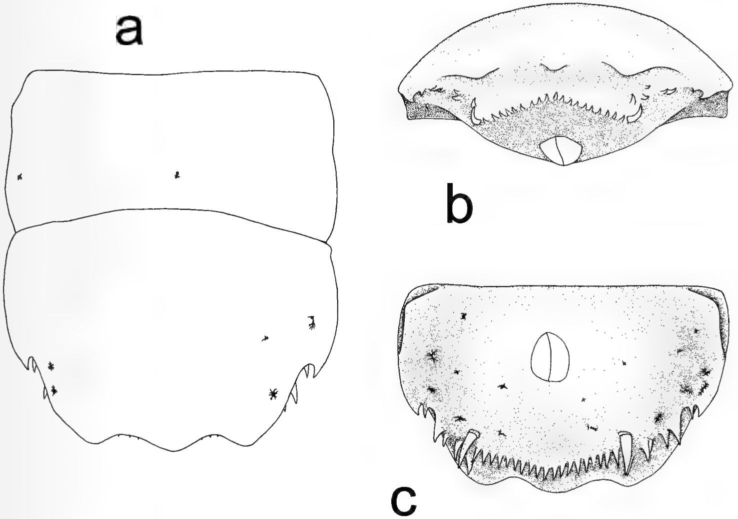

Fig. 2. *Nannosquilla raymanningi*, new species, female holotype. a, sixth abdominal somite and telson, dorsal view; b, telson, posterior view; c, telson, ventral view (EMU-4620).

8 to 10 (holotype with 9-9), lower shorter with 4 free articles; antennular process visible laterally, projecting beyond sides of rostral plate and overreaching anterolateral corners of rostral plate. Antennal peduncles short, not overreaching eyes, flagella with 11 articles; antennal scale not extending beyond midpoint of last segment of antennal peduncle. Rostral plate subrectangular, wider than long, covering only proximal margin of ocular peduncles; lateral margins subparallel, slightly convex, anterolateral corners rounded, anterior margins slightly concave, apex angled, not ending in spine. Mandibular palp absent, four epipods present. Propodus of raptorial claw with four movable teeth on proximal inner margin; dactylus with two proximal notches (in most specimens) and 9 to 11 teeth (9-10 in holotype), including terminal one. Sixth abdominal somite with posterolateral corners acute but not produced as spines. Telson short in dorsal view, aproximately 1.3 times wider than long. False eave trilobed, the median distinctly wider, rounded; lateral lobes obtuse in dorsal view; dorsum of telson with short, shallow sulcus on each side of median projection of false eave, converging to level of median projection; median projection of false eave low, ventrally curved posteriorly, flanked on each side by narrow, deeply concave depressions; submedian projections rounded. False eave merges with true margin at about level of last fixed lateral tooth. Marginal armature on each side of midline consisting of 9–12 denticles (holotype with 9-10), entire row forming an inverted (widely open) "V" in posterior view; 1 movable submedian tooth, originating anteriorly, and seven fixed lateral teeth and denticles; third denticle small and inserted at a lower (ventrally) level than second denticle; outermost denticle located on false eave. Basal segment of uropod

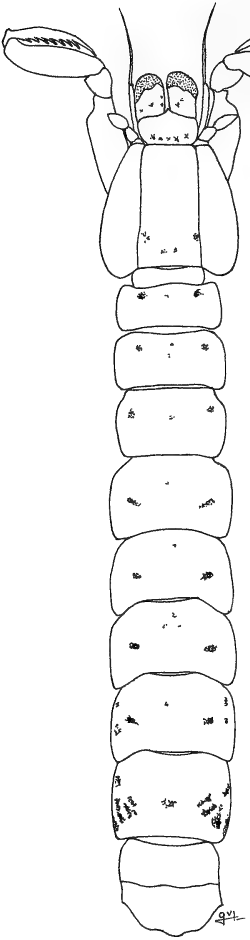

Fig. 3. *Nannosquilla raymanningi*, new species, dorsal view of female paratype (EMU-4622).

with ventral, proximal tubercle. Dorsal spine of basal segment of uropod short, not extending to midpoint of endopod. Outer spine of basal prolongation curved, much longer than inner one which is much narrower and almost straight. Proximal segment of exopod with 1–4 stiff setae (holotype with 2 on each side) on inner distal corner, and 5 to 6 spatulate spines on outer distal margin (holotype with 5-5).

Color.—Specimens in ethanol are pale, with few, variable, stellate chromatophores distributed over the eyes, rostral plate and dorsum. Carapace, thoracic and abdominal segments 1–4 with sparse chromatophores; a pair of chromatophores lateral to the dorsal midline. Fifth abdominal somite with posterolateral regions bearing a symmetrical dark area (Fig. 3).

Remarks.—*Nannosquilla raymanningi* is so far the only species of *Nannosquilla* from the eastern Pacific with the external spine of the basal prolongation of the uropod considerably longer than the inner spine. Five out of the seven species of *Nannosquilla* previously reported from this region feature a longer inner spine: *N. decemspinosa* (Rathbun, 1910); *N. similis* Manning, 1972b; *N. galapagensis* Manning, 1972b; *N. canica* Manning & Reaka, 1979; *N. anomala* Manning, 1967. The other two species feature subequal spines. The new species, however, does not show the 10–12 projections seen on the false eave of *N. californiensis* (Manning, 1961a); it also possesses 9–12 submedian fixed denticles on the telson instead of eight denticles, and rounded anterolateral angles of the rostral plate contrary to acute angles in *N. californiensis*. It is also easily distinguished from *N. chilensis* (Dahl, 1954), a species with rostral plate with a broadly rounded anterolateral angle, and the dactylus of the raptorial claw with 17 teeth (9–11 in *N. raymanningi*). The Atlantic species of *Nannosquilla* with the external spine of the basal prolongation of the uropod either longer or similar in size to the inner spine, have few (4–7) submedian denticles and, at most, nine teeth on the dactylus of the raptorial claw; these species are *Nannosquilla adkinsoni* Camp & Manning, 1982; *N. antillensis* (Manning, 1961b); *N. carolinensis* Manning, 1970; *N. disca* Camp & Manning, 1986; *N. heardi* Camp & Manning, 1982; *N. tobagoensis* Schotte & Manning, 1993; *N. virginalis* Camp & Manning, 1986; *N. yucatanica* Camp & Manning, 1986.

The specimens were collected in an area inhabited by the gregarious "garden eel", *Taenioconger digueti* Pellegrin, on sandy bottom, near reefs. Although the specimens of *N. raymanningi* and *T. digueti* were obtained in the same sample, there is no evidence the stomatopods use the burrows of eels as a shelter.

Etymology.—We are pleased to name this new species in honor of Raymond B. Manning, worldwide expert in stomatopod taxonomy and ecology, for his astounding contribution to the knowledge of this group of crustaceans.

Family Gonodactylidae Giesbrecht, 1910

Neogonodactylus lalibertadensis (Schmitt, 1940)

Fig. 4

Gonodactylus festae lalibertadensis Schmitt, 1940:223, fig. 33.

Gonodactylus lalibertadensis.—Manning, 1974:102.—Reaka & Manning, 1980: 5.—Hendrickx & Salgado-Barragán, 1991:29 (table 6).

Neogonodactylus lalibertadensis.—Manning, 1995:80.

Material examined.—Sayulita Bay, Jalisco (20°52.3′N, 105°28.0′W), 10 Apr 1996, 1 male (TL 20.6 mm) and 1 female (TL 16.7 mm), rocks and algae, 2 m (EMU-4623).—Chilenos Bay, Baja California Sur (22°56.0′N, 109°48.0′W), 1 female (TL 13.1 mm), coral and algae, 4 m, 20 Jul 1996 (EMU-4624).

Previous records.—Known only from La Libertad, Santa Elena Bay, Ecuador (type locality), and Taboga, Panama (Manning 1974).

Color.—The three specimens examined were preserved in ethanol. They have a very similar pattern of chromatophores and dark spots, with only slight variations. Propodus and dactylus of first maxilliped darkened; a dark spot close to the colored spot of the merus of the raptorial claw. There are two submedian spots in the posterior dorsal half of the carapace. The female specimen from Chilenos features two additional marginal spots anteriorly. The male sixth thoracic somite bears two submedian spots, two intermediate spots, and a lateral spot; females show a similar pattern. Abdominal segments 1–5 bear a pair of large submedian boomerang-shaped spots and a pair of intermediate spots; spots are more difuse in the female specimens. The fifth abdominal segment has an additional central spot on all three examined specimens. There are two anterior submedian spots on the telson of the Sayulita male and Chilenos female (Fig. 4).

Remarks.—The specimens examined agree well with the original description of *N. lalibertadensis*, including the laterally projected ocular scales and the anterolateral angle of rostral plate which is apically blunt [not spiny or sharp, as in *N. festae* (Schmitt, 1940) or *N. bahiahondensis* (Schmitt, 1940)]. Number and location of spines and spinules also correspond to the original description of *N. lalibertadensis*, except for a higher number of spines on the intermediate accesory carinae of examined females (Table 1). The only male specimen collected presents an inflated telson with a reduced number of dorsal spines.

The material cited under *G. lalibertadensis* by Manning (1972a) was later recognized by Manning & Reaka (1979) as an undescribed species, which they described and named *G. costaricensis.*

Neogonodactylus stanschi (Schmitt, 1940)

Gonodactylus stanschi Schmitt, 1940:215, Fig. 30.—Steinbeck & Ricketts, 1941: 429.—Manning, 1972a:110.—Reaka & Manning, 1980:8.—Hendrickx & Salgado-Barragán, 1989:244 (table 6); 1991: 36, fig. 17.

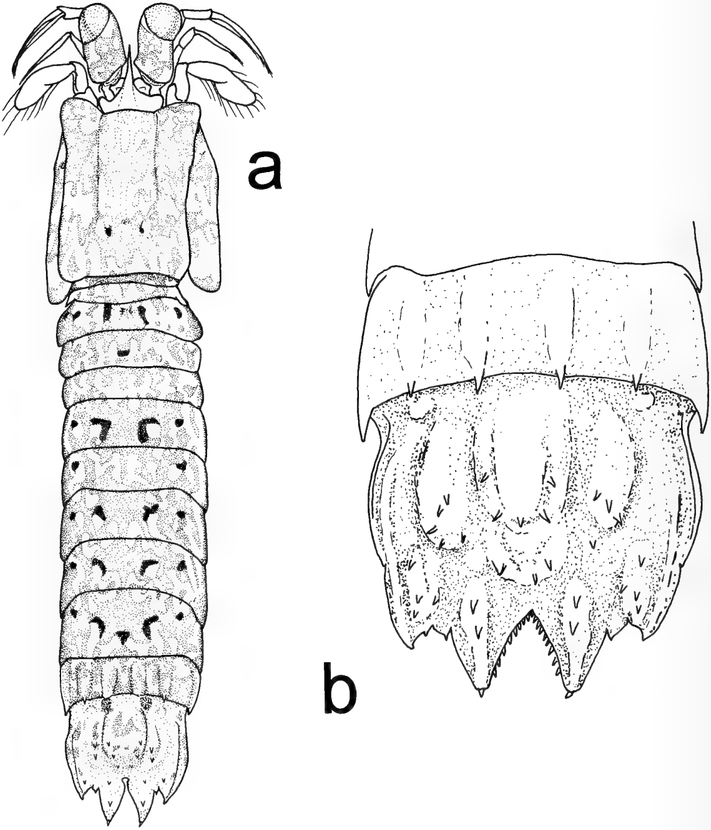

Fig. 4. *Neogonodactylus lalibertadensis* (Schmitt, 1940). a, body of male in dorsal view; b, telson of female, dorsal view (EMU-4623).

Neogonodactylus stanschi.—Manning, 1995:80.

Material examined.—San Juan de Alima, Michoacán (18°36.1′N, 103°42.1′W), 5 Nov 1996, 1 male (TL 9.8 mm), intertidal, rocks and algae (EMU-4233).—Punta Santiago, Manzanillo, Colima, (19°06.5′N, 104°21.0′W), 6 Nov 1996, 1 male (TL 30.5 mm) and 1 juvenile (TL 7.2 mm), 2–3 m, rocks and algae (EMU-4234).—El Tamarindo Beach, Tenacatita Bay, Jalisco (19°15.9′N, 104°47.9′W), 4 Nov 1996, 2 males (TL 13.2 and 18.8 mm), 1 female (TL 11.8 mm), and 2 juveniles (TL 7.4 and 7.5 mm), 1–2 m, rocks and algae (EMU-4235).—Ensenada de Litigu, Nayarit

Table 1.—Pattern of dorsal spination of telson in several *Neogonodactylus* from the eastern Pacific region. Modified from Manning (1972a) and Schmitt (1940).

						lalibertadensis		
	bahiahondensis	*festae*	*costaricensis*	*stanschi*	*laliberta-densis*	Male from Sayulita	Female from Sayulita	Female from Chilenos Bay
Median Carina	1	0–1	1	1	1	1	1	1
Accessory Median	0–1	0–4	1	1	2–3	2	2	3
Anchor	absent	3–4	absent	absent	absent	absent	absent	absent
Knob	2	4–5	4	—	2–4	2–3?	3	4
Anterior Submedian	1 + 1–2	1 + 0–3	1 + 1	1	2–5	2 + 2	5 + 4	3 + 3
Submedian	1–3	4–6	2	0–1	2–5	2	2	2
Accessory Intermediate	in 1 row	in 2 rows	in 1 row	—	2–3	1 + 1	4 + 4	3 + 4
Lateral Denticle	—	+	—	—	—	—	—	—

(20°47.4′N, 105°31.9′W), 9 Apr 1996, 1 female (TL 29.4 mm), 1 m, dead coral (EMU-4236).—Chilenos Bay, Baja California Sur (22°56.0′N, 109°48.0′W), 20 Jul 1996, 2 females (TL 29.1 and 30.5 mm), 3–5 m, coral and rocks (EMU-4237).—Playa Calerita, La Paz, Baja California Sur (24°21.0′N, 110°16.0′W), 18 Jul 1996, 1 male (TL 23.7 mm), 1 juvenile (TL 13 mm), 2–3 m, rocks and algae (EMU-4238).—Los Algodones Bay, Guaymas, Sonora (27°58.6′N, 111°07.7′W), 25 Mar 1997, 1 female (TL 18.3 mm), 1.5–2.5 m, rocks and algae (EMU 4239).

Previous records.—El Dátil, Espíritu Santo, Angel de La Guarda, Isabel and Tres Marías Islands, Gulf of California; San Carlos Bay, Sonora, Tangola-Tangola Bay and Puerto Huatulco, Oaxaca; Punta Mita, Nayarit; Guaymas, Sonora; Teacapán, Sinaloa; Barra de Navidad, Jalisco; Zihuatanejo, Guerrero; Puerto Lobos and Punta Márquez, Baja California Sur; Chamela, Jalisco, Mexico. Salera and del Caño Islands, Costa Rica (Hendrickx & Salgado-Barragán 1991).

Remarks.—Present records are the first available for the coast of Colima and Michoacán, Mexico.

Neogonodactylus zacae (Manning, 1972a)

Gonodactylus oerstedii Schmitt, 1940:221 (part) figs. 27–28 (not fig. 26 = *G. oerstedii* Hansen, 1895; not fig. 29 = *G. pumilus* Manning, 1970).—Steinbeck & Ricketts, 1941:428 (not *G. oerstedii* Hansen, 1895).

Gonodactylus zacae Manning, 1972a:107, fig. 3; 1974:103, fig. 1; 1976:223.—Reaka & Manning, 1980:8.—Brusca, 1980:244, figs. 13-10.—Hernández-Aguilera et al., 1986:190.—Hendrickx & Salgado-Barragán, 1991:39, fig. 19.

Neogonodactylus zacae.—Manning, 1995: 80.

Material examined.—El Tesoro Beach, La Paz, Baja California Sur (24°18.0′N, 110°19.0′W), 17 Jul 1996, 5 males (TL 25.2–33.5 mm) and 5 females (TL 25.2–35.8 mm), intertidal to 1 m, rocks and algae (EMU-4240).—Calerita Beach, La Paz, Baja California Sur (24°21.0′N, 110°16.0′W), 18 Jul 1996, 1 male (TL 23.7 mm), 1 female (TL 13 mm), 1.5–2.5 m, rocks, algae and sponges (EMU-4625).—San Juan de la Costa, La Paz, Baja California Sur (24°27.0′N, 110°42.0′W), 19 Jul 1996, 4 males (TL 11.5–27.7 mm), 3 females (TL 10.8–32.9 mm), and 10 juveniles (TL 5.8–9.3 mm), rocks, algae and sponges, 1-2 m (EMU-4626).—Sendero Viejo Bay, Guaymas, Sonora (27°52.0′N, 110°52.4′W), 27 Mar 1997, 1 male (TL 13 mm), 1–3 m, rocks and algae (EMU-4627).

Previous records.—Puerto Huatulco, Oaxaca; Santa Inés Bay, Concepción Bay, Arena Bank, Gorda bank and Puerto Escondido, Baja California Sur; Revillagigedo and Tres Marías Islands, Mexico. Puerto Parker and Isla del Coco, Costa Rica. Honda Bay, San José and Perlas Islands, Panama. La Plata and Galapagos Islands, Ecuador (Camp & Kuck 1990, Hendrickx & Salgado-Barragán 1991).

Remarks.—Material from Guaymas, Sonora, corresponds to the first continental record on the east coast of the Gulf of California. It also represents a slight extension of the northernmost distribution limit of *N. zacae*.

Acknowledgments

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A revision of the southeast Asian freshwater crabs of the genus *Isolapotamon* Bott, 1968 (Crustacea: Decapoda: Brachyura: Potamidae)

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Abstract.—The taxonomy of the potamid freshwater crab genus *Isolapotamon* Bott, 1968, is revised. Fifteen Bornean species (including two new ones) and three Philippine species are recognized. The fifteen Bornean species are: *I. anomalum* (Chace, 1938) (type species), *I. bauense* Ng, 1987, *I. beeliae* Ng, 1986, *I. borneense,* new species, *I. collinsi* Holthuis, 1979, *I. consobrinum* (De Man 1899), *I. doriae* (Nobili 1900), *I. griswoldi* (Chace, 1938), *I. grusophallus* Ng & Yang, 1986, *I. ingeri,* new species, *I. kinabaluense* (Rathbun, 1904), *I. mahakkamense* (De Man, 1899), *I. naiadis* Ng, 1986, *I. nimboni* Ng, 1987, and *I. stuebingi* Ng, 1995. The three Philippine species are: *I. mindanaoense* (Rathbun, 1904), *I. sinuatifrons* (H. Milne Edwards, 1853) and *I. spatha* Ng & Takeda, 1992. These species are distinguished mainly by means of their gonopodal and carapace features.

The family Potamidae is represented by three genera in the island of Borneo (Brunei, Malaysian Sarawak and Sabah, and Indonesian Kalimantan), i.e., *Isolapotamon* Bott, 1968, *Cerberusa* Holthuis, 1979, and *Ibanum* Ng, 1995. *Cerberusa* contains only two troglobitic species, known only from the caves in northern Gunung Mulu Sarawak (Holthuis 1979). *Ibanum* contains two non-troglobitic species, one from central Kalimantan and the other from Sarawak (Ng 1995). *Isolapotamon* is the largest genus, with 13 described species (Bott 1970b, Ng 1986, 1987, 1995). Three other species are known from the island of Mindanao in the southern Philippines (Bott 1970b, Ng & Takeda 1992).

Bott (1970b) included *Isolapotamon*, *Malayopotamon* Bott, 1968, and *Nanhaipotamon* Bott, 1968, in a new family, Isolapotamidae, which he defined as having stout or elongate male first pleopods, and whose members presumably occurred mainly in Sumatra, Java, Borneo and the Philippines, with some species present in Taiwan, southern China and Peninsular Malaysia. The Isolapotamidae, however, lacks sufficient distinguishing characters from typical potamids to warrant its recognition as a separate family (Ng 1986, 1987, 1988a, 1988b; Ng & Yang 1985, 1986). None of the three genera in the Isolapotamidae (*Isolapotamon*, *Malayopotamon* and *Nanhaipotamon*) possess characters unique to themselves. Substantial changes have also occured with the discovery of additional Sundaic species of, for example *Cerberusa* and *Ibanum* and clarification of various genera such as *Nanhaipotamon* (see Ng & Dudgeon 1992, Ng & Takeda 1992, Dai & Ng 1994, Dai 1997), which casts serious doubts on the validity of the Isolapotamidae. In this paper, the genus *Isolapotamon* is revised and placed in the family Potamidae Ortmann, 1896 (sensu Ng 1988a).

All measurements, in millimeters, are included as carapace widths by lengths. The terminology used follows that used by Ng (1988a). Specimens are deposited in the Museum of Comparative Zoology, Harvard

University (MCZ); National Museum of Natural History (USNM), Washington, D.C; National Natuurhistorische Museum (former Rijksmuseum van Natuurlijke Historie), Leiden (NNM); The National History Museum, London (NHM); Museum Civico di Storia Naturale, Genoa (MGE); Museo ed Istituto di Zoologia Sistematica della Universita di Torino, Turin (MUT); National Science Museum, Tokyo (NSMT); Zoological Reference Collection, School of Biological Sciences, National University of Singapore (ZRC); Museum of Zoology, Cambridge University, (CMZ); Muséum National d'Histoire naturelle, Paris (MNHN); Sarawak Museum, Kuching (SM); and the Museum Zoologicum Bogoriense, Bogor (MZB).

The abbreviations G1 and G2 are used for the male first and second pleopods respectively; Mt. and Sg., for Mount and Sungai respectively, the latter term meaning river in Malay. Altitudes above sea level are indicated in meters (m). Localities of collecting sites have been derived from Anon (1971) or from the field collector's data.

Taxonomy

Family Potamidae Ortmann, 1896

Genus *Isolapotamon* Bott, 1968

Isolapotamon (Isolapotamon) Bott, 1968: 119.

Isolapotamon.—Bott, 1970a:333; Bott, 1970b:190.

Diagnosis.—Carapace broader than long; epigastric and postorbital cristae well developed, separate; anterolateral margin convex, serrated; external orbital angle usually broadly triangular, outer margin distinctly longer than inner margin; epibranchial tooth present. Exopod of third maxilliped very broad, especially proximally, outer margin distinctly convex outwards; distal tip reaches or slightly exceeds half length of merus; flagellum distinct, longer than width of merus. Male abdomen distinctly triangular, lateral margins of last segment convex or almost straight; telson triangular. G1 slender, elongated; terminal segment subequal to or longer than subterminal segment, slender, tip often dilated. G2 slender, elongated; distal segment distinct, subequal to half length of basal segment.

Type species.—*Potamon anomalus* Chace, 1938, by original designation.

Remarks.—Bott (1968) erected *Isolapotamon* with three subgenera, i.e. *Isolapotamon*, *Malayopotamon* Bott, 1968, and *Nanhaipotamon* Bott, 1968. Bott (1970a) subsequently raised all three to distinct genera and placed them in a new family, the Isolapotamidae (Bott 1970b), recognising eight species in the genus *Isolapotamon*. Bott (1970b) also excluded the Philippine species "*Telphusa artifrons* Bürger, 1894," which he had earlier (1968) placed in *Isolapotamon* (*Isolapotamon*), and referred it to the genus *Tiwaripotamon* Bott, 1970. Ng (1992) reviewed the problems associated with Bott's genus *Tiwaripotamon*, and subsequently Ng & Takeda (1992) established a new genus, *Ovitamon*, for Bürger's species as well as two new species from the Philippines.

Bott (1970b) placed *Potamon* (*Potamiscus*) *chaseni* Roux, 1934, in the genus *Isolapotamon*, noting that it was the only member of the genus from Peninsular Malaysia. *Isolapotamon chaseni* differs from typical *Isolapotamon* species in at least one very major character, the form of the exopod of the third maxilliped. In the Bornean and Philippine *Isolapotamon*, the exopod of the third maxilliped is very broad, especially proximally, and the outer margin is distinctly convex outwards. When the exopod is appressed against the endopod, the outer margin of the third maxilliped has a rounded appearance. This type of third maxilliped exopod is known in only one other sundaic taxon, *Allopotamon tambelanense* (Rathbun, 1905), from the Tambelan Islands west of Borneo (Ng 1988b). In *I. chaseni*, the exopod is proportionately more narrow, the outer margin being almost straight or only slightly convex, giving the third maxilliped a more quadrate appearance (see Ng 1988).

The structure of the G1 of *I. chaseni*, and the absence of a flagellum on the third maxilliped exopod, suggests that this species should be excluded from the genus *Isolapotamon*. Ng (1988b) referred this species to the Malayan genus *Stoliczia* Bott, 1966.

Seven *Isolapotamon* species have been described from China, viz. *I. sinense* Tai & Sung, 1975, *I. papilionaceum* Dai, Song, He, Cao, Xu & Zhong, 1975, *I. physalisum* Dai, Song, Li, Chen, Wang & Hu, 1984, *I. aflagellum* Dai, Song, Li & Liang, 1980, *I. nasicum* Dai, Chen, Song, Fan, Lin & Zeng, 1979, *I. sheni* Dai, Chen, Liu, Luo, Yi, Liu, Gu & Liu, 1990, and *I. obtortum* Dai, Song, Li, Chen, Wang & Hu, 1984. All these Chinese *Isolapotamon* species, however, have the exopod of the third maxilliped slender (not broad) and the outer margin being straight (not convex outwards). In addition, the G1 terminal segment of the Chinese species is proportionately much longer than the subterminal segment, where as it is equal to or more than half the length of the subterminal segment in *Isolapotamon*. In a recent reappraisal of these species using the above features as well as the structures of the external orbital angle, exopod of the third maxilliped, male abdomen and G1, Dai & Türkay (1997) referred the Chinese species to four new genera, viz. *Neilupotamon*, *Yarepotamon*, *Minpotamon*, *Vadosapotamon* and *Latopotamon*. As a result of this, *Isolapotamon* s. str. has a wholly Bornean and Philippine distribution.

The form of the exopod of the third maxilliped exopod in *Malayopotamon* and *Nanhaipotamon* is very different from that of *Isolapotamon*. Examination of *Malayopotamon* and *Nanhaipotamon* specimens shows that, like other Southeast Asian potamids, their exopods are slender and the outer margins slightly concave. This observation, together with the fact that the G1s of the three genera are markedly different, indicates that the three genera are not closely related, contrary to Bott's (1970b) belief.

The generic diagnostic characters defined by Bott (1968) for *Isolapotamon* are generally valid and are used here in a modified form. Ng (1986, 1987) and Ng & Yang (1986) partially revised the genus, adding five new species to the Bornean fauna and resurrecting another species which Bott (1970b) had synonymised with *I. mahakkamense* (De Man, 1899). A total of 15 Bornean species are now recognized, two of which are here described as new: *I. anomalum* (Chace, 1938) (type species), *I. bauense* Ng, 1987, *I. beeliae* Ng, 1986, *I. borneense*, new species, *I. collinsi* Holthuis, 1979, *I. consobrinum* (De Man, 1899), *I. doriae* (Nobili, 1900), *I. griswoldi* (Chace, 1938), *I. grusophallus* Ng & Yang, 1986, *I. ingeri*, new species, *I. kinabaluense* (Rathbun, 1904), *I. mahakkamense* (De Man, 1899), *I. naiadis* Ng, 1986, *I. nimboni* Ng, 1987, and *I. stuebingi* Ng, 1995.

Although the present paper deals essentially with Bornean potamids, three poorly known Philippines species, *I. mindanaoense* (Rathbun, 1904), *I. sinuatifrons* (H. Milne Edwards, 1853) and *I. spatha* Ng & Takeda, 1992, are also discussed for completeness.

Key to the Species of *Isolapotamon*

1a. Carapace relatively deep, carapace height to width ratio 0.4–0.5; G1 terminal segment about equal to subterminal segment, terminal segment sinuous, tip dilated, forming a right-angled triangular projection (Fig. 1E–H) (Sarawak) . . . . *I. bauense*

1b. Carapace normal or flat, carapace height to width ratio distinctly less than 0.4; G1 terminal segment equal or subequal to subterminal segment, terminal segment sinuous or straight, tip dilated, laterally flattened, rounded, or with a secondary projection 2

2a. Dorsal surface of carapace evenly flat; epibranchial tooth distinct, well developed, separated from the anterolateral margin by distinct triangular cleft . . . 3

2b. Dorsal surface of carapace inflated or only inflated in 1 or 2 regions; epibranchial tooth indistinct or distinct but separated from anterolateral margin by shallow cleft 4

3a. Carapace wider than long to almost squarish (Fig. 3), dorsal surfaces smooth; anterolateral regions striated; intestinal region smooth; epibranchial tooth well developed, tip sharp, separated from anterolateral margin by deep, distinctly triangular cleft; epigastric cristae sharp; G1 terminal segment tip dilated to form "knob-like" structure or appearing vaguely triangular (Figs. 5E–H) (Sarawak, northwestern Kalimantan) .... *I. consobrinum*

3b. Carapace wider than long, dorsal surfaces rugose, especially anterolateral and posterolateral regions; intestinal regions granulose; epibranchial tooth prominent but tip not sharp, separated from anterolateral margin by relatively shallower triangular cleft; epigastric cristae rugose; G1 terminal segment tip not dilated or rounded (Fig. 12E–H) (Sarawak, northwestern Kalimantan) .... *I. stuebingi*

4a. Dorsal surface of carapace granulated, especially on anterolateral, posterolateral, epigastric, postorbital, branchial and intestinal regions (Fig. 9); epigastric cristae rugose but low; posterolateral margins distinctly convex; outer margin of external orbital angle about 4 times longer than inner margin; cervical groove shallow; no groove discernible between cardiac and intestinal regions; G1 not known (central Kalimantan) .... *I. mahakkamense*

4b. Dorsal surface of carapace granulated or striated only on anterolateral and/or posterolateral regions; epigastric cristae not rugose, distinct and usually prominent; posterolateral margins straight to concave; external orbital angle about 2 or 3 times longer than internal orbital angle; cervical groove shallow or deep, groove between cardiac and intestinal region present or absent; G1 straight to or sinuous ... 5

5a. Epigastric cristae distinct, sloping from centre and merging gradually with postorbital cristae; dactylus of last ambulatory leg very short; G1 sinuous, terminal segment subequal in length to subterminal segment, distal part bifurcated, subdistal process subequal in length to distal process (Fig. 5M–P) (Sabah) .... *I. griswoldi*

5b. Epigastric cristae indistinct, distinctly separated from postorbital cristae by wide, disjunct notch; dactylus of last ambulatory leg long or medium lengthed; G1 sinuous to almost straight, terminal segment of varying lengths, distal part of various forms 6

6a. G1 slightly sinuous to almost straight, not distinctly sinuous, tip foming head-like structure or bifurcated 7

6b. G1 very slender, distinctly sinuous, tip rounded, forming "knob-like" structure 14

7a. Distal part of G1 terminal segment forming a "head-like" structure 8

7b. Distal part of G1 terminal segment bifurcated 16

8a. Tip of distal part of G1 terminal segment distinctly rounded, outer margin of dilated part gradually curving to meet cylindrical part of terminal segment, inner margin of distal part curving gradually without distinct hump 9

8b. Tip of distal part of G1 terminal segment not rounded, usually trapezoidal or triangular, outer margin of dilated part gradually curving to meet cylindrical part of terminal segment, inner margin of distal part curving gradually with or without distinct hump 11

9a. Distal part of G1 terminal segment at right angles to the G1, forming an inverted "boot-like" structure (Figs. 10M–P) (Mindanao) ..... *I. sinuatifrons*

9b. Distal part of G1 terminal segment not at right angles, usually directed at 45° to the perpendicular, forming a "knob-like" structure 10

10a. G1 tip dilated, twice as long as broad (Fig. 10A–D) (Mindanao) .... *I. mindanaoense*

10b. G1 tip dilated, as long as broad (Fig. 12A–D) (Mindanao) .... *I. spatha*

11a. G1 gently sinuous, especially terminal segment, tip resembling a "chicken head" (Figs. 1M–P) (Sarawak ?) ... . *I. borneense*

11b. G1 almost straight, terminal segment tip dilated, trapezoidal or triangular, not resembling a "chicken head" . . . 12

12a. G1 subterminal segment with distinct notch at proximal end, terminal segment tip dilated, rounded, forming a "club-like" structure (Fig. 8) (Sabah) . . . . *I. kinabaluense*

12b. G1 subterminal segment without distinct notch at proximal end, terminal segment tip dilated, flattened, forming a "horse head-like" structure 13

13a. Distal side of G1 tip longer than proximal side (Fig. 1A–D) (Sabah) . . . . *I. anomalum*

13b. Distal side of G1 tip shorter than proximal side (Figs. 6E–H) (Sabah) . . *I. ingeri*

14a. G1 terminal segment distinctly longer than subterminal segment, tip evenly rounded (Fig. 5I–L) (Sarawak) . . *I. doriae*

14b. G1 terminal segment subequal to or slightly longer than subterminal segment, distal part unevenly dilated, upper margins gently convex to almost straight 15

15a. Outer part of dilated G1 terminal segment tip projecting slightly outwards, upper margin gently convex, curving gently downwards about 90° to form dilation (Fig. 10E–H) (southeastern Kalimantan) . . . . *I. naiadis*

15b. Dilated part of distal part of G1 terminal segment almost triangular, upper margin almost straight, sloping downwards sharply (Fig. 1I–L) (southeastern Kalimantan) . . . . *I. beeliae*

16a. Subdistal process of distal part of G1 terminal segment twice as long as distal process (Fig. 6A–D) (Sarawak) . . . . *I. grusophallus*

16b. Subdistal process of distal part of G1 terminal segment subequal in length to distal process 17

17a. Distal and subdistal projections of distal part of G1 terminal segment meeting at right angles at outer margin, distal process approximately equal in length to subdistal process (Fig. 10I–L) (Sarawak) . . . . *I. nimboni*

17b. Distal and subdistal projections of distal part of G1 terminal segment meeting gradually (sloping) at outer margin, subdistal process appears longer (but less than 1.5 times) than distal process (Fig. 5A–D) (Sarawak) . . . . *I. collinsi*

Isolapotamon anomalum (Chace, 1938)
Fig. 1A–D

Potamon anomalus Chace, 1938:14, pl. 2.
Potamon (*Potamon*) *anomalus*.—Yang, 1979:17.
Isolapotamon (*Isolapotamon*) *anomalum*.—Bott, 1968:120, fig. 1.
Isolapotamon anomalum.—Bott, 1970b: 191, pl. 41 fig. 77, pl. 56 fig. 82.
Stoliczia leoi.—Ng, 1988b: fig. 35A, B (not *Potamiscus leoi* Ng & Yang, 1985).

Material examined.—Paratypes, 1 male (34.2 by 26.3 mm), 1 female (27.4 by 21.6 mm) (ZRC 1990.461–462), Borneo, Sabah: Mount Kinabalu, Bundutan (Bundu Tuhan), Luidan River, ca. 5°58′N, 116°32′E, coll. J. A. Griswold Jr., 11 Jul 1937. Paratypes, 2 males (dry) (USNM 075896), Borneo, Sabah, coll. Asiatic Primate Expedition, 11 Jul 1937. Others—2 males, 1 female, 2 juveniles (largest 27.2 by 20.9 mm) (ZRC 1990.3641–3645), Borneo, Sabah: stagnant pools, Sg. Mengalum, Mendolong, ca. 4°45′N, 115°40′E, Sipitang District, coll. R. B. Stuebing, 8 Aug 1989. 2 males, 2 females (USMN 96334), North Borneo: Tenompok, stn. 27, coll. B. C. Walton, 25 Mar 1954.

Diagnosis.—Carapace dorsal surface smooth; anterolateral margins convex, not distinctly cristate; epibranchial regions striated, striae low; postorbital and epigastric ridge low; epibranchial tooth low, blunt; external orbital angle triangular, distinctly behind frontal margin. Dactylus of last ambulatory leg long. G1 sinuous, subdistal process truncate, forming "horse head-like" structure.

Remarks.—Bott (1968) recorded this species from the Luidan River, at an altitude of 1000 m above sea level. This is one of the three species of *Isolapotamon* in the Kinabalu area of Sabah. *Isolapotamon anomalum* is easily distinguished from *I. griswoldi* by having a proportionately longer dactylus on the last ambulatory leg. *Isolapotamon anomalum* resembles *I. kinabaluense* with regards to the long dactylus of

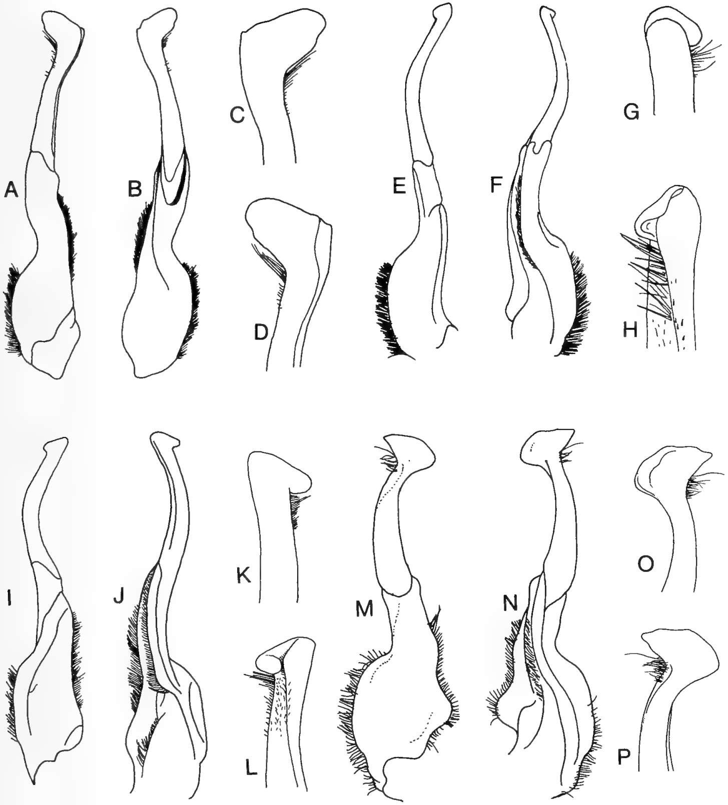

Fig. 1. G1s. A–D: *I. anomalum*, paratype male (ZRC 1990.461); E–H: *I. bauense*, holotype male (SM Cru Nr. 1986.9) (after Ng, 1987); I–L: *I. beeliae*, holotype male (MZB Cru Nr. 464) (after Ng, 1986); M–P: *I. borneense*, holotype male (ZRC 1984.7042). A, E, I, M: dorsal view; B, F, J, N: ventral view; C, G, K, O: dorsal view, tip of terminal segment; D, H, L, P: ventral view, tip of terminal segment.

the last ambulatory leg. In adult specimens of *I. anomalum*, the striae on the epibrachial regions are very low. This makes the crab appear smooth on the dorsal surface of the carapace. The smoother carapace and "horse-head" distal part of the G1 terminal segment easily distinguishes *I. anomalum* from *I. kinabaluense*.

The postorbital and epigastric ridge is remarkably low in adult specimens. It is also not distinctly cristate. In juveniles, both ridges are distinct and cristate.

The figures of the carapace supposedly of "*Stoliczia leoi*" published in Ng (1988b: fig. 35A, B) do not belong to that species but to *Isolapotamon anomalum* (Chace,

1938) instead. The incorrect negatives were accidentally printed. The correct photographs of *Stoliczia leoi* are depicted in the original description of the species by Ng & Yang (1985). The figures of the gonopods and mouthparts of *S. leoi* in (Ng 1988b: fig. 35C–G), however, are correct.

Isolapotamon bauense Ng, 1987
Fig. 1E–H

Isolapotamon (*Isolapotamon*) *mahakkamense*.—Bott, 1968:120 (part), fig. 7a, b (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Isolapotamon mahakhamense.—Bott, 1970b: 193 (part), pl. 41 fig. 81, pl. 56 fig. 81 (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Potamon (*Potamon*) *mahakkamense*.—Leh, 1982:4 (part) (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Isolapotamon bauensis Ng, 1987:145, fig. 3A–E, pls. 8, 9.

Material examined.—Holotype, male (66.3 by 51.0 mm) (SM Cru Nr. 1986.9), Borneo, Sarawak: Serian, cave stream, in total darkness, Lobang Siri, Gua Siri Paya (Kampong) Bentang, 27 miles, ca. 1°22′N, 110°09′E, coll. Lord Medway, 10 Dec 1957. Paratype, 1 male (62.5 by 49.0 mm) (SM Cru Nr 1986.10), same data as holotype. 1 male (85.1 by 61.8 mm) (SM Cru Nr 1986.3), Borneo, Sarawak: Bidi Caves, Bau district, ca. 1°23′N, 110°06′E, coll. C. J. Brooks, Jun 1903. 1 male (71.0 by 53.1 mm), 1 female (58.2 by 42.9 mm) (NHM 1911.2.3.1–2), Borneo: Bidi, Upper Sarawak, coll. C. J. Brooks. 1 male (71.0 by 53.1 mm), 1 female (58.2 by 42.9 mm) (NHM 1911.2.3.1–2), Bidi, upper Sarawak, presented by C. J. Brooks. 1 male (ZRC 1997.782), Borneo, Sarawak: Serian, Gua Sireh, coll. Charles Leh & Mahmuad, Oct 1982.

Diagnosis.—Carapace high, but dorsal surfaces flat, surfaces rugose, epigastric and postorbital cristae low but visible, anterolateral margins very convex, distinctly serrated, epibranchial tooth very small, external orbital angle broadly triangular, margin straight or slightly convex, serrated. Dactylus of last ambulatory leg long. G1 long, slender, sinuous, terminal segment sinuous, tip slightly dilated on outer margin of distal part.

Remarks.—Bott (1968, 1970b) referred several specimens from the Bau district of Sarawak to *I. mahakkamense*, a species originally described from a single large female from the upper stretches of the Mahakkam river, a locality which is 340 km from Bau. Ng (1987), however, showed that two separate taxa were involved, and established a new species, *I. bauensis*, for the Sarawakian specimens.

The locality of the holotype should be Serian (not Senian). This is a small town east of Bau and Kuching. Bau (locality of the paratype) is to the west of Kuching. The specific name should be "bauense" as the genus *Isolapotamon* is neuter. The details of its taxonomy can be found in Ng (1987). *Isolapotamon bauense* is probably the largest known potamid, indeed the largest known freshwater crab, from Southeast Asia, with the largest specimen measuring 85.1 by 61.8 mm (SM Cru Nr 1986.3).

The form and ornamentation on the carapace of *I. bauense* appears to vary somewhat. A heterosexual pair of specimens of *I. bauense* from Bidi (NHM 1911.2.3.1–2) closely resemble *I. mahakkamense* superficially, especially with regards to the finely granulated dorsal surface of the carapace (rugose in the types of *I. bauense*). The G1 of the male specimen, however, is identical to that of the holotype of *I. bauense*. In addition, we have discerned three additional non-sexual differences which can serve to separate *I. bauense* from *I. mahakkamense*. Firstly, in *I. bauense*, the distal part of the third maxilliped exopod tapers gradually, giving it a subcylindrical appearance, whilst in *I. mahakkamense*, however, it tapers sharply, with the structure appearing distinctly acute. Secondly, the frontal margin of *I. bauense* is also entire, whereas in *I.*

Fig. 2. *Isolapotamon borneense*, new species. Holotype male (32.0 by 23.6 mm) (ZRC 1984.7042).

mahakkamense, the median lobes are separated from the lateral lobes by a distinct notch. Thirdly, the median lobe of the posterior margin of the epistome in *I. bauense* is evenly triangular in shape with the lateral margins almost straight, whereas in *I. mahakkamense*, the lateral margins are concave, with the distal part and tip appearing elongate.

Isolapotamon beeliae Ng, 1986
Fig. 1I–L

Isolapotamon beeliae Ng, 1986:219, figs. 3, 4.

Material examined.—Holotype, male (61.0 by 44.9 mm) (MZB Cru Nr. 464), Borneo, Kalimantan: Alai R. Datar, Barabai, Meratus Mountains, 2°36′44″S, 115°22′02″E, coll. M. A. Rifai, 22 Oct 1972.

Diagnosis.—Carapace tranverse, postorbital cristae straight, parallel with the frontal margin. Dactylus of last ambulatory leg long. G1 terminal segment sinuous, slightly shorter than subterminal, with short but distinct subterminal process.

Remarks.—Ng (1986) described this species on the basis of a single large male from Barabai in southern Kalimantan, but the G1 of *I. beeliae* is very distinct and hence easily separated from all known congeners. The details of its taxonomy and affinities with other *Isolapotamon* have been discussed in detail by Ng (1986).

Isolapotamon borneense, new species
Figs. 1M–P, 2

Material examined.—Holotype, male (32.0 by 23.6 mm) (ZRC 1984.7042), Borneo, probably Sarawak, no other data.

Diagnosis.—Carapace wider than long, postorbital cristae subparallel with frontal margin. Dactylus of last ambulatory leg long. G1 terminal segment gently sinuous, subequal to subterminal segment, with "chicken head-like" structure.

Description.—Carapace wider than long, surface flat, smooth with numerous small pits; anterolateral margins convex, gradually merging with posterolateral margins; posterolateral margins straight, converging towards posterior margin, posterior margin straight; gastric, branchial, intestinal regions slightly inflated, epigastric groove distinct, cervical groove prominent, H-shape depression strong; epigastric region sparsely granulated, epigastric cristae distinct, slightly in front of postorbital cristae, subparallel to frontal margin, epigastric lobes trapezoidal; postorbital cristae prominent, subparallel to frontal margin, not confluent with epigastric cristae, confluent with epibranchial teeth base; frontal margin raised, forming cristae anteriorly, sinuous, about 0.3 of carapace width, forming four lobes, each median lobe about 1.5 times wider than a lateral lobe; outer orbital angle broad. Anterolateral margin evenly carinate, striated, distinct epibranchial incision. Eyes well developed; supra- and infraorbital cristae prominent, granulated; suborbital regions sparsely granulated. Pterygostomial region striated. Median frontal triangle absent.

Third maxillipeds covering entire oral field, except efferent opening; ischium with longitudinal median groove; exopod with well developed flagellum.

Chelipeds unequal, merus ventral surface with two distinct cristae, anterior cristae distinctly granulated, posterior cristae less granulated; frontal surface of cheliped with numerous pits, inner surface of palm smooth, about 5–6 low ridges on lower part of pollex, finger with 5–6 shallow grooves.

Ambulatory legs normal, merus without subterminal spine, second pair longest, dactylus of last pair long.

Holotype male abdomen triangular and elongate, widest at third segment, narrows gradually towards telson.

G1 gently sinuous, terminal segment about equal to subterminal segment; terminal segment tip enlarged, shaped like a "chicken head." G2 sinuous, bent at two points, one at joint between subterminal and terminal segment, the other at proximal one-third of terminal segment, tip pointed. Terminal segment slightly shorter than subterminal segment.

Remarks.—The exact locality where the holotype and only known specimen of this species was collected is uncertain. It was found in a sealed bottle, without any data, with specimens of *Stygothelphusa bidiense* (Lanchester, 1900), a gecarcinucid species known only from the Bau area in western Sarawak. It is possible that the specimen was obtained from or near that site (see Ng 1989a). *Isolapotamon bauense* Ng, 1987, also described from the Bau area, has a very different carapace physiognomy and G1 structure compared to *I. borneense*.

The provenance of the present specimen poses some problems as it is not known from which part of Borneo it was obtained. Considering that prior to the mid-1980s, all the ZRC material from Borneo came from either Sarawak or Sabah, it seems likely that the present specimen of *I. borneense* is from either of these two states. As all the specimens in ZRC from Sabah have been reported in the literature (with no species fitting description of *I. borneense*), there is a good chance that the type specimen was in fact obtained from somewhere in Sarawak.

The G1 of the *I. borneense* is very distinctive and quite unlike any *Isolapotamon* species described thus far. The "chicken head-like" distal part of the terminal segment bears some similarity to that of *I. griswoldi*, *I. kinabaluense* and *I. anomalum*, but *I. borneense* can easily be separated by its terminal segment being very sinuous (only slightly sinuous in *I. griswoldi* and almost straight in *I. kinablauense* and *I. anomalum*). The long dactylus of the last ambulatory leg of *I. borneense* also distinguishes it from *I. griswoldi*.

Etymology.—Named after the island of Borneo.

Isolapotamon collinsi Holthuis, 1979
Fig. 5A–D

Isolapotamon collinsi Holthuis, 1979:21, pl. 4, fig 4.

Isolapotamon collinsi.—Holthuis, 1986: 593; Ng, 1987:147, fig. 3F; Guinot, 1988: 13.

Material examined.—Holotype, male (56.0 by 40.0 mm) (NNM), Borneo, Sarawak: Gunong Mulu National Park, Hidden Valley, Sinkhole of Clearwater River next to camp 6, coll. P. Chapman, 27 Mar 1978. Paratype, male (50.0 by 35.0 mm) (NNM), same data as holotype. Others—2 females (ZRC 1997.795), Borneo, Brunei: tributary of Sg. Temburong, near plot 2, East Ridge, at night, coll. I. Das, 23 Apr 1992. 2 females, 2 juveniles (ZRC 1997.794), Borneo, Brunei: Belalong, Sg. Engkabang, coll. S. Choy, 8 Feb 1991. 1 male, 3 juveniles (ZRC 1997.793), Borneo, Brunei: Temburong, Sg. Belalong at Kuala Belalong, coll. K. Lim et al., 14–17 Jun 1995. 1 male (NHM 1928.12.1.84), Borneo, Sarawak: Kuching, Stebbing Collection, coll. C. Hose.

Diagnosis.—Carapace flat, surfaces rugose, especially on anterolateral, posterolateral and gastric regions; epibranchial tooth low but distinct, with distinct notch separating it from external orbital angle; anterolateral margins gently serrated, external orbital angle broadly triangular. Surfaces of chelipeds and ambulatory legs rugose. Dactylus of last ambulatory leg long. G1 sinuous, terminal segment sinuous, tip bifurcated, subdistal process subequal or slightly longer than distal process.

Remarks.—The structure of the G1 of *I. collinsi* allies it with species like *I. griswoldi*, *I. grusophallus* and *I. nimboni*. The taxonomy and biology of this species has been well documented by Holthuis (1979). It was described from from two specimens, but we have examined some specimens from Brunei and Sarawak which agree with the types well. The G1s of the specimens have a thicker thumb-like projection and are gently curved outwards than that figured in Holthuis (1979). The distal projection of the terminal segment is also slightly thicker when compared to that figured by Holthuis (1979). However, the angle produced between the tip and the thumb-like projection is more than right angles. This character can be used to easily distinguish *I. collinsi* from *I. nimboni* (see remarks under *I. nimboni*). A specimen collected from Kuching (NHM 1928.12.1.84) was incorrectly identified as *I. mahakkamense*. The G1 of this specimen is very similar to that illustrated by Holthuis (1979) and there is no doubt that it is conspecific with *I. collinsi*.

With regards to its habits, Ng (1987) commented that in all likelihood, *I. collinsi* is a troglophile like *I. bauense*. All the Bruneian specimens of *I. collinsi* were collected from fast flowing streams not associated with caves.

One specimen (NHM 1928.12.1.84) is noteworthy as it was supposedly obtained from Kuching. The present study has shown that all *Isolapotamon* specimens examined thus far from Kuching and western Borneo are either *I. consobrinum* or *I. bauense*, with *I. collinsi* found only in northeastern Sarawak and Brunei. The NHM specimen is, however, clearly conspecific with *I. collinsi*. There is another specimen (NHM 1928.12.1.83) from the same lot as this one and it is *I. consobrinum*, which is known from the Kuching area. We therefore suspect that the locality data for the specimen of *I. collinsi* is incorrect, and it was actually collected much further north. In the earlier part of this century, many specimens from Sarawak were simply labelled as being from the main city, Kuching, even though they had been collected further afield (see Ng 1989b).

Isolapotamon consobrinum
(De Man, 1899)
Figs. 3, 5E–H

?*Telphusa sinuatifron*.—Miers, 1880:305 (not *Potamon sinuatifrons* H. Milne Edwards, 1853).

Potamon (*Potamon*) *consobrinus* De Man,

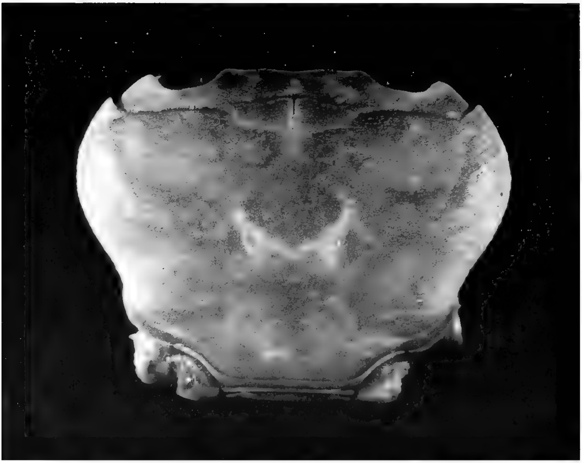

Fig. 3. *Isolapotamon consobrinum*. Lectotype male (45.0 by 33.0 mm) (NNM Cru Nr. 1299).

1899: 99 (part), pl. 9 fig. 10b, f, pl. 10 fig. 10.

Potamon (*Potamon*) *mahakkamense*.—Nobili, 1903b:14 (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Potamon (*Potamon*) *mahakkamense*.—Rathbun, 1904:268 (part) (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Potamon (*Potamon*) *consobrinus*.—Rathbun, 1904:269 (part).

Potamon (*Potamon*) *consobrinus*.—Yang, 1979:17.

Isolapotamon (*Isolapotamon*) *consobrinum*.—Bott, 1968:121, fig. 4a, b.

Isolapotamon consobrinus.—Bott, 1970b: 194, pl. 41 fig. 82, pl. 56 fig. 83.

Potamon (*Potamon*) *consobrinum*.—Leh, 1982:4.

Potamon (*Potamon*) *mahakkamense*.—Leh, 1982:4 (part) (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Isolapotamon consobrinum.—Ng, 1987: 140, fig. 1, pls. 4, 5.

Material examined.—Lectotype, male (45.0 by 33.0 mm) (NNM Cru Nr. 1299); Borneo, Kalimantan: Mount Damoes, Sambas, coll. Hallier, Oct 1893. Others—1 female (NHM 1928.12.1.83), Borneo, Sarawak: Kuching, Stebbing Collection, coll. C. Hose. 1 male (NHM 1928.12.1.82), Borneo, Sarawak: Kuching, Stebbing Collection. 1 female (NHM 1880:6), West Borneo, coll. E. Gerrard; 1 female (MZB Cru No. 1986.1257), Borneo, Kalimantan: S. Nagadan, Sanggauledo, Sinkawang, Kal. Sambas, ca. 0°30′N, 109°45′E, coll. F. Sabar & D. Harjono, 8 Sep 1981. 2 females (larger 40.0 by 31.5 mm), 3 males (largest 49.5 by 37.0 mm) (SM Cru Nr. 1986.139–143), Borneo, Sarawak: Simunjan, Upper Simunjan River, 10th Mile Rock Road, foot of Klingkang, ca. 1°22′N, 110°44′E, coll. Loong Tak, Jun 1901. 7 males, 6 females, 4 juveniles (SM Cru Nr 1986.122–138), Borneo, Sarawak: Gunong Matang (present Gunong Serapi), 1°33′16″N, 110°12′51″E, ca. 1000 m asl, Mar 1901. 2 females (ZRC 1997.789), Borneo, Sarawak: just outside Fairy Caves (Gua Kapo), 6.8 km from junction of road to Wind Cave and main road, 1°22′55.9″N, 110°7′4.7″E, coll. H. H. Tan & D. C. J. Yeo, 7 Sep 1995. 1 male, 1 female, 1 juvenile (ZRC 1997.801), Borneo, Sarawak: Sg. Kuhas tributary (feeder stream), 0.5 km towards Kg. Lanchang, 6.9 km left at Tebelu Tebakang turnoff, 5.8 km into right trail, 1°9′23.1″N, 110°29′29.9″E, coll. P. K. L. Ng et al., 31 Aug 1996. 3 males, 2 females (ZRC 1984.7037–7041), Borneo, Sarawak: Sadong River, ca. 1°55′N, 113°08′E, coll. Loong Tak, Jan 1901. 3 males, 3 females, 1 juveniles (ZRC 1997.791), Borneo, Sarawak: Sg. Isu, km 20 on road to Simunjan, after branching from Kuching-Sri Aman Road, M. Kottelat, 11 May 1994. 1 male, 1 female, 3 juveniles (ZRC 1997.787), Borneo, Sarawak: Sg. Semabang, ca. km 22 on road to Simunjan, after it branches from road Kuching-Sri Aman, 1°12′52.0″N, 110°55′38.7″E, M. Kottelat, 11 May 1994. 3 males, 1 female (ZRC 1997.790), Borneo, Sarawak: Sg. Kuhas, 1°9′10.0″N, 110°29′22.7″E, P. K. L. Ng et al., 14 Jan 1996.

Diagnosis.—Carapace appearing squarish to wider than long, dorsal surfaces flat, regions slightly rough but not strongly rugose; anterolateral margins convex; epibranchial tooth very prominent, sharp, separated from external orbital angle by distinct V-shaped cleft; external orbital angle triangular, tip level with frontal margin. Ischial sulcus on third maxilliped shallow. Dactylus of last ambulatory leg short. G1 straight or slightly sinuous, terminal segment straight, tip dilated to form rounded flap.

Remarks.—The taxonomic problems, infraspecific variation and general biology of this species have already been discussed in detail by Ng (1987), who argued that the type series (a male and a female from two different localities) of De Man (1899) was heterogeneous, and designated the male as the lectotype.

The third maxilliped exopod of *I. consobrinum* is the most narrow of the known *Isolapotamon* species and the outer margin is also less convex. The ischial groove on the third maxilliped is also very shallow. Whether these characters (and perhaps the G1 as well) justify separating *I. consobrinum* out into a separate genus remains to be evaluated.

Other than recent material from Sarawak which expands its distribution in western Sarawak, there are no new observations to add to Ng's (1987) comments of this species.

Isolapotamon doriae (Nobili, 1900)
Figs. 5I–L, 4

Potamon (*Potamon*) *doriae* Nobili, 1900: 501.

Potamon sp.—Shelford, 1916:265.

Potamon (*Potamon*) *doriae*.—Rathbun, 1904:268.

Isolapotamon mahakkamense.—Bott, 1970b:193 (part) (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Potamon (*Potamon*) *mahakkamense*.—Leh, 1982:4 (part) (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Isolapotamon doriae.—Ng, 1987:143, fig. 2A–G, pl. 6.

Isolapotamon sp.—Ng, 1987:148, fig. 3I–K.

Material examined.—Holotype, male (55.0 by 42.0 mm) (MGE III 228), Sarawak, coll. G. Doria & O. Beccari, between 1865 and 1868. Others—2 males, 3 females, 5 juveniles (SM Cru Nr. 1986.102–111), Penrissen Mountains, Sarawak, 1°16′20″N, 110°08′10″E, coll. R. Shelford, May 1899. 1 male (SM Cru. Nr. 1986.112), Penrissen Mountains, Sarawak, 1°16′20″N, 110°08′10″E, ca. 1000 m, coll. R. Shelford, May 1899.

Diagnosis.—Carapace dorsal surfaces slightly convex, distinctly rugose on lateral regions; anterolateral margins convex, appearing serrated due to strong oblique striae; epibranchial tooth sharp, distinct; outer margin of external orbital

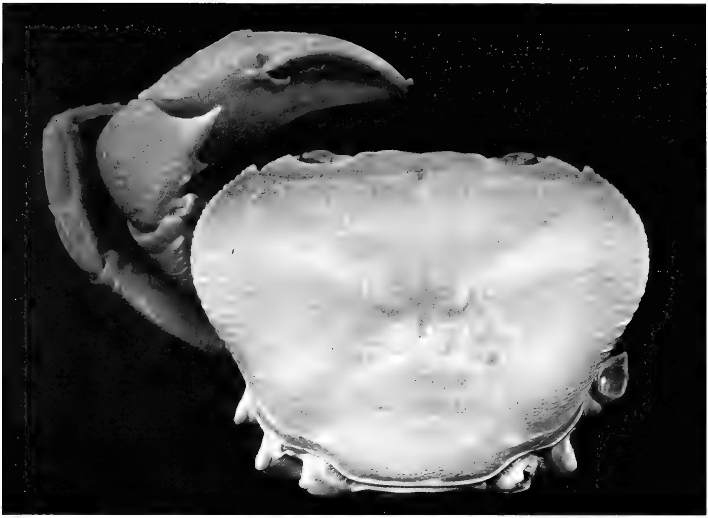

Fig. 4. *Isolapotamon doriae.* Holotype male (55.0 by 42.0 mm) (MGE III 228.9).

angle convex. Dactylus of last ambulatory leg long. G1 very long, gently sinuous, terminal segment sinuous, tip slightly dilated, rounded.

Remarks.—Ng (1987) resurrected the poorly known *I. doriae* after comparing the type material with specimens from the Penrissen Mountains in the Sarawak Museum. Although the G1 terminal segment of this species is quite similar to that of *I. consobrinum*, the external features are so different that there is no doubt that two separate species are involved. Details of the taxonomy of this species can be found in Ng (1987).

Ng (1987), on examining a young specimen of *Isolapotamon* from the Penrissen Mountains collected with the material of *I. doriae*, could not refer it to any known species from Sarawak at that time. We have reexamined the juvenile specimens and now believe that they are conspecific with *I. doriae*. Slight differences observed in the shape of the G1 are probably due to intraspecific variation.

Isolapotamon griswoldi (Chace, 1938)
Fig. 5M–P

Potamon (*Thelphusa*) *consobrinum.*—Borradaile, 1900:94 (not *Potamon consobrinum* De Man, 1899).

Potamon griswoldi Chace, 1938:9.

Potamon (*Potamon*) *griswoldi.*—Yang, 1979:17.

Isolapotamon (*Isolapotamon*) *griswoldi.*—Bott, 1968:120, fig. 2.

Isolapotamon griswoldi.—Bott, 1970b:192, pl. 41 fig. 78, pl. 56 fig. 78.

Material examined.—Paratypes, 3 males (ZRC 1965.12.7.1, ZRC 1990.463–464), Borneo, Sabah: Mt. Kinabalu, Bundutan, Luidan River coll. J. A. Griswold Jr., 1 Jul 1937. Others—3 males, 3 females, 2 juveniles (ZRC 1984.7050–7057), 6 males, 3 female, 3 juveniles (ZRC 1984.7668–

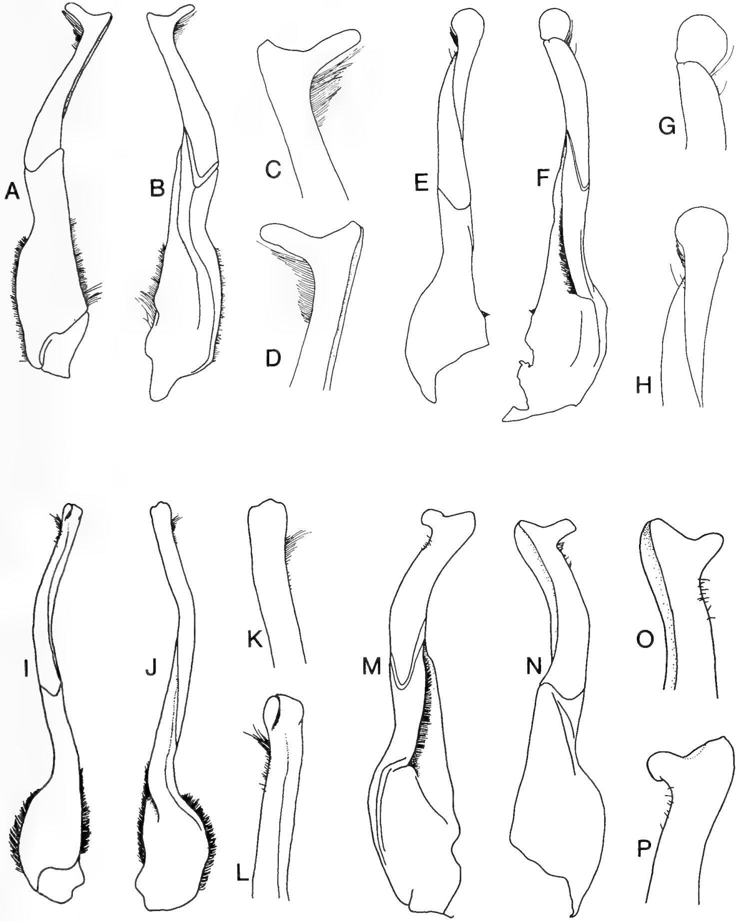

Fig. 5. G1s. A–D: *I. collinsi*, male (ZRC 1997.792); E–H: *I. consobrinum*, lectotype male (NNM Cru. Nr. 1299); I–L: *I. doriae*, holotype male (MGE III 228); M–P: *I. griswoldi*, male (ZRC 984.7050). A, E, I, M: dorsal view; B, F, J, N: ventral view; C, G, K, O: dorsal view, tip of terminal segment; D, H, L, P: ventral view, tip of terminal segment.

7679), 1 male, 1 female (MZB Cru No. 1144), Borneo, Sabah: Mt. Kinabalu, Kadamaian (Kadamayan) River, ca. 6°22′N, 116°26′E, coll. R. Hanitsch, 1900. 1 male (immature), 2 females (CMZ Reg. Nr. 11.1.00), Borneo, Sabah: Mt. Kinabalu, Kadamaian River, ca. 6°22′N, 116°26′E, ca. 630 m asl, coll. R. Hanitsch, 26 Mar 1899. 2 juveniles (ZRC 1997.783), Borneo, Sabah: Kinabalu National Park, Sg. Silan-Silan, near headquarters, under rocks, P. K. L. Ng, 26 Dec 1992.

Diagnosis.—Carapace slightly convex, surfaces slightly rugose; epibranchial tooth distinct, sharp; external orbital angle triangular, outer margin convex. Dactylus of last ambulatory leg short. G1 gently sinuous, terminal segment bifurcated, subequal in length to subterminal segment, distal part bifurcated, subdistal process subequal to distal process.

Remarks.—*Isolapotamon griswoldi* was described by Chace (1938) from several hundred specimens collected by J. A. Griswold Jr. in 1937 from Mt. Kinabalu in Sabah. The species is easily characterised by its G1 terminal segment which resembles a horse's head. The subdistal process is stout, the tip sloping, and the distal process is very stout and rounded. The propodus of the last pair of ambulatory legs is also very broad and the dactylus short.

Chace (1938) in describing *I. griswoldi* suggested that specimens identified as "*Potamon consobrinum*" by Borradaile (1900) may in fact be conspecific with his species. Hanitsch (1900) recorded these specimens as being present in the then Raffles Museum, but they were probably given to the CMZ where Borradaile was based. The first author has examined Borradaile's specimens of "*Potamon consobrinum*" in the CMZ and Chace's suspicions are verified. Although the male is still very young (its G1 is poorly developed) the other morphological features of all three specimens are identical to *I. griswoldi*.

Isolapotamon griswoldi is one of the three species of *Isolapotamon* found in and around the vicinity of Mount Kinabalu, the highest mountain in Borneo; the other two being *I. anomalum* and *I. kinabaluense*.

Isolapotamon grusophallus
Ng & Yang, 1986
Fig. 6A–D

Potamon (*Potamon*) *sinuatifrons.*—Yang, 1979:18 (not *Thelphusa sinuatifrons* H. Milne Edwards, 1853).

Isolapotamon grusophallus Ng & Yang, 1986:15, fig. 1.

Isolapotamon grusophallus.—Ng, 1987: 147, fig. 3G–H, pl. 10.

Material examined.—Holotype, 1 male (42.5 by 31.0 mm) (ZRC 1984.7044), Sarawak, coll. native collector, 1902.—Paratypes—2 females (larger 71.0 by 53.9 mm) (ZRC 1984.7045–7046), 1 female (SM), same data as holotype.

Diagnosis.—Carapace smooth to slightly rugose, lateral regions rugose; anterolateral margins distinctly convex, serrated; epibranchial tooth small, barely separated from triangular external orbital angle. Dactylus of last ambulatory leg long. G1 sinuous, terminal segment sinuous, tip bifurcated, subdistal process long, twice length of distal process.

Remarks.—*Isolapotamon grusophallus* is closest to *I. collinsi*. It is unfortunate that the exact locality where *I. grusophallus* was collected is not known, the only data on the label being somewhere in Sarawak. The details of its taxonomy can be found in Ng & Yang (1986) and Ng (1987).

Isolapotamon ingeri, new species
Figs. 6E–H, 7

Isolapotamon sp.—Ng & Goh, 1987:328, pl. 3, D.

Material examined.—Holotype, male (44.3 by 33.3 mm) (ZRC 1997.796), Borneo, Sabah: Tawau, Tawau Hills Park, Sg. Tawau, coll. Paul Yam, 14 Dec 1991. Paratypes—1 female, (41.4 by 31.0 mm) (ZRC 1997.797), same data as holotype. Others—

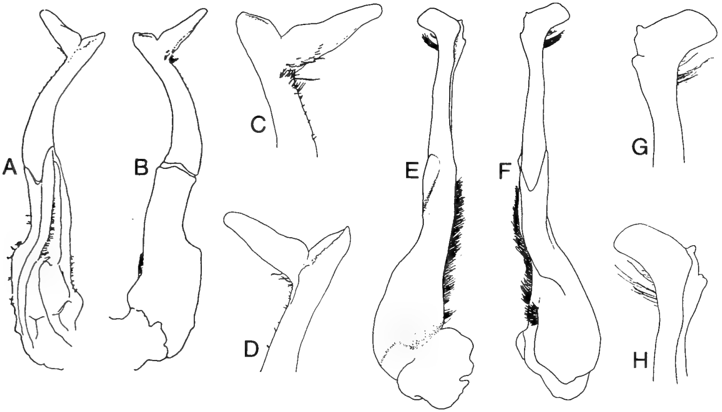

Fig. 6. G1s. A–D: *I. grusophallus*, holotype male (ZRC 1984.7044) (after Ng, 1986); E–H: *I. ingeri*, holotype male (ZRC 1997.796). A, E: dorsal view; B, F: ventral view; C, G: dorsal view, tip of terminal segment; D, H: ventral view, tip of terminal segment.

Fig. 7. *Isolapotamon ingeri*, new species. Holotype male (44.3 by 33.3 mm) (ZRC 1997.796).

1 male (57.4 by 44.8 mm) (ZRC 1997.798), Borneo, Sabah: Lahad Datu, Sg. Palum Tambum, near Danum Valley Field Centre, coll. K. Martin-Smith, Aug 1996. 1 female (ZRC 1989.3419), Borneo, Sabah: Lahad Datu, Madai Caves, Sg. Madai, coll. 27 Jan 1985. 5 males, 1 female (ZRC 1997.799), Borneo, Sabah: near Danum Valley Field Centre, Tambun, Sg. Palum, coll. K. M. Martin-Smith, 9 Oct 1996. 1 male (ZRC 1997.802), Borneo, Sabah: Tawau, Jalan Madai, Gua Madai, Sg. Matarid, 4°43′8.7″N, 118°9′14.7″E, H. H. Tan et al., 6 Oct 1996.

Diagnosis.—Carapace wider than long, relatively smooth; anterolateral margins convex, carinate; epibranchial tooth distinct; external orbital angle acute. Dactylus of last ambulatory leg short. G1 relatively straight, terminal segment subequal to subterminal segment, tip enlarged and flattened, forming rectangular structure.

Description.—Carapace wider than long, surface flat, relatively smooth with numerous small pits; anterolateral margins convex, gradually merging with posterolateral margins; posterolateral margins straight, converging towards posterior margin, posterior margin straight; branchial regions slightly inflated, epigastric groove shallow to indistinct, cervical groove shallow, H-shape depression distinct; epigastric region lightly granulated, epigastric cristae distinct, subparallel to frontal margin, epigastric lobes rectangular, in front of postorbital cristae; postorbital cristae prominent, relatively parallel to frontal margin, not confluent with epigastric cristae or base of epibranchial teeth; frontal margin raised, forming a cristae anteriorly, sinuous, about one-quarter of carapace width, forming four lobes, with two median lobes being wider than lateral lobes; outer orbital angle acute. Anterolateral margin evenly carinate, striated with distinct epibranchial incision. Eyes well developed; supra- and infraorbital cristae prominent, granulated; suborbital regions granulated. Pterygostomial region smooth. Median frontal triangle absent.

Third maxillipeds cover entire oral field, except efferent opening; ischium with longitudinal median groove; exopod with well developed flagellum.

Chelipeds unequal, ventral surface of merus with two distinct cristae, anterior cristae distinctly granulated, posterior cristae less granulated; frontal surface of cheliped with numerous low ridges on lower part, arranged obliquely. Finger of cheliped with shallow grooves.

Ambulatory legs normal, merus without subterminal spine, second pair longest, dactylus of last pair relatively short.

Male abdomen triangular and elongate, widest at third segment, narrows gradually towards telson.

G1 relatively straight, terminal segment subequal to the subterminal segment; tip of terminal segment flattened, forming a rectangular structure. G2 relatively straight, bent at a slight angle at proximal one quarter of terminal segment, tip pointed. Terminal segment slightly shorter than subterminal segment.

Remarks.—Ng & Goh (1987) reported an unidentified *Isolapotamon* from Madai caves in Lahad Datu. We have compared this specimen with the type series of *I. ingeri* and they agree very well in all external asexual characters. *Isolapotamon ingeri* appears to be restricted to the northeastern part of Borneo, being found from Tawau Hills Park, Madai Caves, Danum Valley Conservation Area and Lower Segama River. All these localities are in Sabah.

The shape of the G1 of *I. ingeri* affiliates it with *I. kinabaluense* and *I. anomalum.* It can be differentiated from *I. kinabaluense* by having the distal part of the terminal segment rectangular in shape (vs. "club-like") and subterminal segment without a distinct notch at the proximal end (vs. notch present). *Isolapotamon ingeri* can be differentiated from *I. anomalum* by having the distal side of the G1 tip shorter than the proximal side (vs. distal side longer than proximal side).

Etymology.—We take great pleasure in

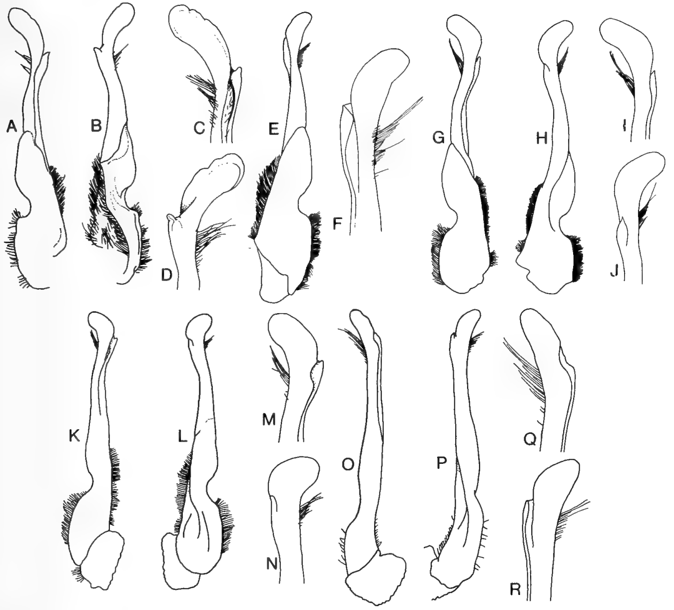

Fig. 8. G1s. of *Isolapotamon kinabaluense* showing variation. A–D: male (41.1 by 30.6 mm) (ZRC 1990.450, Sabah); E–F: same specimen as previous, right G1; G–J: male (40.1 by 30.2 mm) (MCZ 10066, Sabah: Mt. Kinabalu, Kadamayan river); K–N: male (28.0 by 21.0 mm) (ZRC 1997.786, Sabah: Keningau, Sg. Kouran); O–R: male (24.8 by 19.0 mm) (ZRC 1990.449, Sabah: Kota Marud district, Marak Parak, Sg. Surinsin). A, G, K, O: left G1, dorsal view; B, H, L, P: left G1, ventral view; C, I, M, Q: tip of left G1 terminal segment, dorsal view; D, J, N, R: tip of left G1 terminal segment, ventral view; E: right G1, dorsal view; F: tip of right G1 terminal segment, ventral view.

naming this crab after an old friend, Robert F. Inger for helping us collect so many interesting Bornean freshwater crabs over the years.

Isolapotamon kinabaluense (Rathbun, 1904)

Fig. 8

Potamon (*Potamon*) *kinabaluensis* Rathbun, 1904:269, fig. 9, pl. 10 fig. 2.

Potamon kinabaluensis.—Chace, 1938:13, fig. 2.

Potamon (*Potamon*) *kinabaluensis.*—Yang, 1979:17.

Isolapotamon (*Isolapotamon*) *kinabaluensis.*—Bott, 1968:120, fig. 3.

Isolapotamon kinabaluensis.—Bott, 1970b: 193, pl. 41 fig. 80, pl. 56 fig. 80.

Material examined.—Syntype, 1 female (USNM 29990), Borneo, Sabah: Kinabalu, coll. Whitehead. Others—1 male, 1 female (USNM 75900), Borneo, Sabah: Mt. Kinabalu, Bundutan, coll. Asiatic Primate Expedition, 15 Jul 1937. 1 male (42.2 by 31.6 mm) (MCZ 10065), Borneo, Sabah: Mt. Kinabalu, Bundutuan, Luidan River (G1 figured by Chace 1938), coll. J. A. Griswold Asiatic Primate Expedition, 15 Jul 1937. 1 male (24.2 by 18.8 mm), 1 female (MCZ 10065), Borneo, Sabah: Mt. Kinabalu, Bundutuan, Luidan River, coll. J. A. Griswold, Asiatic Primate Expedition, 15 Jul 1937. 7 male (MCZ 10065), Borneo, Sabah: Mt. Kinabalu, Bundutuan, Luidan River, coll. J. A. Griswold Asiatic Primate Expedition, 15 Jul 1937. 1 male (39.7 by 30.1 mm) (MCZ 10066), Borneo, Sabah: Mt. Kinabalu, Kadamaian (Kadamayan River), ca. 6°22′N, 116°26′E, coll. J. A. Griswold Asiatic Primate Expedition, Nov 1937. 1 male (41.0 by 30.9 mm), 2 female (ZRC 1990.450–452), Borneo, Sabah: Sg. Kindingan, Marak, Parak, Kota Marudu District, ca. 6°17′N, 116°43′E, coll. R. B. Stuebing, 11 Nov 1988. 1 male (25.0 by 19.0 mm) (ZRC 1990.449), Borneo, Sabah: Kota Marudu, Marak Parak, Sg. Sorinsim, rapids, rock bottom, ca. 6°17′N, 116°43′E, coll. R. F. Inger & F. L. Tan, 9 Nov 1988. 1 male (16.5 by 13.1 mm), 1 juvenile (ZRC 1990.453–454), Borneo, Sabah: Tenom, Melalap, Sg. Malutut, 14.5 km north of Tenom, ca. 5°13′N, 115°58′E, coll. R. F. Inger & F. L. Tan, 20 Nov 1988. 1 female (ZRC 1990.455), Borneo, Sabah: Tenom, Crocker Range, Melalap, Sg. Malutut, in tire rut of temporary road, 300 m asl, ca. 5°13′N, 115°58′E, coll. R. B. Stuebing, 1 Dec 1988. 1 female (ZRC 1990.456), Borneo, Sabah: Kota Marudu, Marak Parak, Sg. Tahobang, tributary of Sg. Sorinsim, coll. UKM Sabah, 1988; 1 male (ZRC 1997. 786), Borneo, Sabah: Sg. Kouran, coll. 30 Jan 1991. 4 males, 1 female, 13 juveniles (ZRC 1997.800), Borneo, Sabah: Keningau, Sg. Kouran, coll. 31 Jan 1991. 1 female (42.0 by 33.1 mm) (ZRC 1965.12.7.12), Borneo, Sabah: Bundutan (Bundu Tuhan), Luidan River, ca. 5°58′N, 116°32′E, coll. J. A. Griswold Jr., 15 Jul 1937. 1 male, 1 female (ZRC 1990.465–466), Borneo, Sabah: Bundutan, Luidan River, coll. J. A. Griswold Jr., 15 Jul 1937

Diagnosis.—Carapace slightly convex; epibranchial tooth low but distinct, sharp; anterolateral margin gently serrate; external orbital angle triangular, tip level with frontal margin, outer margin straight. Dactylus of last ambulatory leg long. G1 almost straight, distal part of G1 terminal segment dilated to form "club-like" structure, tip tapering, outer margin of dilated part meeting inner margin at sharp angle, inner margin of distal part projects inwards to form distinct hump.

Remarks.—Rathbun (1904) described this species from three females collected by M. Whitehead in Mount Kinabalu. However, she did not designate any holotype. Since the identification of *Isolapotamon* species is highly dependent on the male G1, we felt that the designation of a lectotype in the present instance is unnecessary. In any case, the syntype female in the USNM agrees well with the other specimens of *I. kinabaluense* we have seen. Chace (1938), while studying the specimens collected by J. A. Griswold Jr. from the Mount Kinabalu area was the first to provide a figure and detailed redescription of this species, including the G1. The ZRC has a large female specimen from the Griswold collection donated by the MCZ in the days of the Raffles Museum (ZRC 1965.12.7.12). This female has the original number of MCZ No. 10065, and the label indicated that there was also a male specimen. The whereabouts of this male is not known. It was probably sent to Bott by the Raffles Museum (M. W. F. Tweedie, pers. comm.) and used by him in his studies (Bott 1968, 1970b). Bott (1970b) lists a male (SMF 2841) from exactly the same locality as the ZRC female, and he had probably retained the Raffles Museum specimen in the SMF. Through the kindness of Dr. A. Johnston, the ZRC has since obtained another pair of *I. kinabaluense* from the Griswold collection (ZRC 1990.465–466) from MCZ by exchange.

The G1 terminal segment of *I. kinabaluense* is quite characteristic. The terminal and subterminal segments are generally in a straight line, the entire G1 being only slightly sinuous. The distal part of the terminal segment is expanded into a broad flap which varies in shape slightly. The form of the flap is consistent for all the male specimens examined from Luidan River, the type locality; whereas those from the Kadamayan River (MCZ 10066) and Sungai Kindingan (ZRC 1990.450) have a slightly but distinctly different shape. The shapes of the flaps can vary considerably depending on the angle which they are viewed (care was taken to use the same angle of view in this study). The flaps of specimens from the Luidan River are broader; that from Sungai Kindingan the most slender; with the flap from the Kadamayan specimen being approximately intermediate (Fig. 8). The flap-like distal part of the terminal segment is actually an extension of the ventral fold, the dorsal fold ending at the base of the flap as a short, blunt projection, sometimes so low as to appear hump-like. The dorsal and ventral folds are connected by a stiff sloping membrane which extends from the base of the flap to the dorsal fold projection (or hump). This membrane is visible only from the dorsal view. The G2 distal segment protrudes from beneath this membrane, which is the distal part of the G2 groove. The dorsal projection appears as a sharp knob on the dorsal margin, just below the flap-like expansion at the distal part of the terminal segment in Bott's (1968) figure of the G1 of a male of *I. kinabaluense*. This knob is absent in Chace's (1938) specimen and figure, the projection being hump-like instead. All the G1s examined from the Luidan River specimens have a blunt, hump-like dorsal projection. Those from the Kindingan (Fig. 8A–D) and Kadamayan (Fig. 8G–J) rivers have more produced projections. A juvenile G1 is also figured (Fig. 8O–R) for comparison.

For the moment, considering the few specimens from the Kindingan and Kadamayan rivers, the differences noted in the form of the flap and dorsal fold projections with the Luidan River specimens are not regarded as significant supraspecifically. All other features of the G1, as well as the external characters in specimens from all three areas are constant.

There is also often a distinct small dorsal hump at the base of the terminal segment formed by the subterminal segment. This hump is pronounced in most specimens. *Isolapotamon anomalum* is not known to have this feature, whereas it varies somewhat for *I. griswoldi*. It is also present in *I. borneense*, and does not appear to be very useful as a taxonomic character.

The specific name of the species should be "kinabaluense", not "kinabaluensis", since the gender of the genus is neuter.

Isolapotamon mahakkamense
(De Man, 1899)
Fig. 9

Potamon (*Potamon*) *mahakkamense* De Man, 1899:92, pl. 12 fig. 8.

Potamon (*Potamon*) *mahakkamensis*.—Rathbun, 1904:268 (part).

Material examined.—Lectotype, female (61.0 by 45.0 mm) (NNM Cru Nr. 1300), Borneo: Kalimantan, Upper Mahakkam, Bloe-oe, coll. Nieuwenhuis.

Diagnosis.—Carapace surfaces very rugose, covered with numerous small granules, outer margin of external orbital angle slightly longer than inner margin, appearing almost smooth. Closed fingers of larger cheliped without wide gape. G1 not known.

Remarks.—This species is known only from one large female and has not been reported since the original description. Although the G1 of *I. mahakkamense*, is not known, it is nevertheless a distinctive species on the basis of its external morphology. Its highly granulated lateral regions and convex posterolateral margins gives the species a very distinctive appearance. The species closest to *I. mahakkamense* is *I. bauense*. Specimens identified as this species by Bott (1968, 1970b) were referred to *I. bauense* by Ng (1987). See remarks under *I. bauense* for a detailed discussion.

De Man (1899) in his description of this species did not designate a holotype but he

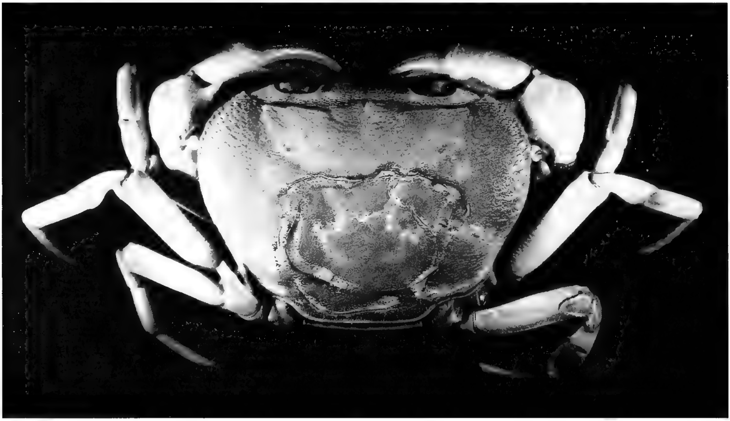

Fig. 9. *Isolapotamon mahakamense*. Lectotype female (61.0 by 45.0 mm), (NNM Cru Nr. 1300).

probably had only one specimen. The present specimen (NNM 1300) is hereby designated as the lectotype of this species.

Isolapotamon mindanaoense
(Rathbun, 1904)
Fig. 10A–D

Potamon (*Potamon*) *mindanaoensis* Rathbun, 1904:268, fig. 8, pl. 10 fig. 5.

Isolapotamon (*Isolapotamon*) *mindanaoense*.—Bott, 1968:121, fig. 5.

Isolapotamon mindanaoense.—Bott, 1970b:192, pl. 41 fig. 79, pl. 56 fig. 79.

Material examined.—Holotype, male (30.5 by 24.0 mm) (MNHN-B 5297), Philippines, Mindanao, coll. M. Montano. Others—5 males (largest 38.1 by 28.8 mm), 13 females (largest 41.9 by 31.3 mm), 3 juveniles (USMN 46985), Philippine Islands, coll. G. A. Mearne. 2 ex. (USNM 032110), Philippines, East Mindanao: Gulf of Davao, Tibuan River.

Diagnosis.—Carapace broader than long; anterolateral margin gently serrated; frontal margin sinous, median lobes slightly forward of lateral lobes; epibranchial regions striated; epigastric cristae forward of postorbital cristae; epibranchial tooth small, separated from external orbital angle by small notch. Chela dorsal surface rugose, smooth ventrally. Telson broader than long. G1 relatively straight, outer margin slightly sinuous, especially on terminal segment, distal part of terminal segment with broad and rounded obliquely directed process. G1 terminal segment tip flap-like, facing outwards.

Remarks.—This species from Mindanao, Philippines, was originally known only from one male type specimen (MNHN-B 5297) (30.5 by 24.5 mm). On a recent sabatical trip to the Smithsonian Museum of Natural History, the first author found a collection of *Isolapotamon* from the Philippines. Examination of the specimens reveals that the G1 and the shape of the abdomen also matches that of *I. mindanaonse* very closely. Unfortunately, the collection locality is stated as Philippines islands. It is therefore still not known whether *I. mindanaoense* extends to other parts of the Philippines.

Isolapotamon mindanaoense is closely related to *I. kinabaluense* especially with regards to the G1. The G1 of *I. kinabaluense* has a prominent flap on the inner side of the

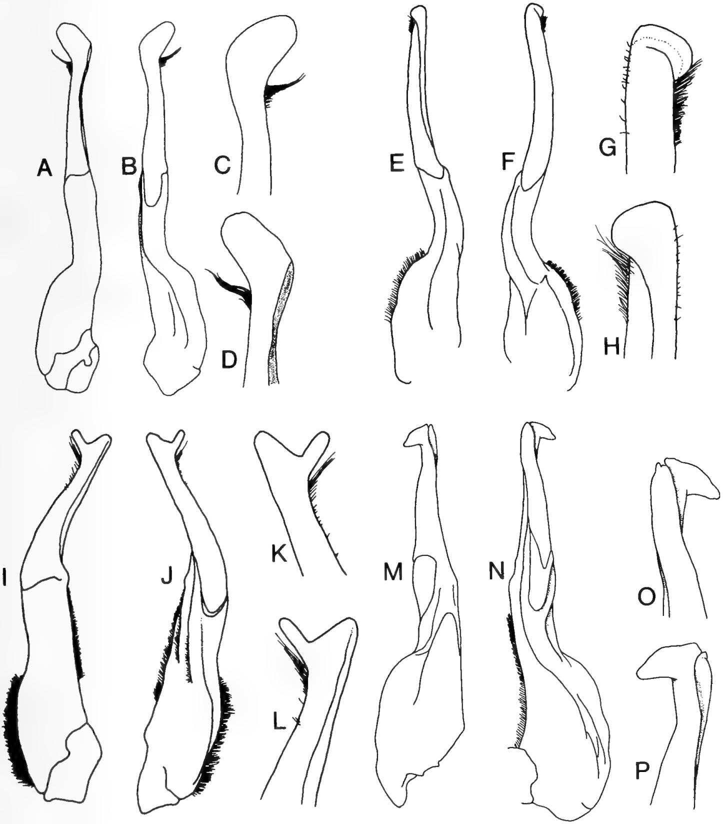

Fig. 10. G1s. A–D: *I. mindanoense*, holotype male (MNHN-B 5297); E–H: *I. naiadis*, holotype male (MZB Cru Nr. 466) (after Ng, 1986); I–L: *I. nimboni*, holotype male (SM Cru Nr 1986.11); M–P: *I. sinuatifrons*, lectotype male (MNHN BP-4353 S). A, E, I, M: dorsal view; B, F, J, N: ventral view; C, G, K, O: dorsal view, tip of terminal segment; D, H, L, P: ventral view, tip of terminal segment.

gonopod whereas the flap is located on the tip of the terminal segment in *I. mindanaoense*. The telson of *I. mindanaoense* is as broad as long. The telson of *I. kinabaluense* is longer than broad. The chela of *I. mindanaoense* possess low flat granules, but is the granules are prominant and distinct in *I. kinabaluense*. The ventral surface of the cheliped carpus is smooth in *I. mindanaoense*. In *I. kinabaluense*, the carpus is rugose.

Isolapotamon mindanaoense can be distinguished from *I. sinuatifrons* and *I. spatha* by the shape of the G1. The G1 terminal segment of *I. sinuatifrons* is twisted at right angles whereas it is not in *I. mindanaoense*.

The distal part of the G1 terminal segment is more pronounced and longer in *I. mindanaoense*. The distal part is less pronounced and shorter. The carapace of *I. mindanaoense* is more convex and higher, whereas the carapace is lower in *I. spatha*.

Isolapotamon naiadis Ng, 1986
Fig. 10E–H

Isolapotamon naiadis Ng, 1986:216, Figs. 1, 2.

Material examined.—Holotype, male (51.6 by 39.3 mm) (MZB Cru Nr. 466), Borneo, Kalimantan: Njapa Mountains, 1°51′26″ N, 117°17′58″ E. coll. S. S. Liem, 27 Oct 1963. Others—2 males (ZRC 1997.785), Borneo, Kalimantan: Bekeleau, Sg. Magang (Setakak), 3°20′29″N, 116° 59′12.5″E, coll. R. Diesel, 6 Sep 1995.

Diagnosis.—Carapace wider than long, flat, surfaces glabrous, postorbital cristae sloping distinctly backwards. Dactylus of last ambulatory leg long. G1 terminal segment long, not distinctly sinuous, tip rounded, slightly dilated.

Remarks.—This species was previously known from only one large specimen. Comparison of recently collected material from East Kalimantan with the holotype indicates that the G1 diagnostic characters used by Ng (1986) are valid. The form of the frontal margin, however, is less reliable, being less "sunken" (relative to the external orbital angles) in the present specimens. In addition to the ZRC specimens, we have also examined another large specimen, which is now in the collections of Rudolf Diesel in Bielefeld, Germany.

This species is only one of the two species known from eastern Kalimantan, the other being *I. beeliae*. Details of its taxonomy can be found in Ng (1986).

Isolapotamon nimboni Ng, 1987
Fig. 10I–L

Potamon sinuatifrons.—Nobili, 1901:4 (not *Potamon sinuatifrons* H. Milne Edwards, 1853).

Potamon (*Potamon*) *consobrinum*.—Nobili, 1903:15 (not *Potamon* (*Potamon*) *consobrinus* De Man, 1899).

Potamon (*Potamon*) *consobrinus*.—Rathbun, 1904:269 (part) (not *Potamon* (*Potamon*) *consobrinus* De Man, 1899).

Potamon (*Potamon*) *sinuatifrons*.—Colosi, 1920:31 (not *Potamon sinuatifrons* H. Milne Edwards, 1853).

Potamon (*Potamon*) *mahakkamense*.—Leh, 1982:4 (part) (not *Potamon* (*Potamon*) *mahakkamense* De Man, 1899).

Isolapotamon nimboni Ng, 1987:144, fig. 2H–L, pl. 7; postscript pg. 150.

Material examined.—Holotype, male (40.5 by 30.0 mm) (SM Cru Nr 1986.11), Borneo, Sarawak: Simmangang, 1°15′N, 111°26′E), Sep 1894. Paratypes—1 male (27.0 by 21.0 mm), 2 females (largest 23.5 by 17.0 mm), 2 juveniles (SM Cru Nr 1986.12–16), same data as holotype. Others—1 male (MUT), same data as holotype (det. as *Potamon* (*Potamon*) *consobrinum* by Nobili 1903b). 1 male (50.1 by 36.2 mm) (ZRC 1997.784), Borneo, Sarawak: Kapit, Rumah Temanggong Koh, coll. loggers of logging company, 10 May 1996.

Diagnosis.—Carapace dorsal surfaces flat, regions very clear; anterolateral regions with numerous short striae; epibranchial tooth low, blunt, separated from external orbital angle by narrow cleft; outer margin of external orbital angle convex. Dactylus of last ambulatory leg long. G1 sinuous, terminal segment bifurcated at distal part, distal and subdistal processes positioned at right angles to each other, subdistal process very slender, subequal in length to distal process.

Remarks.—This species from Sarawak is distinguished primarily on the basis of its characteristic G1, which bears a general resemblance to that of *I. griswoldi*, *I. collinsi* and *I. grusophallus*. A larger specimen (ZRC 1997.784) has since been made available to us and some taxonomic characters are noted herewith.

Isolapotamon nimboni is closest to *I. col-*

linsi. Ng (1987) mentioned that the two can be differentiated mainly by the angle of the processes of the G1 terminal segment, the angle in *I. collinsi* being more obtuse than that of *I. nimboni*, and the subdistal process being shorter than the distal. No other taxonomic characters were offered to differentiate between the two species. However, in larger specimens of *I. nimboni*, this character becomes difficult to use as the distal process is nearly twice as broad as the subdistal process. The subdistal process is about equal in length to the distal process. The angle between the two processes also becomes very difficult to determine with any accuracy. Comparison of specimens of *I. nimboni* and *I. collinsi* reveals the following differences in asexual characters: branchial region of *I. nimboni* is deeply concave on both sides of the carapace whereas it is slightly concave in *I. collinsi*; mesogastric region is flat in *I. nimboni* but inflated in *I. collinsi*; *I. nimboni* possess glabrous ambulatory legs, whereas the ambulatory legs of *I. collinsi* is pubescent.

Isolapotamon sinuatifrons (H. Milne Edwards, 1853)

Figs. 10M–P, 11

Thelphusa sinuatifrons H. Milne Edwards, 1853:211; A. Milne Edwards, 1869: 167, pl. 10, fig. 2.

Thelphusa sinuatifrons. (?) var.—Miers, 1886:214, pl. 18, fig. 1.

Telphusa sinuatifrons.—De Man, 1892: 296; Bürger, 1894: 2.

Potamon sinuatifrons.—De Man, 1898:404.

Potamon (*Potamon*) *sinuatifrons*.—Rathbun, 1904:266, pl. 10 fig. 9; De Man, 1899:92, 100, pls. 8, 9 fig. 9.

Potamon mindanaoensis.—Balss, 1937: 162, fig. 22.

Isolapotamon (*Isolapotamon*) *sinuatifrons*.—Bott, 1968:121, fig. 6.

Isolapotamon sinuatifrons.—Bott, 1970b: 192, pl. 41 fig. 83.

Material examined.—Lectotype, male (53.0 by 39.0 mm) (MNHN BP-4353 S) (listed as *Potamon sinuatifrons*), male, G1 and G2 only. Paralectotypes—male (abdomen with G1 and G2 attached only) (MNHN BP 3845 S, listed as *Potamon sinuatifrons*). Others—1 male, 1 female (NHM 1884:31), Philippines, Mindanao: Pasauanca, coll. HMS Challenger.

Diagnosis.—Carapace width longer than length, dorsal surface smooth; anterolateral margin with low striae; anterolateral and posterolateral regions striated, striae low; epigastric cristae slightly forward of postorbital cristae; epibranchial tooth distinct, sharp, separated from external orbital angle by distinct V-shaped cleft; frontal margin sinuous; dactylus of last ambulatory legs long. G1 straight, not strongly elongated, distal part of terminal segment with large subdistal process, perpendicular to distal process, appearing "hammer-like".

Remarks.—This species has had a confused taxonomic history, with Bornean species having been confounded with it (Nobili 1901). Ng (1987) showed that the Bornean records of this species belong to *I. nimboni* instead.

The tip of the G1 of *I. sinuatifrons* is closest to *I. griswoldi* from Sabah, but the distal and subdistal processes are more distinctly right-angled in *I. sinuatifrons*. The overall length of the G1 is also proportionately distinctly shorter in *I. sinuatifrons*.

Miers (1886) reported specimens from Pasananca (Mindanao) which apparently differed slightly in their carapace features, but a re-examination of those specimens (NHM 1884:31) revealed that it is *I. sinuatifrons*. Differences observed of the carapace features are variation. Slight differences are also observed in the male G1. The distal part of the G1 terminal segment of the lectotype of *I. sinuatifrons* is twisted and the tip is pointed and faces towards the sternum. Specimens examined from NHM display the twisted distal portion of the G1 terminal segment, but the tip of the terminal segment is rounded and not pointed. This is probably part of the intraspecific variation.

Examination of the photographs of a syn-

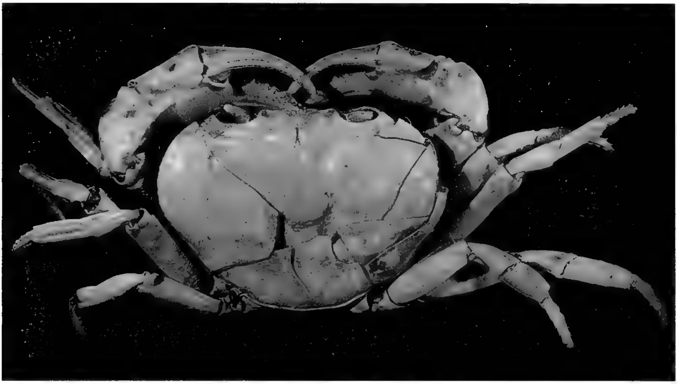

Fig. 11. *Isolapotamon sinuatifrons*. Lectotype male (53.0 by 39.0 mm) (MNHN BP-4353 S).

type male, purportedly from the same expedition as the lecotype, indicates that it differs from photographs of the lectotype in the following characters: the tip of the G1 terminal segment lies flat on the sternum and not twisted, whereas it is twisted and facing towards the sternum in the lectotype; the syntype male has a proportionately shorter ambulatory merus; the left ambulatory leg propodus of the syntype male is proportionately half as short as that on the lectotype; there are four low spines on the posterior margin of the ambulatory propodus of the syntype male but it is smooth in the lectotype; and the syntype male has relatively flatter branchial regions. It is very possible that this specimen in fact represents a separate species. But in the absence of fresh material and more characters, we regard this specimen tentatively as *I. sinuatifrons*.

The type specimens were collected by the Voyage de la Zélée. This makes the locality of the type specimens uncertain as the voyage collected specimens from various localities in Southeast Asia. Specimens from NHM that we had examined were collected in Mindanao, Philippines.

Isolapotamon spatha Ng & Takeda, 1992
Fig. 12A–D

Isolapotamon spatha Ng & Takeda, 1992: 163, fig. 7.

Material examined.—Holotype, male (28.0 by 22.7 mm) (NSMT-Cr 11225), Kraan, 100 m, Sultan Kradarat Province, Mindanao, coll. Y. Nishikawa, 12 Aug 1985. Paratypes.—1 male (30.6 by 224.3 mm), 1 female (NSMT-Cr 11226), same data as holotype.

Diagnosis.—Carapace dorsal surface flat, smooth; epigastric cristae slightly forward of postorbital cristae; epibranchial tooth distinct, blunt, separated from external orbital angle by deep V-shaped cleft; frontal margin sinuous, finely beaded. G1 gently sinuous, laterally flattened, tip dilated, outer distal part of subterminal segment with broad truncate cleft.

Remarks.—This species is superficially similar to *Isolapotamon consobrinum* but can be distinguished by the presence of only a blunt epibranchial tooth and the structure of the G1. The G1 of *I. spatha* resembles that of *I. kinabaluense* in possessing a club-shaped tip but it does not

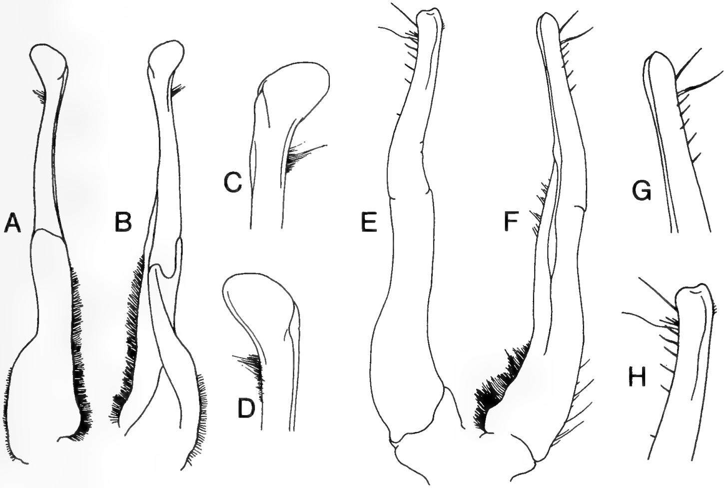

Fig. 12. A–D: *I. spatha*, holotype male (NSMT-Cr 11225) (after Ng & Takeda, 1992); E–H: *I. stuebingi*, holotype male (ZRC 1995.273) (after Ng, 1995). A, E: dorsal view; B, F: ventral view; C, G: doral view, tip of terminal segment; D, H: ventral view, tip of terminal segment.

have a deep concave curvature on the outer distal margin of the subterminal segment. For a more detailed discussion of the taxonomy of this species, see Ng & Takeda (1992).

Isolapotamon stuebingi Ng, 1995
Fig. 12E–H

Isolapotamon stuebingi Ng, 1995:65, figs. 7, 8A–E.

Material examined.—Holotype, male (22.0 by 16.6 mm) (ZRC 1995.273), Borneo, Sarawak: Lanjak-Entimau, Sg. Sekerang, station 90, coll. R. B. Stuebing, 8 Oct 1993. Paratype—male (20.5 by 15.0 mm) (NNM D 4629), Borneo, Sarawak: Lanjak-Entimau Widelife Sanctuary, in stomach of frog (*Rana ibanorum*, Ranidae), coll. C. H. Diong, 17–23 May 1994. Others—1 male (ZRC), Borneo, Sarawak: Sg. Adir (Stn. 5), coll. R. B. Stuebing, 30 Jun 1994.

Diagnosis.—Carapace wider than long, dorsal surfaces flat, regions rugose to granulose, especially lateral region, anterolateral margins distinctly granulated, epibranchial tooth low but distinct, separated from external orbital angle by cleft, external orbital angle broadly triangular. Dactylus of last ambulatory leg short. G1 gently sinuous, terminal segment shorter than subterminal segment, tip subtruncate.

Remarks.—The holotype and all known specimens of *I. stuebingi* are all rather small but the characters used by Ng (1995) to distinguish this species from the closely allied *I. consobrinum* are of diagnostic value even for specimens of comparable sizes.

Discussion

The known distribution of the genus *Isolapotamon* s. str. strongly supports the concept of Wallace's Line which demarcates the Australian and Asian fauna. Of the other two potamid genera in Borneo, *Cer-*

berusa is a wholly cavernicolous taxon (Holthuis 1979) whilst *Ibanum* is probably semi-terrestrial in habits (Ng 1995). *Isolapotamon* is the most speciose genus, and its members extend into Mindanao, but is not known from the Palawan islands or areas further north (Ng & Takeda 1992, 1993). *Isolapotamon* is absent from Sulawesi. In the Tambelan Islands to the west of Borneo, the genus appears to be replaced by the allied *Allopotamon* (Ng 1988b). *Allopotamon tambelanense* (Rathbun 1905), the only species known from the genus, shares many of the external features of *Isolapotamon* (including the form of the third maxilliped exopod) but has a very different G1. As yet, no potamids are known from the Natuna and Anambas islands northwest of Borneo, which might be simply due only to a lack of collecting.

The easternmost species on Borneo appear to be *I. ingeri* whereas *I. consobrinum* is the westernmost taxon. It is striking that there are no species of *Isolapotamon* or any genus even close to *Isolapotamon* in Peninsular Malaysia, Sumatra, Java or the Lesser Sunda Islands. In Borneo, while *Cerberusa* and *Ibanum* are probably sister genera (see Ng 1995), neither seems to be very close to *Isolapotamon*.

The distribution of the various *Isolapotamon* species is also interesting. There are only three known non-Bornean species—*I. mindanaoense, I. spatha* and *I. sinuatifrons*, all from the island of Mindanao in southern Philippines. In the morphology of the G1, two of the Philippine species, *I. mindanaoënse* and *I. spatha*, appear to be most closely related to the Sabahan species like *I. kinabaluense* and *I. anomalum*. The overall shape of the G1 is similar to that of *I. kinabaluense*, but the shape and position of the dorsal and ventral folds of the distal part are closer to the condition in *I. anomalum*. The G1 of *I. sinuatifrons* generally resembles that of *I. anomalum*, although the distal dilation of the terminal segment in the former species is positioned at sharply right angles to the rest of the segment. The likelihood that the Mindanao *Isolapotamon* originated from species in northern Borneo thus seems high. The absence of *Isolapotamon* on Palawan is also of interest. Recent collections in Palawan uncovered numerous new species (including a new genus of potamid, *Insulamon* Ng & Takeda, 1992), but no species of *Isolapotamon* (see Ng & Takeda 1992, 1993). Similarly, another genus of potamid, *Ovitamon* Ng & Takeda, 1992, occurs on southern Luzon and the nearby islands in the Philippines (Ng & Takeda 1992).

The richness and diversity of the *Isolapotamon* fauna in Borneo and their restricted distribution in the Philippines (only in Mindanao) seems to indicate that *Isolapotamon* entered Philippines from Borneo. The islands southwest of Mindanao (Sulu Islands) were almost certainly connected to Mindanao during the last ice age in the Pleistocene, and the proximity of these islands to Borneo together with the shallow adjacent seas would have resulted in a land bridge between Mindanao and north Borneo during the last ice age.

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A new species of crayfish of the genus *Procambarus*, subgenus *Ortmannicus* (Decapoda: Cambaridae), from the Waccamaw River basin, North and South Carolina

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Abstract.—*Procambarus* (*Ortmannicus*) *braswelli* is a new species of crayfish from the Waccamaw River basin in North and South Carolina. A primitive member of the Pictus Group, *P. braswelli* has its closest affinities with *P.* (*O.*) *chacei*, *P.* (*O.*) *enoplosternum*, and *P.* (*O.*) *pictus*. The new species is less closely related to *P.* (*O.*) *epicyrtus*, and distantly related to its geographically nearest relative, *P.* (*O.*) *lepidodactylus*, with which it has been confounded. The occurrence of *P. lepidodactylus* in North Carolina is currently unconfirmed. *Procambarus braswelli* may be distinguished from the other members of the Pictus Group by its combination on the form I male gonopod (first pleopod) of a prominent, truncated, distally directed caudal knob; a large, somewhat bulbous adventitious process; and a long, caudodistally directed mesial process; and by a long acumen.

The Waccamaw River basin of southeastern North Carolina and northeastern South Carolina has long been known as home to a number of animal species that are either endemic or are shared with a single other river basin. The endemic fauna includes several fishes and mollusks. Information on the fishes can be found in Hubbs & Raney (1946), Frey (1951), Shute et al. (1981), Menhinick (1991), and Rohde et al. (1994). The mollusks are discussed in Fuller (1977), Johnson (1984), and Porter & Horn (1984). Teulings & Cooper (1977: 414–415) provided a list of the endemic species.

Included in the Waccamaw invertebrate fauna is a crayfish previously assigned to *Procambarus* (*Ortmannicus*) *lepidodactylus* Hobbs, 1947a, a species considered the northernmost representative of the primitive Pictus Group (Hobbs 1958a, 1962, 1968, 1972, 1974, 1989; Cooper & Cooper 1977a, 1977b). Few specimens of this Waccamaw crayfish have been collected, and the only published locality was "canal off Waccamaw River, apparently 7.5 air mi. [12.0 air km] south of Lake Waccamaw, Columbus County (1949)" (Cooper & Cooper 1977b: 206). This record was based on a female in the collections of the National Museum of Natural History, Smithsonian Institution (USNM 129841), collected on 29 March 1949 by E. C. Raney. It is the only North Carolina specimen identified as *P. lepidodactylus* in the catalogued collections of that institution, and the locality is obviously the same one referred to as "Columbus County" by Hobbs (1968:K9, 1972:61, 1974:57, 1989:68). None of the North Carolina specimens later assigned to *P. lepidodactylus* had received critical examination. Prompted by a form I male collected by David R. Lenat, North Carolina Division of Water Quality, I determined that these specimens represent an undescribed species of the Pictus Group that appears to be endemic to the Waccamaw River basin and that is only distantly related to *P. lepidodactylus*. This new species is currently known only from Columbus County, North

Carolina, and from a single locality in Horry County, South Carolina, but it may be found elsewhere within the Waccamaw basin.

Because *P. lepidodactylus* (s.s.) occurs in the Pee Dee River basin in South Carolina, Cooper & Cooper (1977b:207) speculated that it "may yet be discovered in tributaries of the Lumber River of North Carolina . . . . " A distribution map showing localities for members of the Pictus Group (Hobbs 1958a:72) contains a single North Carolina site for "*P. lepidodactylus*." The site indicated by a dot in the map lies just west of the 79th meridian, which would place the locality in the Lumber River basin. However, the dot undoubtedly was meant to represent the Columbus County record in the Waccamaw basin (USNM 129841). I know of no specimens of *Procambarus* from North Carolina that incontrovertibly can be assigned to *P. lepidodactylus*. Several specimens that could belong to this species have been collected in the Lumber basin (Cooper & Braswell 1995:120), but form I males have yet to be seen.

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

Procambarus (*Ortmannicus*) *braswelli*, new species
Fig. 1

Procambarus lepidodactylus.—Hobbs, 1958a:72 (p.p.; map locality for North Carolina), 75, 76 (p.p.; southeastern North Carolina).—Hobbs, 1962:284 (p.p.; southeastern North Carolina).—Hobbs, 1968:K9 (p.p.; Columbus County, North Carolina).—Hobbs, 1972:151 (p.p., North Carolina).—Franz & Lee, 1982:61 (p.p.; North Carolina).—LeGrand & Hall, 1997:32 (p.p.; Waccamaw drainage, North Carolina).

Procambarus (*Ortmannicus*) *lepidodactylus*.—Cooper & Cooper, 1977a:198, 1977b:206, 207 (p.p.; North Carolina).—Cooper & Cooper, 1977a:200 (p.p.; by implication, North Carolina).—Hobbs, 1972:61, 1974:57, 1989:68 (p.p.; Columbus County, North Carolina).—Hobbs & Peters, 1977:8 (p.p.; North Carolina).—Hobbs et al., 1977:19 (p.p.; North Carolina).—Teulings & Cooper, 1977:415 (p.p.; North Carolina).—Fitzpatrick, 1983:214 (p.p.; Carolinas, viz. North Carolina).—Hobbs & Franz, 1986:516 (p.p.; North Carolina).—Hobbs, 1989:86 (p.p.; North Carolina).

Procambarus leptodactylus.—Williams et al., 1989:26, 64 (p.p.; by implication, North Carolina; erroneous spelling).—LeGrand, 1993:23, LeGrand & Hall, 1995:31 (p.p.; Waccamaw drainage, North Carolina; erroneous spelling).

"Undescribed species."—Cooper & Braswell, 1995:120.

Diagnosis.—Body and eyes pigmented, eyes large ($\bar{X}$ adult diam 2.4 mm, n = 11). Rostrum acarinate, margins narrow, parallel to subparallel near base, slightly convex between orbits, then recurving and tapering to base of long acumen, which delineated by strong marginal spines; acumen comprising 41.9 to 49.1% ($\bar{X}$ = 44.8%, n = 12) of rostrum length, latter comprising 31.7 to 37.9% ($\bar{X}$ = 34.4%) of TCL. Areola 2.1 to 4.2 ($\bar{X}$ = 2.9, n = 13) times as long as broad and constituting 26.3 to 28.2% ($\bar{X}$ = 26.9%, n = 12) of TCL and 39.4 to 42.8% ($\bar{X}$ = 41.3%, n = 13) of PCL, and with 6 to 9 (usually 7–8) punctations across narrowest part. Carapace densely granulate, cephalic section constituting 71.8 to 74.8% ($\bar{X}$ = 73.1%, n = 12) of TCL. Cervical spines strong, 1 each side; cervical groove inter-

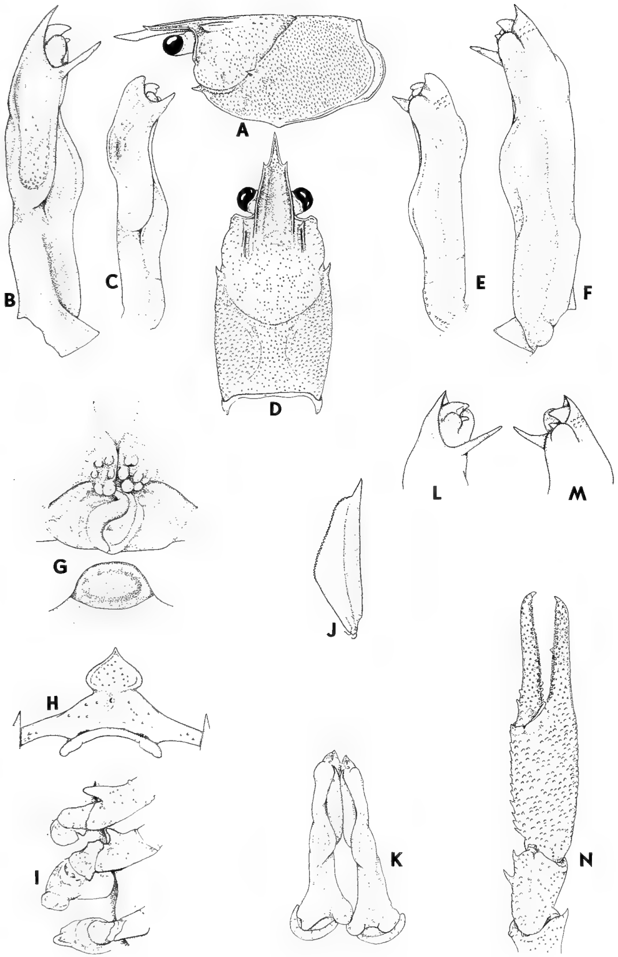

Fig. 1. *Procambarus* (*Ortmannicus*) *braswelli*, new species (all from holotypic male, form I, except C, E, from morphotypic male, form II, and G, from allotypic female; setae not illustrated): A, lateral aspect of cephalothorax; B, C, mesial aspect of left gonopod (first pleopod); D, dorsal aspect of cephalothorax; E, F, lateral aspect of left gonopod; G, annulus ventralis and associated structures; H, epistome; I, basal podomeres of third, fourth, and fifth pereiopods; J, antennal scale; K, caudal aspect of in situ gonopods; L, M, caudomesial and caudolateral aspects, respectively, of tip of left gonopod; N, dorsal aspect of distal podomeres of right cheliped.

rupted. Branchiostegal spine strong; hepatic area with some weak tubercles. Suborbital angle obtuse to obsolete. Postorbital ridge moderately strong, with nearly obliterated groove and strong cephalic spine. Antennal scale 2.9 to 3.4 ($\bar{X}$ = 3.2, n = 13) times as long as broad, widest proximal to midlength; lateral margin thickened and terminating in acute spine, mesial (lamellar) margin subangular.

Palm of chela of cheliped 1.1 to 1.7 ($\bar{X}$ = 1.4, n = 13) times wider than deep, 1.3 to 1.8 ($\bar{X}$ = 1.6, n = 13) times longer than wide, and constituting 40.2 to 46.7% ($\bar{X}$ = 42.5%, n = 12) of chela length; mesial margin of palm with staggered row of 5 to 13 small, subconical tubercles. Fingers without gape, without dense setae at opposable bases; dactyl 1.1 to 1.4 ($\bar{X}$ = 1.2, n = 13) times length of mesial margin of palm.

Hooks on ischia of third and fourth pereiopods of male; in form I male (Fig. 1I), hook on third pereiopod oblique, subconical, overreaching basioischial articulation by most of length, not opposed by tubercle on basis; hook on fourth pereiopod smaller, vertically disposed, not reaching articulation, and opposed by prominent protuberance on basis, center of protuberance with curved, setiferous depression; coxa of fourth pereiopod with low, vertically disposed caudomesial boss, that of fifth pereiopod with compressed ridgelike boss at caudomesial angle (Fig. 1I).

Gonopods (first pleopods) of form I male (Fig. 1B, F, K, L, M) asymmetrical, proximomesial apophyses strong, tapering, generally rounded but with subacute tip caudally, overlapping; total length of gonopod 22.1 to 25.6% ($\bar{X}$ = 23.8%, n = 4) of TCL; distal ¼ of shaft weakly inclined caudodistally, cephalic surface with narrow convexity subjacent to base of cephalic process; mesial process long, slender, noncorneous, directed caudodistally and inclined laterally, tip acute to subtruncate; central projection and cephalic process corneous, subequal in length; cephalic process with acute apex, directed distally and slightly caudally, and with expanded base forming cowl around cephalic base of central projection; latter subtriangular, directed caudodistally at much greater angle than cephalic process; caudal element consisting of: prominent distolateral caudal knob, directed distally and delimited cephalically by groove; small, toothlike caudal process, originating on mesial surface of central projection and directed caudodistally; and inflated adventitious process, originating at proximomesial base of cephalic process, lying wholly mesial or cephalomesial to caudal process, and obscuring part of proximomesial bases of central projection and caudal process.

Annulus ventralis (Fig. 1G) symmetrical, subovate, 2.4 times as wide as long, movable; cephalic margin broadly arched, caudal margin mildly convex and with weak caudomedian labiellum; median ⅓ of annulus ventrally elevated, moundlike; dextral half of mound hemitubular, C-shaped, sinistral half slightly narrower, following contours of dextral half; both parts of central mound descending cephalically as pair of short, narrow, curved ridges, which tapering cephalically and terminating sinistral to midline of cephalic margin of annulus; narrow, somewhat C-shaped ridge dextrolateral to central mound at about midlength of annulus, and short horizontal ridge sinistrolateral to mound at same level; deep subtriangular depression cephalolateral to central mound on either side of curved ridges, each depression with prominent protuberance near cephalolateral margin.

Measurements of type specimens provided in Table 1.

Description of holotypic male, form I.—Body and eyes pigmented, eye 2.9 mm diam. Cephalothorax (Fig. 1A, D) subcylindrical; maximum width of carapace 1.1 times depth, cephalic section 2.8 times length of areola and constituting 73.4% of TCL. Areola 3.3 times as long as wide, constituting 26.6% of TCL (39.5% of PCL), densely punctate, with 7 to 8 punctations across narrowest part; branchiocardiac

Table 1.—Measurements (mm) of types of *Procambarus* (*Ortmannicus*) *braswelli*, new species.

	Holotype	Allotype	Morphotype
Carapace			
Total length	27.4	29.6*	20.2
Postorbital length	18.5	19.4	13.8
Length cephalic section	20.1	21.3*	14.5
Width	11.8	13.5	9.0
Depth	10.4	12.4	9.1
Rostrum			
Length	9.0	9.7*	6.4
Width at base	4.0	4.6	3.4
Length acumen	3.8	off	2.7
Areola			
Length	7.3	8.3	5.7
Width	2.2	2.0	2.1
Antennal scale			
Length	9.1	9.8	7.4
Width	2.7	3.4	2.3
Abdomen			
Length	28.3	34.6	22.0
Width	10.5	12.9	7.3
Cheliped			
Length lateral margin chela	19.8	15.9	10.5
Length mesial margin palm	8.6	6.6	4.9
Width palm	5.2	5.2	2.7
Depth palm	3.9	3.0	2.0
Length dactyl	9.5	8.3	5.5
Length carpus	6.4	6.2	4.1
Width carpus	3.9	4.1	2.3
Length dorsal margin merus	10.6	9.9	6.8
Depth merus	3.7	4.1	1.9
Gonopod length	6.2	NA	4.8

* estimated; acumen damaged.

grooves strong, flaring caudolaterally from about midlength. Rostrum with narrow, elevated margins, extending caudally nearly to caudal margin of postorbital ridges; margins of rostrum parallel near base, slightly convex between orbits, then recurving and converging to base of long, spiculiform acumen which delineated by strong marginal spines; rostrum deeply excavate, margins flanked medially by continuous row of setiferous punctations; walls of rostrum sloping, floor (dorsal surface) slightly concave, punctations most abundant in cephalic half; acumen comprising 42.2% of rostrum length, apex corneous, directed cephalically and extending to distal margin of second article of antennular flagellum; ventral keel of acumen bladelike, broadly subangular in lateral aspect; subrostral ridge visible in dorsal aspect only at base of rostrum. Postorbital ridge moderately strong, with thin dorsal crest and narrow, nearly obliterated lateral groove bearing small punctations; cephalic margin with strong spine. Suborbital angle obsolete, orbital rim subrectilinear and with concavity near base of antennal peduncle. Cervical spines strong, 1 each side, and area also with dense granulations dorsal to spine; cervical groove interrupted just dorsal to spine, with short, broad sulcus cephalic to groove; ventral margin of cephalic portion of groove with row of small tubercles. Carapace with thoracic section densely granulate laterally and dorsally, granules ascending to margins of branchiocardiac grooves; cephalic section of carapace with scattered granules laterally; caudal mandibular region broadly convex, delimited by moderate groove; gastric region with crowded punctations, caudal margin of region in form of low, arcuate ridge.

Branchiostegal spine long, slightly procurved. Antennal peduncle with long distolateral spine on basis and similar spine on ventral surface of ischium; antennular peduncle with strong, semierect ventral spine situated near mesial margin at about midlength of basal podomere, which hirsute mesially and with sparse setae ventrally; tip of antennal flagellum reaching cephalic margin of telson when flagellum adpressed. Antennal scale (Fig. 1J) 3.4 times as long as wide, broadest proximal to midlength; lateral margin thickened and terminating in strong distal spine, tip reaching slightly beyond proximal margin of third article of antennular flagellum; lamella approximately twice as wide as thickened lateral portion, distal margin slightly sloping for short distance then strongly declivous to widest part; mesial margin subangular.

Abdomen slightly longer and narrower than carapace; pleura of most abdominal segments with rounded cephalolateral margins, and slightly rounded to subangular caudoventral margins. Proximal podomere of right uropod (left uropod regenerate, deformed) with very strong caudolateral spine on lateral lobe, and slightly weaker, somewhat laterally situated spine on mesial lobe; mesial ramus of uropod with long caudolateral spine, and strong median ridge terminating in spine situated well cephalic to caudal margin; lateral ramus with broad median ridge on cephalic section, and poorly defined ridge lateral to it; transverse flexure of ramus with margin bearing row of 11 fixed spines, and large movable spine, with small spine at dorsal base, near lateral margin of ramus. Telson with 3 spines in each caudolateral corner of cephalic section, middle one movable, mesial one on left bifurcate; transverse suture strong; caudal margin of telson truncate and with slight median concavity. Uropods and telson with few setae dorsally.

Epistome (Fig. 1H) with subtriangular cephalic lobe bearing long, triangular cephalomedian projection; lobe strongly constricted at base, transverse sulcus indistinct; margins of lobe slightly thickened, elevated (ventrally), somewhat undulant, incomplete at base of projection, and with long, dense setae; lateral apices thicker than rest of margin, rounded, somewhat flared; floor (ventral surface) of lobe slightly convex, very punctate, setiferous; body of epistome with broad central depression bearing shallow cephalomedian fovea; lamellae punctate, tapering laterally to subtruncate margin devoid of tubercles; zygoma moderately arched, flanked cephalolaterally by usual elongate pits.

Third maxilliped with tip of endopodite of ischium extending nearly to distal margin of penultimate podomere of antennal peduncle, tip of exopodite extending to just beyond distal margin of merus of endopodite; basal podomere of exopodite not hirsute; ventrolateral margin of ischium with row of setiferous punctations at base of longitudinal ridge, distolateral corner produced as acute spine; ventrolateral half of ischium with scattered punctations bearing short setae; ventromesial half with longitudinal rows of long setae, moderately obscuring mesial margin; basis of ischium with clumps of long setae, forming brushes. Right mandible with incisor ridge bearing 8 denticles, third from distal end largest, penultimate one small, left incisor ridge with 6 denticles, distalmost largest.

Palm of chela of cheliped (Fig. 1N) subovate in cross section, 1.3 times wider than deep, 1.7 times longer than wide; mesial margin of right palm with mesial row of 11 subconical tubercles (9 on left) of varying sizes, most with distal margin elevated; other obvious tubercles dorsal and ventral to mesial row; distal margin of mesial surface developed as 12th (10th on left) tubercle, with large spiniform tubercle and smaller rounded tubercle proximoventral to it; dorsal, mesial, and lateral surfaces of palm crowded with strong squamous tubercles of varying sizes, and recumbent setae; ventral surface of palm less densely tuberculate, many tubercles subspiniform; articular ridge of palm, dorsally and ventrally, poorly defined, lateral eminence especially weak; lateral eminence ventrally with very strong subdistal spine. Fingers narrow, with opposable surfaces contiguous and lacking prominent setae at bases; fingers slightly curved distoventrally in lateral aspect, dorsal surfaces studded with punctations and tufts of stiff setae. Right dactyl 48.0% of chela length, 1.1 times as long as palm; dorsal surface of dactyl with narrow, weak longitudinal ridge, ventral surface rounded and without ridge; proximal ⅓ of ventral surface with 5 or 6 small tubercles; mesial margin of dactyl with 2 (4 on left) large, semierect tubercles in row near base, and several smaller tubercles dorsal and ventral to them, rest of margin punctate; opposable margin with dense pad of denticles in 6 to

7 rows throughout length of dactyl, pad narrower near base; proximal half of finger with 8 to 9 (5 on left) small tubercles dorsal to denticles, basal 2 largest; ventral to denticles, surface with 1 small, subacute tubercle near base and 2 large contiguous tubercles situated at base of distal ¾ of finger, interrupting denticles (on left, single large tubercle at this site). Fixed finger with narrow longitudinal ridge dorsally, and moderate ridge ventrally; lateral surface of finger rounded, with rows of deep punctations and clumps of stiff setae; opposable margin with dense pad of denticles in 7 to 8 rows throughout length of finger, pad narrower near base; large subconical tubercle ventral to denticles just distal to midlength; proximal ⅓ of finger with 5 (4 on left) small, rounded tubercles dorsal to denticles, third from base largest.

Carpus of cheliped (Fig. 1N) 1.6 times as long as wide, length 74.4% of palm length; dorsal surface with very shallow, slightly oblique sulcus, surface lateral to which punctate, mesial to which with 2 to 3 rows of subconical tubercles extending onto dorsomesial surface; large spine mesial to dorsal articular eminence; ventral surface with very strong distolateral spine, strong distal spine mesial to distolateral one, smaller spine just proximal to distomedian one, 2 small acute tubercles proximal to both of the latter, and 2 weak spines and 4 tubercles near mesial margin; latter with strong, curved subdistal spine and 4 to 5 proximal tubercles. Merus of cheliped 2.9 times longer than deep, depth fairly uniform throughout length, latter 38.3% of TCL; dorsal surface with 2 strong, contiguous subdistal spines, and row of spiniform tubercles along dorsomedian ridge; dorsal spines and tubercles flanked mesially and laterally by other subspiniform to squamous tubercles; distal half of mesial surface tuberculate, lateral surface punctate and with some minute, scattered tubercles; ventrolateral ridge with large distal spine near articular eminence, 3 other strong spines; 8 to 9 small tubercles, and row of small tubercles between distal extremity of ridge and large distal spine; ventromesial ridge with large distal spine, patch of 3 large spines just proximal to distal spine, and 11 or 12 spiniform tubercles; other obvious tubercles on dorsomesial surface, and patch of 5 to 6 tubercles between distal extremities of both ridges; ventral surface of merus between ridges with some small tubercles and dense setae. Ischium with row of 4 (5 on left) subspiniform tubercles on ventral ridge; sufflamen obsolete on right, short on left. Merus of second through fourth pereiopods with prominent distolateral spine.

Hooks on ischia of third and fourth pereiopods simple (Fig. 1I), that on third long, subconical, slightly curved and overreaching basioischial articulation by most of length, not opposed by tubercle on basis; hook on fourth pereiopod short, vertically disposed, not reaching articulation, and as in "Diagnosis." Coxae of fourth and fifth pereiopods also as in "Diagnosis." Sternites between third and fourth pereiopods with long setae.

For description of gonopod see "Diagnosis." In addition, intact subapical setae (not illustrated) flanking mesial, cephalic, and lateral bases of cephalic process and central projection, largely obscuring both elements.

Description of allotypic female.—Differing from holotypic male, except in secondary sexual characters, as follows: Areola 4.2 times as long as broad, constituting approximately 28.0% of TCL (acumen damaged) and 42.8% of PCL, with 6 punctations across narrowest part. Cervical area with 2 tubercles ventral to cervical spine. Cephalolateral corners of cephalic section of telson with 4 spines on left, 3 on right. Antennal scale 2.9 times as long as broad. Chela of cheliped 1.7 times wider than deep; mesial margin of palm with mesial row of 5 to 6 tubercles. Longitudinal ridges on fingers of cheliped well developed. Mesial surface of dactyl with single prominent tubercle and other squamous to subsquamous tubercles near base; opposable surface with 4 rounded tubercles on proximal ⅓ to ¼, and several smaller tubercles distally; denticles in single row; opposable margin of fixed finger with row of 6 tubercles, denticles in single row. Carpus of cheliped 1.5 times as long as wide, length 93.9% of length of mesial margin of palm; merus 2.4 times as long as deep, length 33.4% of TCL; ventrolateral ridge with row of 7 spines or spiniform tubercles in addition to distal spine, ventromesial ridge with 13 spines or tubercles and large distal spine.

For description of annulus ventralis (Fig. 1G) see "Diagnosis." In addition, postannular sclerite nearly twice as wide as long, about half as wide as annulus. Preannular sternite with broadly flared walls, deep median cleft in caudal half, and 5 to 6 protuberant lobes on either side of cleft, caudalmost pair overhanging cephalic margin of annulus. First pleopods uniramous, extending just beyond caudal margin of preannular sternite when abdomen flexed.

Description of morphotypic male, form II.—Differing from holotypic male in following respects: Areola 2.7 times as long as broad, constituting 28.2% of TCL (41.3% of PCL), sparsely punctate; apex of acumen reaching to proximal base of first article of antennular flagellum. Antennal scale 3.2 times as long as wide. Mesial margin of palm of cheliped with mesial row of 8 tubercles; lateral eminence of ventral articular ridge with small tubercle. Mesial margin of dactyl with 3 tubercles; opposable margin with 3 minuscule tubercles ventral to denticles in proximal ¼ of finger, and 2 small tubercles dorsal to denticles near base of finger; denticles in single row. Opposable margin of fixed finger with 3 or 4 small tubercles, denticles in 2 to 3 rows. Carpus of cheliped 1.8 times as long as broad, length 83.7% of length of mesial margin of palm; merus 3.4 times as long as deep, length 33.7% of TCL; ventrolateral ridge with 2 strong spines in addition to large distal spine, ventromesial ridge with 11 small tubercles and large (broken) distal spine; ischium with 5 (4 on left) minuscule tubercles. Hooks on ischia of third and fourth pereiopods reduced; boss on coxa of fourth pereiopod not pronounced, that on fifth pereiopod narrow.

Gonopods (Fig. 1C, E) with proximomesial apophyses separated; mesial process stout, tapering, tip directed caudally; gonopod in lateral aspect with "juvenile suture"; cephalic convexity apparent; all terminal elements blunter and thicker than in form I male, not corneous, all except caudal process identifiable and relationships clearly visible; subapical setae sparse; gonopod in mesial aspect with poorly defined caudal process, and adventitious process reduced to narrow ridge.

Disposition of types.—The holotypic male, allotypic female, and morphotypic male are in the crustacean collections of the NCSM (catalogue numbers NCSM C-2507, C-2549, and C-2550, respectively), as are paratypes consisting of 3 ♂ I, 3 j ♂, 3 ♀, 3 j ♀.

Type locality.—North Carolina, Columbus County, Waccamaw River at NC 130 near Brunswick County line, 8.0 air km (5.6 air mi) SSE of Old Dock (Freeland USGS 7.5′ quadrangle, UTM coordinates 3775210N/726190E).

Range and specimens examined.—Known only from the Waccamaw River basin in North and South Carolina, where the following collections have been made: North Carolina. Columbus Co.—Waccamaw R at NC 130 (type locality); 1 ♂ I (NCSM C-2507), 17 Jun 1991, 1 ♀ (NCSM C-2234), ? Aug 1984, coll. D. R. Lenat; Waccamaw R at Lake Waccamaw dam, S end of SR 1967, ca. 7.4 air km S of town Lake Waccamaw; 1 ♂ I, 1 j ♂, 1 j ♀ (NCSM C-316), 1 ♀ (NCSM C-2549), 22 Oct 1978, coll. A. L. Braswell, R. E. Ashton, Jr., P. S. Ashton; Waccamaw R between spillway & SR 1928; 1 ♂ I, 1 ♀, 2 j ♀ (NCSM C-2066), 29 Mar 1978, coll. W. S. Birkhead; Waccamaw R below Bogue Swamp, "near dam" at Lake Waccamaw; 1 j ♂, 1 j ♀ (NCSM C-2515), 19 Jun 1991, coll. D. R. Lenat, F. Winborne, L. Eaton;

Waccamaw R, N of NC 130 (probably 2.8 river km N); 1 ♂ I (NCSM C-963), 1 ♂ II (NCSM C-2550), 22 Apr 1979, coll. UNC–Wilmington biologists; canal off Waccamaw R, 1.6 km N of river, apparently 12.0 air km S of Lake Waccamaw; 1 ♀ (USNM 129841), 29 Mar 1949, coll. E. C. Raney. South Carolina. Horry Co.—Smith Lake at end of Park Ave, northern Conway; 1 j ♂ (NCSM C-3247), 10 May 1994, coll. R. G. Arndt & students.

Variations.—Significant variations are addressed in the "Diagnosis," but others are also evident. The tubercle on the lateral eminence of the ventral articular ridge of the palm of the chela varies from large and spiniform to small and subsquamous, and is absent in one small female. The tubercles in the mesial row of the mesial margin of the palm range in number from five to thirteen, and in size from barely discernible to large and obvious; in the four form I males they number from ten to thirteen and are conspicuous, while in females they number from five to nine and generally are inconspicuous. The number of tubercles on the opposable margin of the fixed finger, exclusive of the prominent subconical one, varies from one to six, but the usual number is two or three. The number of tubercles on the opposable margin of the dactyl ranges from two to thirteen, but usually is two to five. In most specimens these tubercles are very small, and in several they are scarcely discernible. Some are dorsal to the denticles, but others are either ventral to them or interrupt them ventrally. The tubercles along the dorsomedian ridge of the merus vary in size and configuration, from barely visible, squamous tubercles to small spines. In all specimens there is a single cervical spine on each side of the carapace, but the allotype also has two tubercles ventral to the spine. There almost always are three spines in each caudolateral corner of the cephalic section of the telson, but five specimens have four spines in one corner, three in the other.

In form I males the opposable surfaces of both fingers of the chela are densely packed with denticles, arranged in five to nine somewhat irregular rows. Females and juvenile males have a single row of denticles on these surfaces, and the morphotypic male has two to three rows on the fixed finger and a single row on the dactyl.

Size.—The largest specimen, a female with a damaged acumen, has an estimated TCL of 29.6 mm (PCL 19.4 mm). Four other females range from 18.5 to 25.5 mm TCL (12.0–16.7 mm PCL). The four form I males range from 19.5 to 27.4 mm TCL (12.8–18.5 mm PCL).

Life history notes.—Form I males have been found in March, April, June, and October. No ovigerous females or those with attached young have been collected.

Crayfish associates.—Cooper & Braswell (1995:120–121) briefly discussed the crayfishes of the Waccamaw River basin. The only species that have been taken with *P. braswelli* are *Procambarus* (*Ortmannicus*) *acutus* (Girard, 1852), *Procambarus* (*Ortmannicus*) *ancylus* Hobbs, 1958b, and *Procambarus* (*Ortmannicus*) *blandingii* (Harlan 1830).

Relationships.—Based on the configuration of the form I male gonopod, *P. braswelli* has its closest affinities with *Procambarus* (*Ortmannicus*) *chacei* Hobbs, 1958c, *Procambarus* (*Ortmannicus*) *enoplosternum* Hobbs, 1947b, and *Procambarus* (*Ortmannicus*) *pictus* (Hobbs 1940), is somewhat more distantly related to *Procambarus* (*Ortmannicus*) *epicyrtus* Hobbs, 1958c, and is even more distantly related to its geographically nearest neighbor, *P. lepidodactylus.*

Procambarus braswelli may be distinguished from all other members of the Pictus Group by the combination of: a gonopod whose distal one-fourth is only slightly caudally directed; a small but obvious cephalic convexity; an almost distally directed cephalic process whose caudal base is transversely expanded and forms a cowl or hood around the cephalic base of the slightly longer, caudodistally directed central projection; a long mesial process that is caudodistally directed at about 45° to the shaft of the gonopod; a prominent, distally directed caudal knob that extends only slightly beyond the proximocaudal bases of the cephalic process and central projection; a large adventitious process that in mesial aspect obscures part of the proximomesial bases of the central projection and caudal process; an acumen that on average comprises about 45% of the rostrum length; and a carapace that, caudal to the cervical groove, is granulate both dorsally and laterally.

Etymology.—Despite his being an unrepentant vertebrate zoologist who has always "outcrayfished" me in the field, I take great pleasure in naming this new species for Alvin L. Braswell, Curator of Lower Vertebrates, NCSM, who has been a friend, colleague, and congenial field companion for many years. Suggested vernacular name: Waccamaw Crayfish.

Acknowledgments

My thanks go to those collectors who provided the specimens of this new crayfish, and particularly to David R. Lenat. I am grateful, too, for the reviews of the manuscript by Roger F. Thoma and Steve Busack, and especially for the always astute attentions of Joseph F. Fitzpatrick, Jr. Nancy Childs provided technical assistance in the preparation of the figure. I also express my sincerest gratitude to Alvin L. Braswell, John E. Cooper, Jr., Martha R. Cooper, Jesse Perry, and particularly to Don Howard, without whose unstinting assistance this paper would never have been realized. My greatest debt, which I cannot adequately express, remains to the late Horton H. Hobbs, Jr., mentor and friend, whose outstanding work on the members of the Pictus Group of *Procambarus* provided the framework for understanding the relationships of *P. braswelli.*

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A new species of freshwater crab of the genus *Phallangothelphusa* Pretzmann, 1965 from Colombia (Crustacea: Decapoda: Pseudothelphusidae)

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Abstract.—A new species of the genus *Phallangothelphusa* Pretzmann, 1965 is described. With the addition of the new species, this genus now includes two species endemic to Colombia: *P. dispar* (Zimmer, 1912) and *P. magdalenensis*, new species. Their distribution comprises the upper and middle Magdalena valley region including the adjacent slopes of the Eastern and Central Andes. The two species are distinguished by features of the first male gonopod.

The monotypic genus *Phallangothelphusa* Pretzmann, 1965, was defined to include *P. dispar* (Zimmer, 1912). With the discovery of *P. magdalenensis*, new species, described herein, the genus now comprises two species of freshwater crabs that inhabit lower mountain springs and streams on the upper and middle Magdalena valley region on the adjacent slopes of the Andes, at altitudes ranging from 300 to 1500 m above sea level. The new species is found in the middle Magdalena valley at altitudes ranging from 300 to 900 m above sea level, where a humid climate exists.

As defined by (Rodriguez 1982), species of the genus *Phallangothelphusa* are characterized by an exognath approximately four-fifths the length of the ischium of the third maxilliped; the orifice of the efferent branchial channel is partially closed by the extension of the lateral lobe of the epistome. Also, the first male gonopod is straight; the marginal lobe is simple and straight; the apical portion is formed by two projections and the mesial side, which surround the spermatic channel.

The shape of the orifice of the efferent branchial channel and the length of the exognath are considered primitive features. Thus, it is probable that this genus derives from an ancient stock of the genus *Strengeriana* Pretzmann, 1971. The structure of the first male gonopod in members of *Phallangothelphusa* resembles slightly that found in members of the tribe Kingleyini; however, the apical portion is completely different (Rodríguez 1982)

The systematics of *Phallangothelphusa* were reviewed by Rodríguez (1982). The morphology of the first male gonopod is a critical diagnostic character in species of freshwater crabs. In the present description of *P. magdalenensis*, the terminology established by Smalley (1964) and Rodríguez (1982) is used for the male first gonopods. The material is deposited at Museo de Historia Natural, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN-MHN), and Instituto Venezolano de Investigaciones Científicas (IVIC). The abbreviations cb and cl stand for carapace breadth and carapace length, respectively.

Family Pseudothelphusidae Rathbun, 1893
Tribe Strengerianini Rodríguez, 1982
Genus *Phallangothelphusa*
Pretzmann, 1965
Phallangothelphusa magdalenensis,
new species
Figs. 1, 2

Holotype.—Quebrada La Cristalina, Vereda La Cristalina, Inspección Puerto Rom-

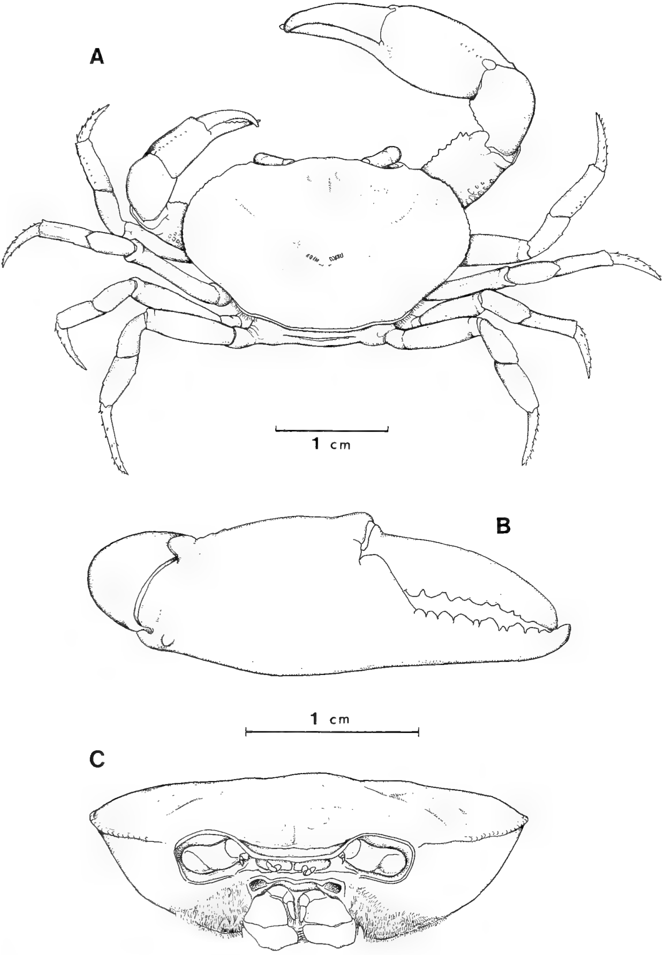

Fig. 1. *Phallangothelphusa magdalenae*, new species, holotype (ICN-MHN-CR 1603): A, dorsal view of carapace and pereiopods; B, chela of largest cheliped, external view; C, frontal view of carapace.

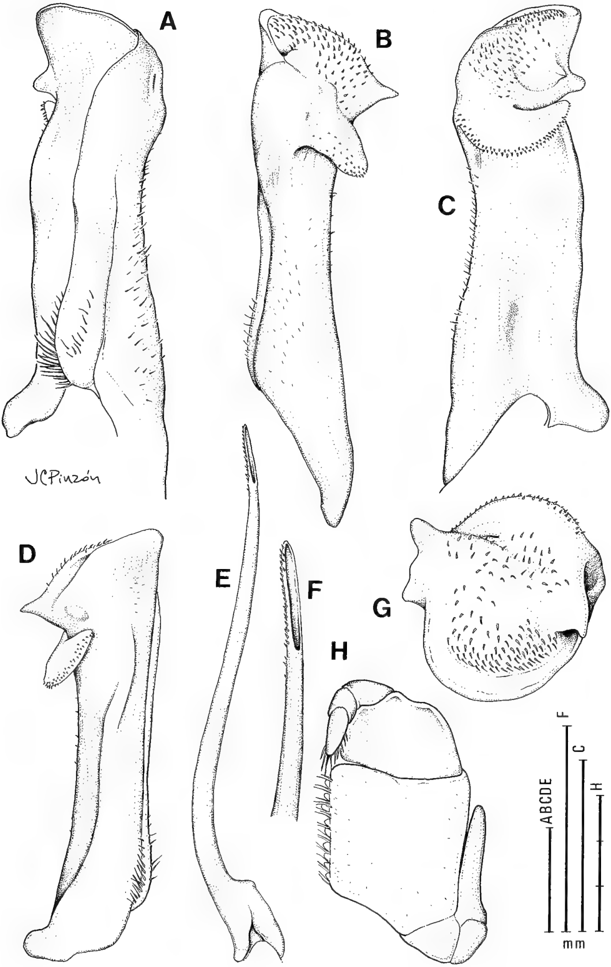

Fig. 2. *Phallangothelphusa magdalenensis*, new species, holotype (ICN-MHN-CR 1603), left first gonopod: A, whole gonopod, caudal view; B, whole gonopod, lateral view; C, whole gonopod, cephalic view; D, whole gonopod, mesial view; G, apex, distal view. Left second gonopod: E, whole gonopod, caudal view; F, detail of apex, caudal view; H, left third maxilliped external view.

ero, Municipio Puerto Boyacá, Boyacá Department, Colombia, 350 m alt., 17 Sep 1996, leg. M. R. Campos: 1 male, cl 18.2 mm, cb 31.0 mm (ICN-MHN-CR 1603).

Paratypes.—20 males, cl 13.7–16.9 mm, cb 22.5–29.4 mm, 13 females, cl 15.1–19.9 mm, cb 24.9–35.0 mm (ICN-MHN-CR 1604).

Additional material examined.—Vereda Dosquebradas, Inspección Puerto Romero, Municipio Puerto Boyacá, Boyacá Department, Colombia, 500 m alt., 18 Sep 1996, leg. M. R. Campos: 5 males, cl 13.7–16.7 mm, cb 24.1–28.5 mm, 3 females, cl 12.3–17.0 mm, cb 20.4–30.1 mm (ICN-MHN-CR 1606). Quebrada Honda, Vereda El Oasis, Municipio Otanche, Boyacá Department, Colombia, 625 m alt., 19 Sep 1996, leg. M. R. Campos: 10 males, cl 12.1–19.6 mm, cb 20.6–33.9 mm, 6 females, cl 13.1–19.5 mm, cb 22.7–34.4 mm (ICN-MHN-CR 1608). Sitio Barbascales, Vereda Gramales, Inspección Guadualito, Municipio Yacopí, Boyacá Department, Colombia, 700 m alt., 2 Nov 1995, leg. M. R. Campos: 17 males, cl 12.9–16.7 mm, cb 20.5–27.8 mm, 9 female, cl 12.6–16.4 mm, cb 18.9–28.5 mm (ICN-MHN-CR 1527). Sitio Barbascales, Vereda Gramales, Inspección Guadualito, Municipio Yacopí, Boyacá Department, Colombia, 700 m alt., 2 Nov 1995, leg. M. R. Campos: 1 male, cl 15.7 mm, cb 26.2 mm (IVIC). Sitio Cajonales, Vereda Gramales, Inspección Guadualito, Municipio Yacopí, Boyacá Department, Colombia, 850 m alt., 30 Oct 1995, leg. M. R. Campos: 1 male, cl 14.0 mm, cb 23.4 mm, 2 females, cl 12.3, 14.3 mm, cb 20.0, 23.8 mm (ICN-MHN-CR 1522).

Diagnosis.—First male gonopod with the apical portion carrying 2 broad projections: distal one ending in 2 lobes directed mesially, and proximal one prominent and projected caudally, with basal part covered with rows of spinules. Apex of mesial side rounded, swollen, and bearing numerous brown spinules.

Description of holotype.—Cervical groove almost straight and narrow, ending near lateral margin. Anterolateral margin with depression behind anteroexternal orbital angle; with 6–7 papillae not well defined anterior to cervical groove, followed by 16 papillae decreasing in size posteriorly. Postfrontal lobes ovally shaped and high; median groove absent. Surface of carapace in front of postfrontal lobes slightly excavated in frontal view and inclined anteriorly. Upper border of front convex in dorsal view, marked with row of tubercles; lower margin almost straight in frontal view. Surface of front between upper and lower borders wide and vertical. Lower orbital margins each with row of tubercles. Surface of carapace smooth, covered with small papillae; limits between regions indistinct (Fig. 1A, C). Merus of endognath of third maxilliped with depression on distal half of external margin; exognath approximately 0.8 length of ischium of third maxilliped (Fig. 2H). Orifice of efferent branchial channel partially closed by extension of lateral lobe of epistome (Fig. 1C).

First pereiopods heterochelous in both sexes; in holotype, 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 3–4 tubercles on internal crest, and prominent blunt distal spine. Palms of both chelipeds smooth and swollen. Fingers of larger chela gaping when closed, tips crossing, and with rows of tubercles; fingers of smaller chela elongated (length 1.76 times length of carpus), not gaping when closed, tips crossing, and with rows of tubercles (Fig. 1B). Walking legs (second to fifth pereiopods) slender, dactyli of pereiopods elongated (length 1.5 times length of propodi), those of second to fifth pereiopods each with 5 rows of large spines diminishing in size proximally; arrangement of spines on dactylus of right third pereiopod as follows: anterolateral and anteroventral rows with 6 spines, external row with 7 spines, posteroventral row with 3 spines, and posterolateral row with 4 spines.

First male gonopod straight, wide in caudal view; marginal lobe simple, straight (Fig. 2A). Apical portion carrying 2 broad projections: distal one ending in 2 lobes directed mesially, proximal one prominent, projected caudally, and with basal part covered by rows of spinules (Fig. 2C, D). Apex of mesial side rounded, swollen, bearing numerous brown spinules (Fig. 2B, G). Second male gonopod with spinules on distal portion, tip cup-shape (Fig. 2E, F).

Color nomenclature follows Smithe 1975. The holotype preserved in alcohol is light brown (near 121C, mikado brown) with 28, olive-brown specks on the dorsal side of carapace. The walking legs are 28, olive-brown. The chelae are 240, kingfisher rufous on the dorsal side, and 132C, orange-rufous on ventral side. The ventral surface of the carapace is 24, buff with 28, olive-brown specks.

Ecology.—The specimens were collected in shady, moist banks of springs and small streams. They were found in soft mud, under rocks, or in burrows. The largest populations were found at the following localities: Quebrada Honda, Vereda El Oasis, Municipio Otanche, and Sitio Barbascales, at Vereda Gramales, Inspección Guadualito, Municipio Yacopí, Boyacá Department.

Etymology.—The specific name refers to the Magdalena valley region, where the specimens were collected.

Remarks.—This species is very similar to *Phallangothelphusa dispar*. The two can be distinguished by the following features of the first male gonopod. The apical portion of *P. dispar* is formed by two narrow and single projections directed mesially, while in *P. magdalenensis* they are broad. In the later species, the distal projection ends in two lobes and the proximal one is prominent and projected caudally. The apex of the mesial side is rounded and swollen in the new species, whereas the apex is funnel-shaped in *P. dispar*.

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Typilobus kishimotoi, a new leucosiid crab (Crustacea: Decapoda: Brachyura) from the Miocene Katsuta Group, Japan

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Abstract.—*Typilobus kishimotoi*, new species, a crab of the family Leucosiidae, is described from the middle Miocene Katsuta Group in Okayama Prefecture, southwest Japan. The discovery of the species shows that *Typilobus* had reached Japan, on the west side of the North Pacific, by middle Miocene.

Typilobus was established within the family Leucosiidae Samouelle, 1819, by Stoliczka, 1871, based on a single species, *Typilobus granulosus* Stoliczka, 1871, from the Lower Miocene of Pakistan. Since then, *Typilobus* spp. have been recorded from the Eocene-Miocene of Europe, the Miocene of Egypt, and the Miocene of Sabah (Glaessner 1969, Quayle & Collins 1981, Förster & Mundlos 1982, Morris & Collins 1991, Müller 1993). Although *Typilobus* is an extinct genus, Via Boada (1969: 422), Quayle & Collins (1981: 743) and Förster & Mundlos (1982: 163) suggested that the genus is closely related to the extant leucosiid genera, *Randallia* Stimpson, 1857, and *Philyra* Leach, 1817.

In this paper a new species of *Typilobus* from the Japanese Miocene is described. The specimens were collected from silty sandstone within the Yoshino Formation of the Katsuta Group exposed at Mino (Loc. T.A.-34 of Kishimoto 1995) and Tanaka (Loc. T.A.-37 of Kishimoto 1995), Katsuou-cho, Katsuta-gun, Okayama Prefecture (Fig. 1). According to Yoshimoto (1979), the Katsuta Group is assigned to Zones N. 8b-9 (earliest middle Miocene) of Blow's (1969) scale of planktonic foraminifera. Karasawa & Kishimoto (1996) reported four additional decapod species, *Cancer sanbonsugii* Imaizumi, 1962, *Scylla* sp. aff. *S. serrata* (Forskål, 1775), *Carcinoplax antiqua* (Ristori, 1889), and *Miosesarma japonicum* Karasawa, 1989, from both localities. Among these, *C. antiqua* and *M. japonicum* are predominant. The decapod assemblage suggests a depositional environment within the upper sublittoral zone on a sandy bottom (Karasawa & Kishimoto 1996).

Systematics

Section Heterotremata Guinot, 1977
Superfamily Leucosioidea Samouelle, 1819
Family Leucosiidae Samouelle, 1819
Genus *Typilobus* Stoliczka, 1871

Type species.—*Typilobus granulosus* Stoliczka, 1871, by monotypy.

Geologic range.—Middle Eocene–Middle Miocene.

Typilobus kishimotoi, new species
(Fig. 2)

Philyra sp.—Kishimoto, 1995: 49, pl. 7, figs. 1–5.

Typilobus sp. nov.—Karasawa & Kishimoto, 1996: 46, fig. 12.

Material examined.—MFM39017 (holotype), carapace length 14.4 mm × carapace width 17.1 mm, Mino, Katsuou-cho, Katsuta-gun, Okayama Prefecture.—MFM39018 (paratype), carapace length 10.6 mm × carapace width 11.5 mm, Tanaka, Katsuou-cho, Katsuta-gun, Okayama Prefecture.

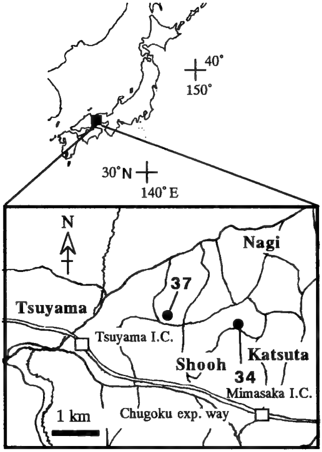

Fig. 1. Locality map.

Diagnosis.—Carapace large, transversely oval in outline, dorsal surface with 2 longitudinal ridges on the postfrontal depression, and with small tubercles on mesogastric and mesobranchial regions.

Etymology.—The specific name is dedicated to Mr. S. Kishimoto who first reported the present species.

Description.—Large sized *Typilobus*, up to 17 mm carapace width. Carapace transversely oval in outline, length about $^4/_5$ its width, widest about midlength. Carapace of small specimen (12 mm in width) subovate in outline, slightly wider than long. Orbitofrontal margin sulcate, upturned, occupying about ¼ of carapace width. Orbit small, concave with small postorbital spine. Anterolateral margin convex; lateral margin developed as thin edge from weak cervical notch to lateral tubercle. Lateral tubercle bluntly rounded, slightly upturned, situated posterior to mid-carapace length. Posterolateral margin nearly straight, about $^4/_5$ length of anterolateral and lateral margins, with small, bluntly rounded tubercle of which tip is directed dorsally and anteriorly. Posterior margin slightly convex, as wide as orbitofrontal margin, posterior angle with small, bluntly rounded tubercle. Dorsal surface of smaller specimen moderately convex, densely covered with small granules of variable diameters, but internal mould of carapace of larger specimen finely pitted. Postorbital depression with two lon-

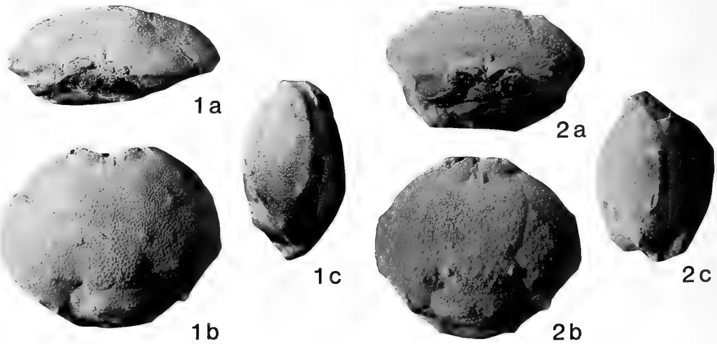

Fig. 2. *Typilobus kishimotoi*, new species. 1a–c, holotype (MFM39017), × 3.0, 1a, frontal; 1b, dorsal; 1c, lateral view. 2a–c, paratype (MFM39018), × 3.5. 2a, frontal; 2b, dorsal; 2c, lateral view.

		Europe	Indian	NW. Pacific
MIOCENE	M	*Typilobus moralejai* Müller, 1993 [Spain]	*Typilobus sadeki* Withers, 1925 [Egypt]	*Typilobus kishimotoi* [Japan] *T. marginatus* Morris & Collins, 1991 [Sabah]
	E	Tethys	*Typilobus granulosus* Stoliczka, 1871 [Pakistan]	*Typilobus* sp., Morris & Collins 1991 [Sabah]
OLIGOCENE		*Typilobus corrodatus* (Noetling, 1885) [Germany] *T.* cfr. *corrodatus*, Förster & Mundlos, 1982 [Germany] *T. birsteini* Förster & Mundlos 1982 [Turkmenistan]		
EOCENE		*Typilobus belli* Quayle & Collins, 1981 [England] *T. boscoi* Via Boada, 1959 [Spain] *T. modregoi* Via Boada, 1959 [Spain] *T. obscurus* Quayle & Collins, 1981 [England] *T. semseyanus* Lőrenthey, 1909 [Hungary]	*Typilobus trispinous* Lőrenthey, 1909 [Egypt]	

Fig. 3. Geological and geographical distribution of the genus *Typilobus* Stoliczka, 1871.

gitudinal ridges behind median sulcus of frontal region. Hepatic region separated from gastric region by shallow groove. Small tubercle on each hepatic region in angle of hepatic and cervical furrows. Cervical furrow distinct, but becoming obsolete before reaching anterolateral margin. Cardiac region strongly tumid, transversely pentagonal in outline, with 3 nodes set in inverted triangle; it is separated from branchial regions by deep grooves and delimited from posterior margin by narrow, flattened intestinal region. Small tubercles on rectangular urogastric lobe near mesogastric lobes.

Ventral aspects unknown.

Remarks.—This new species has close affinities with the type of the genus, *T. granulosus*, from the lower Miocene (Aquitanian) of Kutch, Pakistan, and *Typilobus sadeki* Withers, 1925, from the middle Miocene (Vindobonian) of West Sinai, Egypt. The new species differs in having small tubercles on the gastric and branchial regions, and in having two longitudinal ridges on the postorbital depression. Unlike *T. sadeki*, *T. kishimotoi* has a pair of tubercle on each posterior angle. Small granules on the dorsal surface, and a nongranular anterolateral margin, readily distinguish *T. kishimotoi* from the other middle Miocene species, *Typilobus marginatus* Morris & Collins, 1991, from the Segama Group of Sabah, and from *Typilobus moralejai* Müller, 1993, Langhian, Spain by having marginal tubercles and a well defined cardiac region.

The dorsal surface in the smaller specimen is densely covered with small granules, but it in the larger one is finely pitted. The dorsal regions of the smaller specimen are well defined rather than those of the larger. These differences lie in preservations of both specimens. In the smaller specimen the carapace is well preserved, but the larger one shows only internal surface of the carapace.

Early members of *Typilobus* (*T. belli* Quayle & Collins 1981, *T. boscoi* Via Boada 1959, *T. semseyanus* Lőrenthey 1898, *T. modregoi* Via Boada 1959, *T. obscurus*

Quayle & Collins 1981, *T. trispinosus* Lőrenthey 1909) are known from the middle Eocene of England (Quayle & Collins 1981), Spain (Via Boada 1959) and Egypt (Lőrenthey 1909) (Fig. 3). The genus occurs in Oligocene deposits from Germany (Noetling 1885, Förster & Mundlos 1982) and Turkmenistan (Förster & Mundlos 1982). *Typilobus granulosus* has been known from the lower Miocene of Pakistan (Stoliczka 1871), and an unnamed Lower Miocene species is recorded from Sabah (Morris & Collins 1991). By the Middle Miocene the genus was established in Spain (Müller 1993), Egypt (Withers 1925), Sabah (Morris & Collins 1991), and Japan. This sequence of occurrences suggests that the genus originated in the west Tethys, and that migration from the Tethys region to the Indo-West Pacific regions occurred during the Miocene.

Acknowledgments

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Intraspecific variation in external morphology of the American lobster, *Homarus americanus* (Crustacea: Decapoda: Nephropidae)

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Abstract.—Intraspecific variation in external morphology of *Homarus americanus* H. Milne Edwards was examined in order to interpret better the fossil record of clawed lobsters. Several hundred *H. americanus* were collected from the Gulf of Maine. Lobsters were collected from rocky, shelly and muddy substrates. Detailed examination of 175 specimens indicates that carapace proportions, carapace groove positions, expression of carapace spines and general claw form are virtually constant within the sample—regardless of age, sex or substrate. This corroborates the scarcely published conclusion of taxonomists on modern lobsters: these external features are, in fact, reliable species characters. This study also shows, however, that number and arrangement of spines on the rostrum and claws are variable within the species and, therefore, not good species characters; this variation is unrelated to age, sex or substratum.

The clawed lobsters have a fossil record extending back to the Permo-Triassic (ca. 250 m.y.a.). The extant family Nephropidae sensu Tshudy & Babcock (1997)—to which *Homarus* Weber, 1795 belongs—is known from rocks of Early Cretaceous age (ca. 130 m.y.a.). Observations on fossil lobsters are almost entirely limited to external hard part morphology. Interpretations of the taxonomy and evolution of fossil lobsters are, therefore, based exclusively on external hard parts, especially carapace groove pattern and aspects of carapace ornamentation. An understanding of intraspecific variation is fundamentally important to these interpretations but there is scant published information on intraspecific external variation in lobsters.

Templeton (1935) examined *H. americanus* H. Milne Edwards 1837 from four localities off New Brunswick and Nova Scotia, with the most widely separated locales being approximately 440 km apart. In lobsters approaching sexual maturity, he observed that the claws of males, and the width and thickness of the abdomen in females, increase at a greater rate than does body length. He also observed that these features vary geographically.

Saila & Flowers (1969) studied bathymetrically related external variation in *H. americanus* collected off Rhode Island by analyzing linear measurements of 16 external features, mostly aspects of the appendages and carapace. Using multivariate analyses, they found that inshore and offshore groups were distinguishable by "small shape differences," that these differences were more pronounced in females than in males, and they suggested that there may also be differences among geographically isolated subsets inshore. They also reported that females were relatively bulkier than males. Two of their 16 measurements, carapace length and maximum carapace width, were considered in the present study.

This study of intraspecific variation in *H. americanus* was conducted in order to better interpret the fossil record of *Homarus*-like lobsters. *Homarus*-like fossils have been collected from stratigraphic sections spanning millions of years; these collec-

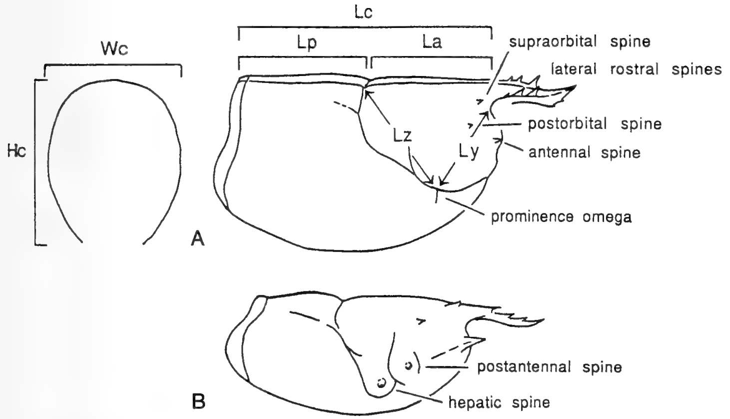


Fig. 1. Locations of carapace spines and orientations of measurements taken on: a, *Homarus americanus* H. Milne Edwards (posterior and lateral views), and b, *Hoploparia stokesi* (Weller). Abbreviations: Hc, carapace height; La, length of anterior portion of carapace; Lc, carapace length; Lp, length of posterior portion of carapace; Ly, distance between prominence omega and orbit; Lz, distance between prominence omega and dorsal end of postcervical groove; Wc, carapace width.

tions provide opportunities to examine lobster morphology through time. Interpretations of these potentially informative fossil collections have been limited, however, by lack of published information on intraspecific variation in modern lobsters.

Hoploparia McCoy, 1849 is a fossil genus considered ancestral to *Homarus* (e.g., Mertin 1941, Secretan 1964, Tshudy & Babcock 1997). In Antarctic (James Ross basin) *Hoploparia stokesi* collected over an area roughly 80 km in longest dimension, five external features are observed to display significant, stratigraphically related variation (Feldmann & Tshudy 1989, Feldmann et al. 1993). These features include: the morphology of the abdominal tergum-pleuron boundary (which on geologically older lobsters bears a prominent boss but, on younger lobsters, bears an oblique ridge), the morphology of the thoracic region (which is more inflated on geologically older lobsters), hepatic and postantennal spines (which are present on geologically older lobsters), and general claw form (being more delicately constructed, less sculptured and more finely ornamented in geologically older lobsters) (Feldmann et al. 1993). In order to infer intraspecific or interspecific morphologic variability within these fossil *Hoploparia*, we examined the nature of intraspecific variation in the same or similar features in *H. americanus*.

Methods

Several hundred live *H. americanus* were collected from the Gulf of Maine in the vicinity of Mount Desert Island, Maine (from Stave Island to Sand Beach on Mount Desert Island, a distance of approximately 15 km) in May–June, 1995. The first 175 specimens were measured and otherwise examined in detail. Specific features examined include (Fig. 1): the proportions of the carapace and some of its regions, the presence or absence of three carapace spines (supraorbital, postorbital and antennal), the

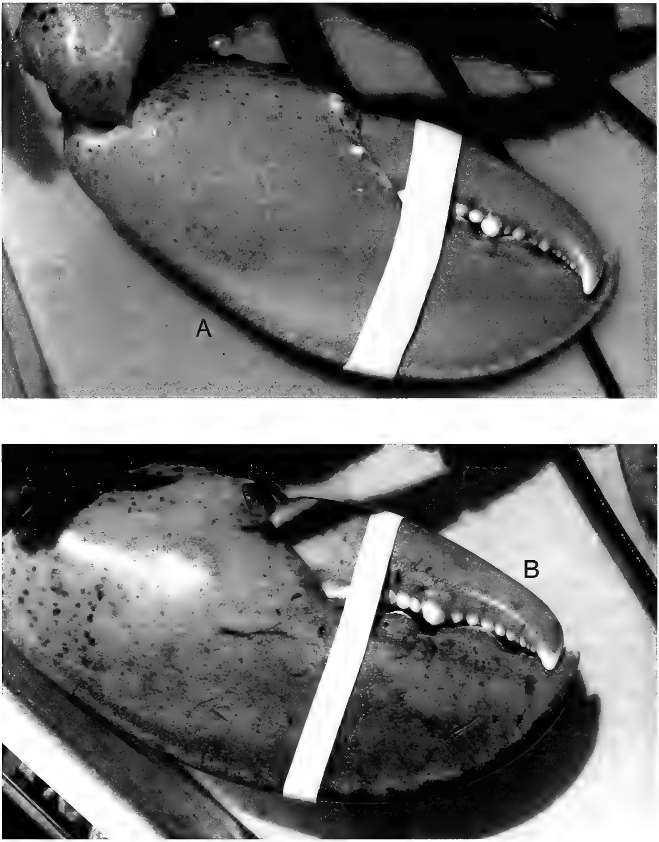
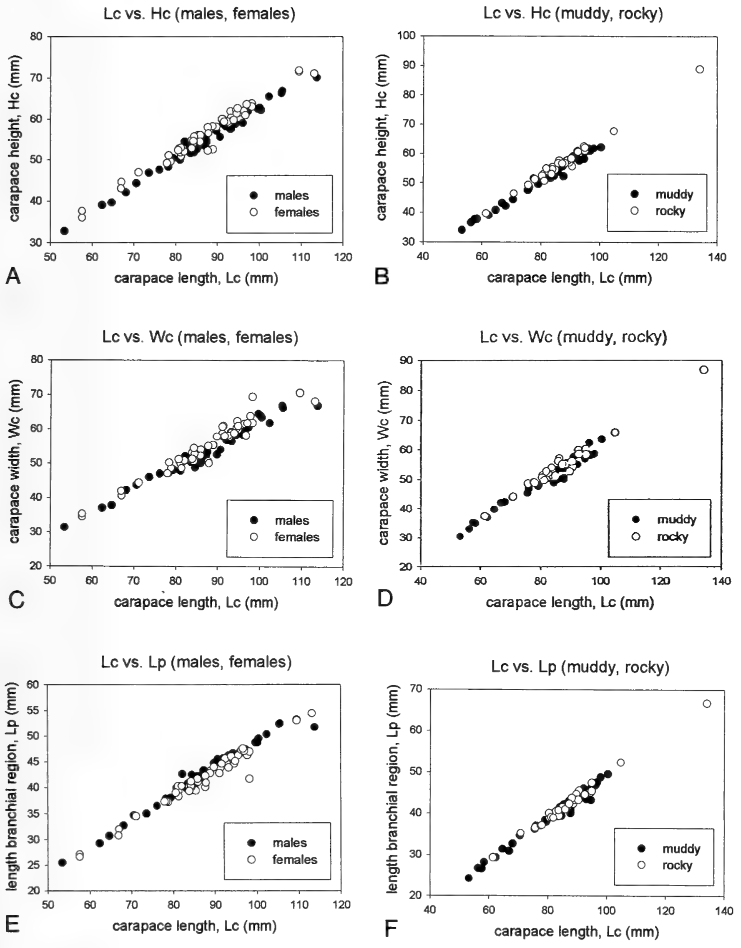


Fig. 2. Unabraded (a) and abraded (b) lower surface of claws on lobsters inhabiting muddy and rocky substrata, respectively.

arrangement and number of rostral spines, and the arrangement and number of spines along the upper, inner margin and lower, inner margin of the palm (propodus) of cutter and crusher claws. Carapace length (Lc), height (Hc), width (Wc), and the distance from the posterior margin of the postcervical groove (Lp) (Fig. 1) were measured in order to gauge the volume of the thoracic region and, by implication, the branchial chamber. The distance from the prominence omega (mandibular external articulation) to the orbit (Ly), and to the postcervical groove on the dorsomedian (Lz) (Fig. 1), were also recorded in order to detect any variation in the proportions of the carapace.



Lc vs. Hc (males, females)

Lc vs. Hc (muddy, rocky)

Lc vs. Wc (males, females)

Lc vs. Wc (muddy, rocky)

Lc vs. Lp (males, females)

Lc vs. Lp (muddy, rocky)

Fig. 3. Scatterplots of various measurements (carapace height, Hc; carapace width, Wc; posterior portion of carapace, Lp) versus carapace length (Lc). Plots indicate that measured features increase linearly through ontogeny and do not vary with sex or substratum.

Table 1.—Frequency of expression of postorbital spine in association with sexes and substrates.

# Postorbital spines	Overall $n = 148$	Male $n = 73$	Female $n = 75$	Mud dweller $n = 32$	Rocky dweller $n = 31$
Spine	66%	71%	60%	75%	71%
Spinule	29%	25%	33%	16%	29%
Absent	5%	4%	7%	9%	0%

Table 2.—Frequency of expression of antennal spines in association with sexes and substrates.

# Antennal spines	Overall $n = 150$	Male $n = 74$	Female $n = 76$	Mud dweller $n = 33$	Rocky dweller $n = 32$
2	8%	7%	9%	0%	16%
1.5	7%	7%	8%	6%	3%
1	84%	86%	82%	94%	81%
0.5	0%	0%	0%	0%	0%
0	1%	0%	1%	0%	0%

Each of these features/distances was examined with respect to age (proxied by carapace length), sex and substratum texture.

Water depth and substratum texture were recorded for each of the lobsters examined. Lobsters were collected from depths ranging from 6 to 50 meters. Substratum texture was interpreted from sonar reflection on a fathometer (American Pioneer Fishscope). Bottom grabs taken at several stations confirmed accuracy in interpreting bottom texture from the fathometer.

Dissolved oxygen for surface and bottom water samples was determined on-board by Winkler titration. Unfortunately, the hypothesis that "thoracic inflation (as observed in Antarctic *Hoploparia*) is an adaptation to living in less oxygenated environments" could not be satisfactorily tested in this study; dissolved oxygen just above the substratum varied insignificantly over the study area during the investigation.

Relationships between morphology and age, sex or environment were evaluated using univariate statistics. Methods included regression and Chi-square analyses.

Testing for any relationships between morphology and environment in *H. americanus* is complicated because many individuals of this species make an annual offshore–onshore migration. Many lobsters found in the study area during the summer spend the winter offshore in deeper waters and, presumably, on finer-grained and, probably, less-oxygenated bottoms. Therefore, collecting a lobster from a particular location is no guarantee that the lobster spent its life, or any large amount of time, there. Fortunately, the substrate a lobster has inhabited, at least since its last molt, can be determined by examining the lower surface of the chelipeds. Lobsters inhabiting

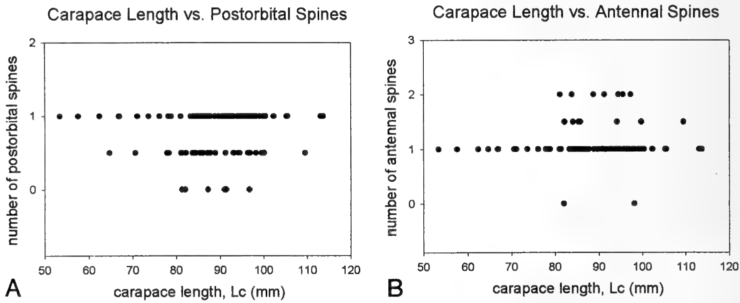


Fig. 4. Scatterplots comparing number of carapace spines with carapace length. Plots indicate that expression of spines is unrelated to age.

Table 3.—Frequency of expression of 0–4 lateral rostral spines in association with sexes and substrates.

# Rostral spines	Overall $n = 172$	Male $n = 88$	Female $n = 84$	Mud dweller $n = 44$	Rocky dweller $n = 31$
4	2%	2%	1%	5%	0%
3	45%	41%	50%	39%	42%
2	51%	56%	47%	52%	58%
1	1%	0%	2%	2%	0%
0	1%	1%	0%	2%	0%

Table 5.—Frequency of expression of 1–4 spines on lower margin of crusher claw in association with sexes and substrates.

# Spines on Cr-low	Overall $n = 60$	Male $n = 38$	Female $n = 22$	Mud dweller $n = 28$	Rocky dweller $n = 32$
1	32%	29%	36%	32%	32%
2	48%	47%	50%	50%	49%
3	18%	21%	14%	18%	19%
4	2%	3%	0%	0%	0%

muddy bottoms have pristine lower claw surfaces, whereas lobsters inhabiting hard, rocky bottoms are badly abraded and scratched over this region (Fig. 2). Those inhabiting gravelly or shelly bottoms exhibit an intermediate condition.

The study area, being approximately 16 km in longest dimension, is small geographically, but the lobsters collected in this area range seasonally over a much larger region. Therefore, we think we are examining variation over an area comparable in size to the James Ross basin, Antarctica, which yielded the fossil *Hoploparia.*

Results and Discussion

General.—Detailed examination of 175 *H. americanus* indicates that carapace proportions, carapace groove positions, carapace spines and general claw form show only a small degree of variation (over the measured size range of individuals in the study area)—regardless of age, sex or substratum. These findings corroborate the generally held but scarcely published conclusion of taxonomists on modern lobsters: these features are essentially constant within species and, therefore, taxonomically useful at the species level. The number and arrangement of spines on the rostrum and claws are, however, variable within the species and, therefore, much less useful taxonomically. This variation is unrelated to age, sex or substratum.

Carapace proportions.—Over the measured size range of adult lobsters, all of the measured features on the carapace increase linearly with an increase in carapace length. These parameters include carapace height (Fig. 3A–B), width (Fig. 3C–D), length of the branchial region (Fig. 3E–F). distance between the orbit and prominence omega, and distance between prominence omega and the postcervical groove at the dorsomedian. The complete overlap of data plotted for males and females, and for dwellers on muddy and rocky substrata, indicates that neither sex nor substratum affects the proportions of the carapace or its regions.

Carapace spines.—On specimens of *H. americanus* from around Mt. Desert Island, the supraorbital spine is invariably present (100%; $n = 84$) and the postorbital and antennal spines are nearly always present in some form. These observations corroborate

Table 4.—Frequency of expression of 4–6 spines on upper margin of crusher claw in association with sexes and substrates.

# Spines on Cr-up	Overall $n = 60$	Male $n = 38$	Female $n = 22$	Mud dweller $n = 28$	Rocky dweller $n = 32$
4	62%	58%	68%	61%	63%
5	32%	37%	23%	36%	28%
6	7%	5%	9%	3%	9%

Table 6.—Frequency of expression of 4–6 spines on upper margin of cutter claw in association with sexes and substrates.

# Spines on Cut-up	Overall $n = 60$	Male $n = 38$	Female $n = 22$	Mud dweller $n = 28$	Rocky dweller $n = 32$
4	56%	54%	57%	52%	58%
5	41%	46%	33%	44%	39%
6	3%	0%	10%	4%	3%

Table 7.—Frequency of expression of 1–3 spines on lower margin of cutter claw in association with sexes and substrates.

# Spines on L-cut	Overall $n = 60$	Male $n = 38$	Female $n = 22$	Mud dweller $n = 28$	Rocky dweller $n = 32$
1	54%	57%	50%	57%	53%
2	39%	38%	40%	41%	37%
3	7%	5%	10%	4%	10%

the observations of taxonomists of modern lobsters (Fenner Chace, Jr., Austin B. Williams, pers. comm.) that carapace spines are reliable diagnostic characters at the species level. The postorbital spine (Table 1) is usually small—much smaller than the supraorbital spine—and is almost always present (95%; $n = 148$), either as a distinct spine (66%) or a subtler, less pointed projection (29%). On a few specimens (9%, $n = 85$), the postorbital spine is expressed differently on the left and right sides of the carapace. The antennal spine (or spines) (Table 2) is almost invariably (99%; $n = 150$) present. although form varies in detail. It usually occurs as a single spine (84%), but also occurs as two spines of different size (7%), or as a pair of spines of equal size (8%). On some specimens (20%; $n = 85$), the antennal spine is expressed differently on the left and right sides of the carapace. Expression of the postorbital and antennal spines is independent of age (Fig. 4), sex or substratum (Table 8).

Lateral rostral spines.—Although not considered in the study of Antarctic *Hoploparia*, one of us (D.T.) has observed, in many other fossil lobsters, intraspecific or interspecific variation in the arrangement and number of spines on the rostrum and inner margins of the claws. Therefore, in this study, we examined variation in these features in *H. americanus*. The number of distinct lateral spines (smaller "spinules" not counted) on each side of the rostrum is variable ($n = 172$), but almost always either 2 (51%) or 3 (45%); 0 (1%), 1 (1%) or 4 (2%) spines occur rarely (Table 3). As with the carapace spines, variation in number of lateral rostral spines is unrelated to age, sex and substratum (Table 8). There is usually (88%; $n = 131$) an equal number of spines on each margin of the rostrum. The number of spinules posterior to these spines is highly variable and often unequal on left and right sides of the carapace.

Claw ornamentation.—Templeton (1935) documented that the claws of male *Homarus* are longer than claws of females of the same carapace length. There is no mention

Table 8.—Results of Chi-square test for independence of morphology from both sex and substratum. Cutoff value is for 95% confidence level. In all cases, calculated value is less than cutoff value, indicating that variation in these features is independent of sex or substratum.

Morphologic feature	Chi-square values for sex	Chi-square values for substratum
Postorbital spine	Calculated = 2.328 Cutoff = 5.991	Calculated = 4.216 Cutoff = 5.991
Antennal spine	Calculated = 1.481 Cutoff = 7.815	Calculated = 5.756 Cutoff = 7.815
Lateral rostral spines	Calculated = 4.838 Cutoff = 9.488	Calculated = 2.978 Cutoff = 9.488
Spines on cutter claw inner, upper margin	Calculated = 4.063 Cutoff = 5.991	Calculated = 0.095 Cutoff = 5.991
Spines on cutter claw inner, lower margin	Calculated = 0.539 Cutoff = 5.991	Calculated = 0.876 Cutoff = 5.991
Spines on crusher claw inner, upper margin	Calculated = 1.422 Cutoff = 5.991	Calculated = 1.035 Cutoff = 5.991
Spines on crusher claw inner, lower margin	Calculated = 1.260 Cutoff = 7.815	Calculated = 0.030 Cutoff = 7.815

in the literature, however, of intraspecific differences in claw shape or ornamentation. Claw shape was not formally evaluated in this study, but observations of hundreds of specimens revealed no obvious variation in claw shape. The surface of the claws in *H. americanus* is consistently smooth, regardless of age, sex or substratum. The number of spines on the inner margin of the palm (propodus) of both cutter and crusher claws is, however, variable, and therefore unsuitable for defining species (Tables 4–7). Variation in these spines is unrelated to age (Fig. 4), sex or substratum (Table 8).

Summary

Examination of 175 *H. americanus* indicates that carapace proportions, carapace groove positions, expression of carapace spines and general claw form are nearly constant on lobsters in the study area—regardless of age, sex or substrate. These findings corroborate the scarcely published conclusion of taxonomists on modern lobsters that these features are reliable species characters. This study also shows, however, that number and arrangement of spines on the rostrum and claws are variable within the species and, therefore, not good species characters; this variation is unrelated to age, sex or substratum.

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A revision of the freshwater crabs of the family Pseudothelphusidae (Decapoda: Brachyura) from Ecuador

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Abstract.—Revised diagnoses and illustrations of the species of pseudothelphusid crabs previously known to occur in Ecuador are provided and five new species. *Hypolobocera esmeraldensis*, *H. konstanzae*, *H. muisnensis*, *H. mindonensis* and *Lindacatalina sumacensis*, are described. The validity of pentanomial names proposed in the literature for some Ecuadorian species is revised in the light of series of specimens collected in their distributional areas. The genera *Hypolobocera*, *Moritschus* and *Lindacatalina* are redefined and several species are reassigned among these genera.

The systematics of Neotropical freshwater crabs of the family Pseudothelphusidae is relatively complex due to lack of dependable taxonomic differences in their carapace and appendages. The male first gonopods provide the most reliable characters of diagnostic value, whereas potential somatic characters, such as the dentition of the lateral border, form and position of the cervical grooves and postfrontal lobes, sculpturing of the front, and proportions of the third maxilliped, display very slight interspecific differences.

In almost all cases it is not possible to establish infraspecific categories that will meet the two criteria accepted for other animal groups, viz., that the differences are slight, but constant through large series of specimens (Mayr 1964), and that no overlap occurs in the geographical distribution of the supposed subspecies (Mayr et al. 1953).

In his revision of the Pseudothelphusidae, Pretzmann (1972) proposed the organization of the taxa into a tetranomial scheme (genus, subgenus, species and subspecies). In further contributions he arranged some crabs from Ecuador into a more elaborate pentanomial nomenclature (Pretzmann 1978, 1983a, 1983b). Thus, for example, what he called *Hypolobocera* (*Hypolobocera*) *aequatorialis aequatorialis* in 1972, became *Hypolobocera* (*Hypolobocera*) [*aequatorialis*] *aequatorialis aequatorialis* in his later contributions. The erection of these infraspecific categories was based usually on one or two specimens. In some cases two infraespecific categories of the same species were reported from the same localities (see for instance *Hypolobocera* (*Hypolobocera*) [*peruviana*] *henrici henrici* and *Hypolobocera* (*Hypolobocera*) [*peruviana*] *henrici nora*). This treatment of the Ecuadorian species has resulted in considerable confusion and serious difficulties for the identification of binomial taxa.

In the present contribution the validity of some of these infraspecific taxa is revised in the light of series of specimens collected in the same areas as Pretzmann's materials (Pretzmann & Radda 1978). All new or critical species reported here are fully illustrated. For other species only figures of the first male gonopods are given, together with references to adequate illustrations in the literature (see "Additional illustrations" under each species). Two species, *Hypolobocera conradi* (Nobili, 1897) and *Lindacatalina hauserae* Pretzmann, 1977b, are not illustrated for lack of material. Terminology for gonopod morphology follows Smalley (1964).

Abbreviations used are cl. for carapace length and cb. for carapace breadth. The materials recorded are deposited in the Reference Collection of the Instituto Venezolano de Investigaciones Científicas, Caracas (IVIC), the British Museum, London (BM), the Museum of Natural History of Tulane University, New Orleans (TU), the National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM), the Muséum nationale d'Histoire naturelle, Paris (MNHN), the Strasbourg Museum (SM) and the Naturmuseum und Forschunginstitut Senckenberg, Frankfurt am Main (SMF).

Systematics

Family Pseudothelphusidae Rathbun, 1893

Key to Genera from Ecuador

1. Lateral margin of first gonopods produced into a defined, although sometimes reduced, lateral lobe 2
–. Lateral margin widening progressively towards the apex which extends considerably laterally, giving the apex in caudal view a characteristic triangular-elongated appearance .... *Moritschus*
2. Lateral lobe densely covered with spinules. Exognath of third maxilliped usually more than 0.45 length of ischium of endognath .... *Lindacatalina*
–. Lateral lobe naked or with a few sparse spinules and short hairs. Exognath of third maxilliped usually less than 0.45 length of ischium of endognath .... *Hypolobocera*

Hypolobocera Ortmann, 1897

Diagnosis.—Exognath of third maxilliped usually less than 0.45 length of ischium of endognath (Table 1). First male gonopods with strong longitudinal ridge on caudal surface, and well defined (although sometimes reduced) lateral lobe (Fig. 1A); apex truncated, either circular or oblong in distal view, with round papilla near spermatic channel (Fig. 1B).

Table 1.—Carapace breadth (cb) of largest males recorded and proportions of the exognath to ischium of endognath of third maxillipeds in Ecuadorian Pseudothelphusidae.

	cb (mm)	Exognath/ endognath
Hypolobocera aequatorialis	66.8	0.35
H. caputii	41.9	0.40
H. conradi	88.0	0.30
H. delsolari	65.1	0.30
H. esmeraldensis	33.8	0.40
H. exuca	61.8	0.30
H. guayaquilensis	44.1	0.30
H. konstanzae	56.8	0.30
H. mindonensis	27.1	0.30
H. muisnensis	51.6	0.35
H. orcesi	23.5	0.30
H. rathbuni	45.0	0.35
Lindacatalina brevipenis	27.5	0.65
L. hauserae	25.0	0.50
L. latipenis	55.7	0.50
L. orientalis	28.0	0.65
L. puyensis	32.3	0.45
L. sumacensis	35.6	0.45
Moritschus ecuadorensis	25.5	0.45
M. henrici	91.1	0.40

Type species.—*Potamia chilensis* H. Milne Edwards & Lucas, 1844.

Distribution.—Panama, Colombia, Venezuela, Ecuador and Peru.

Key to Species from Ecuador

1. Lateral lobe of first gonopods reduced or obsolescent (Figs. 1E, 4A) 2
–. Lateral lobe well developed 6
2. Lateral lobe with small scattered papillae (Fig. 7A) .... *H. mindonensis*
–. Lateral lobe with smooth surface or with scattered short hairs 3
3. One or two prominent tubercles on apex of first gonopods 4
–. No prominent tubercles on apex of first gonopods 5
4. One prominent tubercle; apex produced laterally into extraordinarily long, obtuse lobe (Fig. 4B) .... *H. exuca*
–. Two prominent tubercles on apex of gonopods (Fig. 9A–C) .... *H. orcesi*

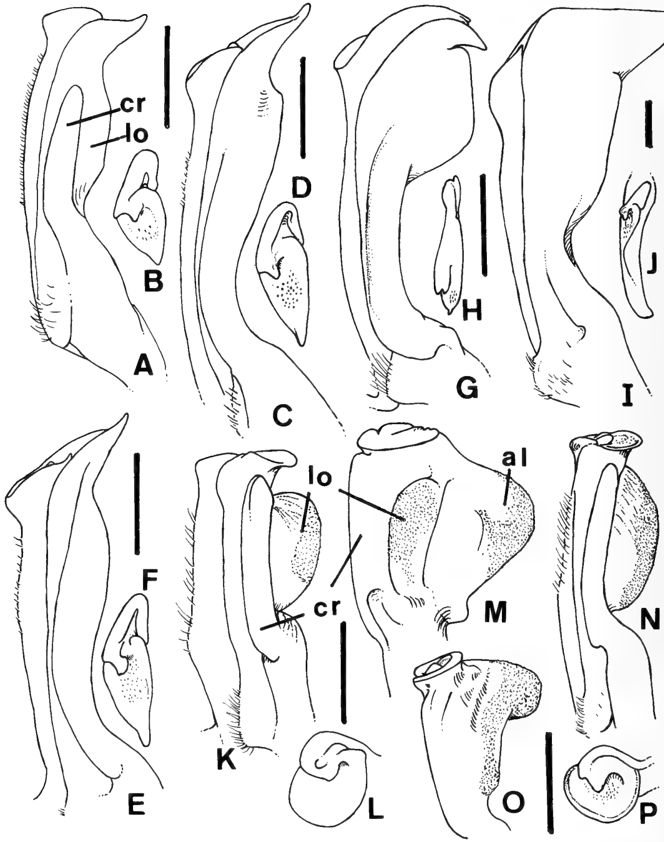

Fig. 1. First left gonopod of Ecuadorian Pseudothelphusidae: A, B, *Hypolobocera aequatorialis* (Ortmann, 1897), holotype from Ecuador (SM); C, D, *H. caputii* (Nobili, 1901), from Río Quevedo (IVIC 628); E, F, *H. rathbuni* Pretzmann, 1968, from Río Peripa, between Aurora en Puerto Limón (IVIC 631); G, H, *Moritschus ecuadorensis* (Rathbun, 1897), from west of Gualea (BM 918.1.31.11); I, J, *M. henrici* (Nobili, 1897), from Ecuador (IVIC 615); K-M, *Lindacatalina brevipenis* (Rodríguez & Díaz), 1981, from Ecuador (IVIC 606); N–P, *L. latipenis* (Pretzmann, 1968), from Ecuador (IVIC 621). A, C, E, G, I, K, N, caudal; M, O, lateral; B, D, F, H, J, L, P, apex, distal; lo, lateral lobe; cr, caudal ridge; al, supplementary lobe. Scales = 2 mm.

5. With large tubercle on external surface of palm .... *H. conradi*
–. Without a large tubercle on external surface of palm .... *H. rathbuni*

6. Lateral lobe of first gonopods long, oblong, with proximal angle rounded and distal angle sloping gently to apex ... 7
–. Lateral lobe triangular or subtriangular... 8

7. A large tubercle on external surface of palm . . . . *H. delsolari*
–. Without a large tubercle on external surface of palm . . . . *H. aequatorialis*
8. Apex of first gonopods in caudal view forms very elongated spine, projected laterally and distally (Figs. 1C, 3A) . . 9
–. Apex in caudal view with lateral border obtuse or with short spine (Figs. 5A,6A,8A) 10
9. Border of lateral lobe straight or slightly convex distally . . . . *H. caputii*
–. Border of lateral lobe rounded distally . . . . *H. esmeraldensis*
10. Apex in distal view with lateral margin acute or ending in a short point directed laterally 11
–. Apex in distal view with lateral margin rounded . . . . *H. muisnensis*
11. Border of lateral lobe expanded and rounded distally . . . . *H. guayaquilensis*
–. Border of lateral lobe narrow and transverse distally . . . . *H. konstanzae*

Hypolobocera aequatorialis
(Ortmann 1897)
Figs. 1A, B

Pseudothelphusa dentata.—Ortmann, 1893: 493 (pro parte ex. b, c).

Potamocarcinus aequatorialis Ortmann, 1897:317, 319, pl. 17, fig. 5.

Pseudothelphusa aequatorialis.—Rathbun, 1898:532, 537.—Young, 1900:213.—Nobili, 1901:38.—Rathbun, 1905:285.—Colosi, 1920:18.—Coifmann, 1939:106.

Strengeria (*Strengeria*) *aequatorerorialis* [sic].—Pretzmann, 1965:7.

Hypolobocera (*Hypolobocera*) *aequatorialis aequatorialis*.—Bott, 1967:368, fig. 3a–c.—Pretzmann, 1971:17; 1972:43, figs. 186–189, 265–267.

Hypolobocera aequatorialis.—Rodriguez, 1982:61 (pro parte and fig. 33e, f).

Hypolobocera (*Hypolobocera*) [*aequatorialis*] *aequatorialis aequatorialis*.—Pretzmann, 1983b:351, figs. 4, 18, 26, 39, 54, 56, 71.

Hypolobocera (*Hypolobocera*) *aequatorialis nigra* Pretzmann, 1968:6; 1972:44, figs. 167–169, 262–264; 1971:17.

Hypolobocera (*Hypolobocera*) [*aequatorialis*] *aequatorialis nigra*.—Pretzmann, 1983b:352, figs. 3, 17, 25, 35, 52, 55, 72.

Material.—Ecuador: Leg. Reiss, 1 male holotype of *Potamocarcinus aequatorialis* Ortmann, 1897 (SM).—Arroyo de Arrayán, N of Baños, Parroquia de Chirgua, Tungurahua Province, 1750 m alt., 7 Nov 1980, leg. H. Díaz, 3 males cl. 31.5, 31.0 and 21.8 mm, cb. 49.8, 48.8 and 33.7 mm, 2 mature females cl. 35.0 and 34.1 mm, cb. 57.0 and 53.5 mm, 1 immature female cl. 27.8 mm, cb. 43.5 mm (IVIC 590).—Baños, Tungurahua Province, Dec 1984, leg. Ferro, 1 male, 1 immature female (IVIC 972).—Quebrada Punsán, Pueblo de Alba, E of Baños, Tungurahua Province, 1600 m alt., 7 Nov 1980, leg. H. Díaz, 1 male cl. 27.8 mm, cb. 43.4 mm, 1 immature female cl. 31.4 mm, cb. 49.5 mm (IVIC 591).—Río Villa, Ponce, 44 km N Machala, Azuay Province, 50 m alt., 11 Nov 1980, leg. H. Díaz, 70 males, the largest cl. 40.8 mm, cb. 66.8 mm, 57 females, the largest cl. 32.5 mm, cb. 51.6 mm (IVIC 624).—Cantón San Miguel, 5 km N of Balsapamba, roadside stream feeding into Río Cristal, Bolívar Province, 20 May 1996, leg. R. von Sternberg, 7 males, the largest cl. 19.4 mm, cb. 30.5 mm, 1 juvenile (IVIC 940).—Town of Pullatanga, Chimborazo Province, 15 Feb 1996, leg. R. von Sternberg, 6 males, 2 females (IVIC 969).—Village of Ocaña, Cañar Province, 8 Jun 1996, leg. F. von Sternberg, 1 male, 10 juveniles (IVIC 970).

Additional illustrations.—Rodríguez (1982, figs. 19k; 22d,i; 23f; 33a–f.)

Diagnosis.—Carapace with upper frontal margin angled, with faintly indicated papillae and deep notch at middle. Larger chela with oblong, but not well developed, dark protuberance near articulation of fingers and smaller dark tubercle above it. Lateral lobe of first male gonopods prominent, square in outline; apex in caudal view funnel-shaped; in distal view elongated laterally and ending in spine directed distally and transversely to main axis of appendage.

Remarks.—Ortmann (1893) identified as *Pseudothelphusa dentata* three lots of crabs from South America. Later he (Ortmann 1897) separated lots b and c, from Río Ucayalli, Perú, and the Eastern Cordillera of Ecuador, respectively, under his new species *Potamocarcinus aequatorialis*, but he used as types only the specimens from the second locality. The first male gonopods of these specimens (Rodríguez 1982, fig. 33e, f) closely correspond with those of the specimens recorded above from the vicinity of Baños and from Ponce, near Machala, but the specimens recorded by Rodríguez (1982, fig. 33a–d) from Río Jubones belong in *Hypolobocera delsolari.* Bott (1967) recorded the species from Paramba, on the headwaters of Río Mira, 75 km from Tulcán, Imbambura Province. In the material reported above from Ponce, near Machala, the first gonopods exactly correspond with those of the type material and with those of our specimens from Baños; the only difference is that in the largest male (cl. 40.8 mm) from the first loclity the spine of the apical lobe is directed laterally and perpendicularly to main axis of the appendage. In the specimens from Ponce the papillae on antero-lateral margins of carapace are more clearly defined. According to these records, *H. aequatorialis* occupies widely separated areas on the eastern and western slopes of the Eastern Cordillera of Ecuador.

Pretzmann used the specific name *Hypolobocera aequatorialis* in several contributions (Pretzmann 1968, 1977b, 1983b). In his most recent one (Pretzmann 1983b) he grouped under this species the following forms: *Hypolobocera* (*Hypolobocera*) [*aequatorialis*] *aequatorialis aequatorialis*, *Hypolobocera* (*Hypolobocera*) [*aequatorialis*] *aequatorialis nigra*, *Hypolobocera* (*Hypolobocera*) [*aequatorialis*] *delsolari delsolari*, *Hypolobocera* (*Hypolobocera*) [*aequatorialis] delsolari isabella.* It is not possible to discern from this pentanomial nomenclature whether the author assigned a subspecific rank to these forms. In the present contribution *Hypolobocera* (*Hypolobocera*) [*aequatorialis*] *delsolari delsolari* is considered as a separate species and *Hypolobocera* (*Hypolobocera*) [*aequatorialis*] *delsolari isabella* a junior synonym of this.

Pretzmann's (1968) original material of *Hypolobocera* (*Hypolobocera*) [*aequatorialis*] *aequatorialis nigra* comprised 1 male holotype, 1 male paratype and 3 females, collected by Cayan in 1883 at an undetermined locality in Ecuador. The first gonopods of the holotype was illustrated in Pretzmann 1972. Subsequently, he (Pretzmann 1977b) recorded the distribution of his taxon as "Westrand der Anden nordwestlich Machala". However, this distribution must refer to two lots of crabs recorded later (Pretzmann 1983b) from 20 and 35 km NE of Machala in the Río Jubones basin. There are no clear cut characters that separate our specimens collected around Machala from the typical *H. aequatorialis*, even in the coloration of the specimens which was given as one of the diagnostic characters. In specimens from a single locality preserved in alcohol, some specimens are dark brown, almost black, on anterior portion, including cervical grooves, while other have cervical grooves and cardiac regions olive. On the other hand, *H. delsolari*, *H. muisnensis* and H. *orcesi* also display this last pattern of coloration, with the cervical grooves and gastric regions of a lighter shade than the dorsal surface of carapace.

Hypolobocera caputii (Nobili 1901)
Fig. 1C, D

Pseudothelphusa caputii Nobili, 1901: 38.—Rathbun, 1905:299.—Colosi, 1920: 20.—Coifmann, 1939:107.—Rodríguez, 1982:190.

Strengeria (*Strengeria*) *caputi* [sic].—Pretzmann, 1965:7 (pro parte).

Strengeria (*Strengeria*) *caputii.*—Pretzmann, 1972:40; 1983b:353.

Hypolobocera (*Hypolobocera*) *caputii caputii.*—Pretzmann, 1971:17; 1972:40 (pro parte) figs. 254, 255, not figs. 270–

272, 302, 303 [=*Hypolocera chilensis* (H. Milne Edwards & Lucas, 1844)]; 1983b:353, figs. 2, 22, 29, 38, 48, 59, 65.

Hypolobocera (*Hypolobocera*) [*chilensis*] *caputii.*—Pretzmann, 1977b:436.

Hypolobocera quevedensis Rodríguez & Díaz, 1981:308, figs. 2, 6, 7.

Material.—Ecuador: Río Quevedo, 36 km N of Quevedo, Pichincha Province, 24 Jun 1976, leg. H. Díaz, 1 male holotype of *H. quevedensis*, cl. 26.8 mm, cb. 41.9 mm (IVIC 628).—Puerto Rico, Quevedo, Los Ríos Province, 3 males cl. 21.5, 17.9 and 14.0 mm, cb. 33.4, 27.8 and 21.2 mm (TU 94-100-1, USNM 273521).

Additional illustrations.—Rodríguez & Díaz (1981, figs. 2, 6, 7).

Diagnosis.—Carapace with upper frontal margin well defined although not projected, with some tubercles faintly indicated and deep notch at middle. Larger chela with small swelling on outer surface, at articulation of dactylus. First male gonopods with lateral lobe well developed, long, subtriangular, with distal margin angled, advanced; apex with conspicuous lanceolate lobe directed distally.

Remarks.—Nobili (1901) in his original description of *Pseudothelphusa caputii* did not give an illustration of the male gonopods, and they were only vaguely described as "lunghe e robuste, troncate e svasate obliquamente all'apice." Since the holotype and only specimen recorded could not be located at the Museo Zoologico di Torino, where it was presumably to be deposited, Rodríguez (1982) considered this species incertae sedis. These circumstances also led Rodríguez & Díaz (1981) to erroneously describe their material from Quevedo under a new species, *H. quevedensis*. Pretzmann (1965, 1971 and 1972) recorded *Hypolobocera caputii* on several occasions, but never stated that he had examined the holotype, although subsequently he (Pretzmann 1983b) illustrated the gonopod, carapace, orbital area and third maxilliped of the holotype, thus validating his report of this species.

Nobili's species has been recorded in the literature from Río Peripa (Nobili 1901, Pretzmann 1983b), 42 km from Quevedo (Rodríguez & Díaz 1981, holotype of *Hypolobocera quevedensis*); Quevedo and Mindo (Pretzmann 1983b). The latter author gives as the general distribution of *Hypolobocera caputii* the basins of the Daule and Vincens rivers.

Hypolobocera conradi (Nobili 1897)

Pseudothelphusa conradi Nobili, 1897:3; 1901:38.—Rathbun, 1898:533, 537 (pro parte); 1905:298, fig. 90a, d (pro parte, not material from Perú and fig. 90b, c).—Young, 1900:217.—Colosi, 1920:19.—Coifmann, 1939:107.—Rodríguez, 1982: 63.

Strengeria (*Strengeria*) *conradi.*—Pretzmann, 1965:7.

Potamocarcinus (*Hypolobocera*) *conradi.*—Bott, 1967:367, fig. 2a, b, c.

Hypolobocera (*Hypolobocera*) *conradi conradi.*—Pretzmann, 1971:17; 1972:41, fig. 273, 274; 1977b:430, fig. 1; 1983b: 356, figs. 74, 79–83.

Pseudothelphusa dubia Colosi, 1920:19.—Coifmann, 1939:107.

Hypolobocera (*Hypolobocera*) *dubia.*—Pretzmann, 1972:48 (pro parte, not the material from Colombia and figs. 224–226, 230–232, 236, 237).

Material.—Ecuador: Sabanilla, 18 km NNE from Loja, headwaters of Río Zamora, Zamora Province, Sep 1985, leg. L. Coloma, 2 males cl. 20.7 and 19.1 mm, cb. 31.5 and 29.2 mm (IVIC 946).

Additional illustrations.—Bott (1967, fig. 2a, b, c).

Diagnosis.—Carapace with upper frontal margin angled, with flat papillae and deep notch at middle. Large flat tubercle on the insertion of the dactylus of the larger chela, fingers conspicuously high. First male gonopods slender, with lateral lobe long, re-

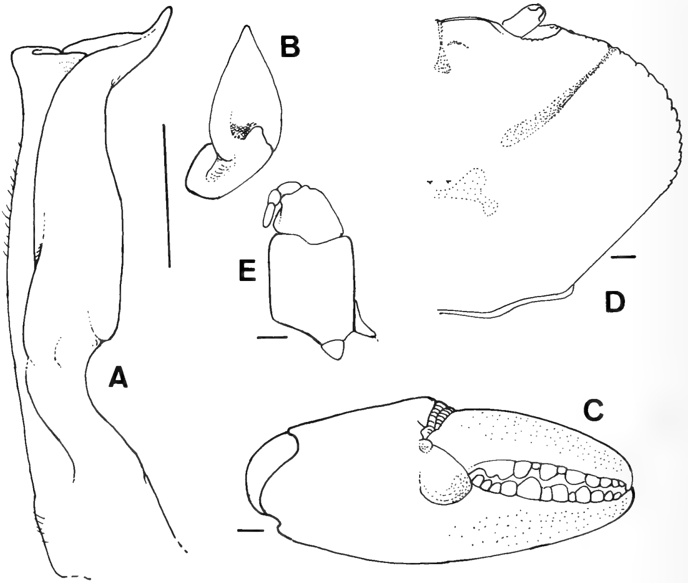

Fig. 2. *Hypolobocera delsolari* Pretzmann, 1978, male from Quebrada Celata, Azuay Province, Ecuador (IVIC 960): A, first left gonopod, caudal; B, apex, distal; C, chela of largest cheliped, external view; D, dorsal view of right side of carapace; E, third maxilliped. Scales = 3 mm.

tracted; apex with conspicuous lateral expansion, in distal view triangular.

Remarks.—The status of Nobili's type material was discussed by Rodríguez (1982), who considered the male recorded by Bott (1970) from Río Santiago as the neotype of the species. Our specimens were collected in a locality within this basin. Since we have examined only the two small males mentioned above, it is not possible to revise the description of the species or to present adequate illustrations. The largest male (20.7 mm cb.) already has a large flat tubercle on the insertion of the dactylus of the larger (left) chela, and the first male gonopods, although not fully developed, present the retracted lateral lobe and the apical expansion characteristic of this species.

Hypolobocera delsolari Pretzmann, 1978
Fig. 2

Hypolobocera (*Hypolobocera*) [*aequatorialis*] *delsolari delsolari* Pretzmann 1977b:436 (nomen nudum); 1978:163, fig. 1; 1983a:304, figs. 11, 12; 1983b: 350, fig. 58.—Rodríguez, 1982:210.

Hypolobocera (*Hypolobocera*) [*aequatorialis*] *delsolari isabella* Pretzmann 1977b: 436 (nomen nudum); 1978:163, fig. 2; 1983a:304, figs. 13, 14;1983b:350.—Rodríguez, 1982:210.

Hypolobocera aequatorialis.—Rodríguez, 1980:61 (pro parte) figs. 19k, 23f, 33a–d.

Material.—Ecuador: Río Jubones, leg. Dr. Bray, 2 males cl. 41.0 and 24.6 mm, cb. 65.1 and 40.9 mm (BM).—Quebrada Celata, 1 km from Girón, Azuay Province, 9 Nov 1980, leg. H. Díaz, 1 male cl. 36.6 mm, cb. 58.5 mm, 3 ripe females cl. 48.5, 48.2 and 44.5 mm, cb. 79.5, 75.0 and 70.9 mm, 1 immature female cl. 28.7 mm, cb. 44.8 mm, 2 juveniles (IVIC 960).—Río Chorro, affluent of Río San Vicente in the Río Jubones basin, near Girón, Azuay Province, 11 Nov 1980, leg. H. Díaz, 1 male cl. 37.6 mm, cb. 60.6 mm, 1 immature female cl. 29.0 mm, cb. 45.3 mm (IVIC 959).—Quera, military checkpoint, border of Azuay and El Oro provinces, stream feeding into Río Jubones, 22 May 1996, leg. R. von Sternberg, chela and portions of carapace of a specimen cl. 36.5 mm, cb. 57.5 mm, 4 juveniles (IVIC 942).—Village of Tres Banderas, Azuay Province, roadside ditch, Río Jubones adjacent, 22 May 1996, leg. R. von Sternberg, 2 young males, the largest cl. 17.6 mm, cb. 26.1 mm, 2 juvenile females (IVIC 941).

Diagnosis.—Carapace with upper frontal margin angled, devoid of papillae, with deep notch at middle. Larger chela with large rounded tubercle below articulation of dactylus. First male gonopods with lateral lobe long, oblong, wider proximally; apex with conspicuous lanceolate lobe directed distally.

Remarks.—The apex of the first gonopods in this species resembles that of *Hypolobocera caputii* (Nobili, 1901) in the lateral apical process, but differs in the shape of the lateral lobe.

Hypolobocera esmeraldensis, new species
Fig. 3

Material.—Ecuador: Esmeraldas Province, leg. Juan Carlos, 1 male holotype cl. 20.6 mm, cb. 33.8 mm, 1 immature female cl. 20.9 mm, cb. 33.6 mm (TU 94-100-2).—Chone River, Manabí Province, 1 mature male, broken carapace (TU 94-100-3).

Diagnosis.—Carapace with upper frontal margin devoid of median notch and tubercles. First gonopods with caudal ridge obsolescent distally; lateral lobe narrow, more prominent and excavated distally; apex in distal view with strong curved point projected laterally and distally, in caudal view very elongated laterally.

Description of holotype.—Upper surface of carapace smooth and polished, with regions only slightly indicated. Lateral border of carapace with shallow postorbital notch, without teeth or papillae up to level of cervical grooves; rest of border with approximately 12 distinct triangular teeth which diminishes in size progressively and end at middle of border. Cervical grooves straight and deep, not reaching margins of carapace. Postfrontal lobes absent, its place marked only by 1 or 2 punctae; median groove absent. Upper margin of front almost straight or slightly convex in dorsal view, without median notch and devoid of tubercles. Lower margin sinuous in frontal view; space between both margins narrow.

Palm of larger cheliped (left) moderately inflated, fingers slightly gaping. Exognath of third maxilliped 0.4 length of ischium of endognath.

First male gonopods strongly arcuate in lateral view; caudal ridge curved, becoming indistinct distally; lateral lobe narrow, excavated and more prominent distally; apex in distal view with strong curved point projected laterally and distally, in caudal view very elongated.

Etymology.—The species is named after the Esmeraldas Province where the species was collected.

Hypolobocera exuca Pretzmann, 1977b
Fig. 4

Hypolobocera (*Hypolobocera*) [*conradi*] *exuca* Pretzmann, 1977b:437, fig. 8; 1983b:357, figs. 91–94.

Hypolobocera riveti Rodríguez, 1980:891; 1982:49, figs. 19b, 20e, j, 23b, 25a–e.

Material.—Ecuador: 10 km N of La Troncal, on Río Culebras/Taura, Cañar Province, in a concrete storm drainage ditch, 6 Jun 1996, leg. R. von Sternberg, 1 male cl. 37.6 mm, cb. 59.3 mm, 1 female

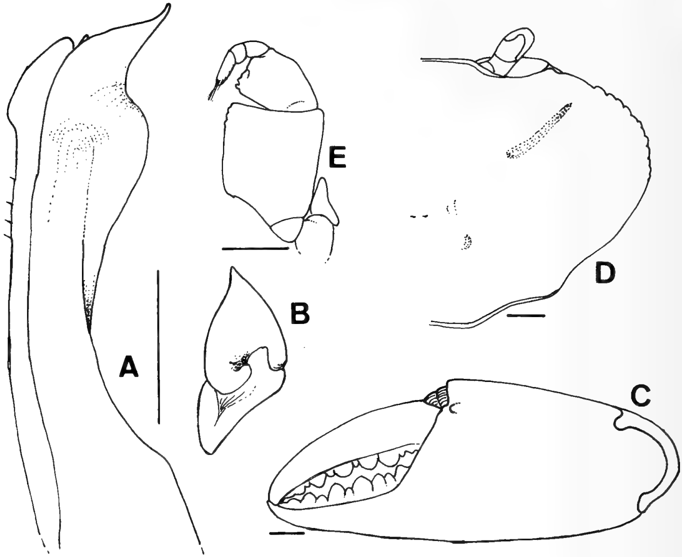

Fig. 3. *Hypolobocera esmeraldensis*, new species, holotype male from Esmeralda Province, Ecuador (TU 94-100-2): A, first left gonopod, caudal; B, apex, distal; C, chela of largest cheliped, external view; D, dorsal view of right side of carapace; E, third maxilliped. Scales = 3 mm.

cl. 21.1 mm, cb. 33.2 mm, 9 juveniles (IVIC 949).—Between La Troncal and Manuel J. Calles, 65 km SE of Guayaquil, Cañar Province, 100 m alt., 10 Nov 1980, leg. H. Diaz, 1 immature male cl. 18.2 mm, cb. 27.2 mm (IVIC 627).—Town of Las Pampas, on Río Toachi, Cotopaxi Province, Oct 1988, leg. G. Onore, 1 male cl.32.4 mm, cb. 50.5 mm (IVIC 950).—Ecuador, without other data, leg. P. Rivet, 2 males cl. 40.8 and 23.6 mm, cb. 61.8 and 37.6 mm, holotype and paratype respectively of *Hypolobocera riveti* Rodríguez, 1980 (MNHN B-5087).

Diagnosis.—Carapace with upper frontal margin angled, with small papillae and deep notch at middle. First male gonopods with lateral lobe absent, replaced by wide depression; apex in lateral view funnel-shaped, with strong elongated projection ending in truncated tip; in distal view strongly expanded cephalically, with conspicuous ridge on caudal side of expansion; prominent subtriangular papilla on caudal side of gonopore; distinct subapical ridge on mesial side.

Remarks.—Pretzmann (1977b) gave as his type locality "Cordillere". The present records fix the area of distribution of the species between the provinces of Cañar and Cotopaxi.

Hypolobocera guayaquilensis Bott, 1967
Fig. 5

Potamocarcinus (*Hypolobocera*) *aequatorialis guayaquilensis* Bott, 1967:368, figs. 4a, b, c.

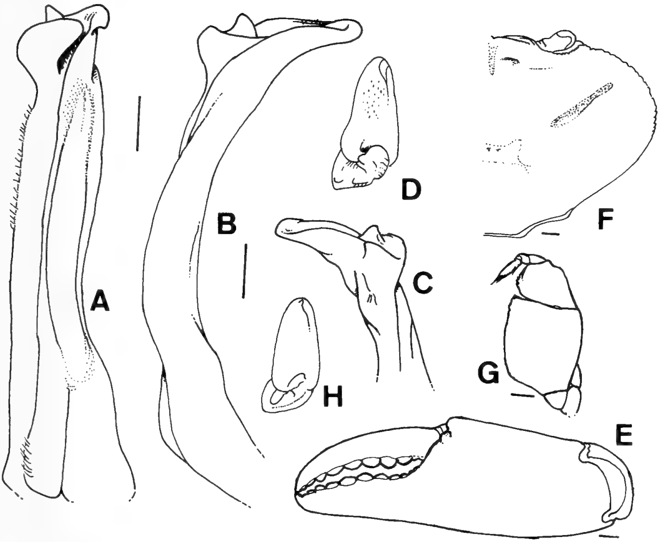

Fig. 4. *Hypolobocera exuca* Pretzmann, 1977b, A–G, male from 10 km N of La Troncal, Cañar Province, Ecuador (IVIC 949): A, first left gonopod, caudal; B, lateral; C, apex, caudo-distal; D, apex, distal; E, chela of largest cheliped, external view; F, dorsal view of right side of carapace; G, third maxilliped. H, specimen from Las Pampas, Cotopaxi Province, Ecuador (IVIC 950), first left gonopod, apex, distal. Scales = 3 mm.

Hypolobocera (*Hypolobocera*) *caputii guayaquilensis.*—Pretzmann, 1971:17 (by inference).

Hypolobocera (*Hypolobocera*) *guayaquilensis.*—Pretzmann, 1972:42, figs. 173–175, textfig 10. *Hypolobocera* (*Hypolobocera*) [*aequatorialis*] *guayaquilensis.*—Pretzmann, 1983b:353, figs. 5, 16, 28, 37, 53, 57, 69.

Hypolobocera guayaquilensis.—Rodríguez, 1982:64.

Material.—Ecuador: Chone, Estero Donde, Manabí Province, 9 Aug 1967, 3 males cl. 26.2, 18.3 and 14.7 mm, cb. 44.1, 29.3 and 23.5 mm, 1 female with young under the abdomen cl. 34.5 mm, cb. 56.2 mm (TU 6374).

Diagnosis.—Carapace with upper frontal margin angulated and devoid of conspicuous tubercles, with notch at middle. First male gonopods strongly arcuate in lateral view; caudal ridge prominent, moderately curved proximally, straight distally; lateral lobe triangular, increasing in width distally, with distal margin rounded; apex in distal view elongated along meso-lateral axis, ending in short lateral point directed laterally.

Remarks.—The type locality is Babahoyo, on the Daule-Vincens basin. The specimens reported above come from a locality 140 km NNW of Babahoyo, on the coastal plain, but the water divide between both basins, on the Conguillo Mountains, is less than 300 m above sea level in some places.

Hypolobocera konstanzae, new species
Fig. 6

Material.—Ecuador: Estero San Agustín, 4 km S from the bridge, Río Banchal, Manabí

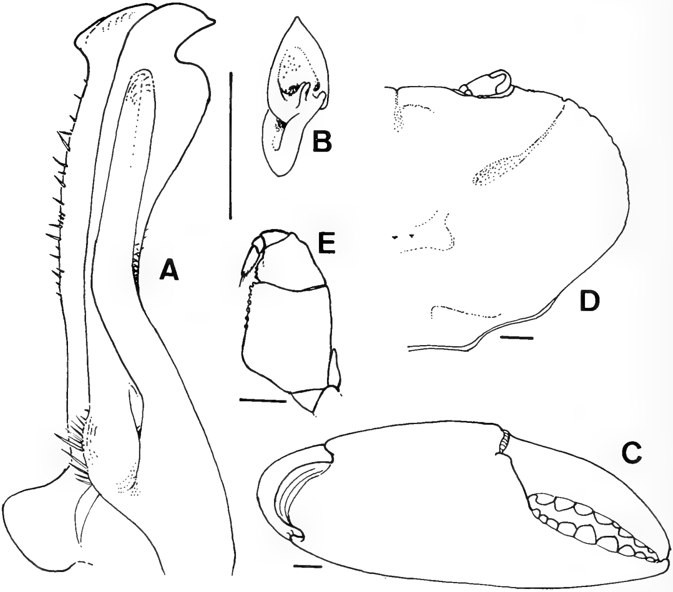

Fig. 5. *Hypolobocera guayaquilensis* Bott, 1967, male from Chone, Manabi Province, Ecuador (TU 6374): A, first left gonopod, caudal; B, apex, distal; C, chela of largest cheliped, external view; D, dorsal view of right side of carapace; E, third maxilliped. Scales = 3 mm.

Province, 6 Jun 1977, leg. H. Díaz, 1 male holotype cl. 37.5 mm, cb. 56.8 mm (IVIC 593).—Village of Cascol, stream adjacent to Río Banchal, lower Río Daule basin, Manabí Province, approx. 1° 40′ S, 80° 30′ W, 4 Jun 1996, leg. R. von Sternberg, 2 young males paratypes (the largest soft shell) cl. 21.8 and 18.9 mm, cb. 33.5 and 29.1 mm respectively, 3 juvenile males, 3 immature females, the largest cl. 22.3 mm, cb. 34.3 mm (IVIC 951).

Diagnosis.—Carapace with upper frontal margin angled, devoid of papillae, with deep notch at middle. First male gonopods with lateral lobe reduced, subtriangular, more expanded distally; apex in caudal view funnel-shaped, moderately elongated laterally, not ending in defined spine; in distal view roughly obtuse-angled, lateral expansion rounded.

Description of holotype.—Carapace narrow (cb/cl = 1.51), surface smooth. Anterolateral margins without shallow notch behind external orbital angles, margin behind it and up to level of cervical grooves smooth, almost straight; approximately 8 small papilliform teeth behind level of cervical grooves, progressively less prominent posteriorly. Cervical grooves almost straight, deep, not reaching margins of carapace. Postfrontal lobes well defined, transverse, with anterior margin rounded; median groove well defined, very narrow anteriorly, making deep incision on upper frontal margin of carapace. Upper frontal margin bilobed in dorsal view; angled, devoid of papillae; lower margin strongly sinuous; space between upper and lower margins narrow.

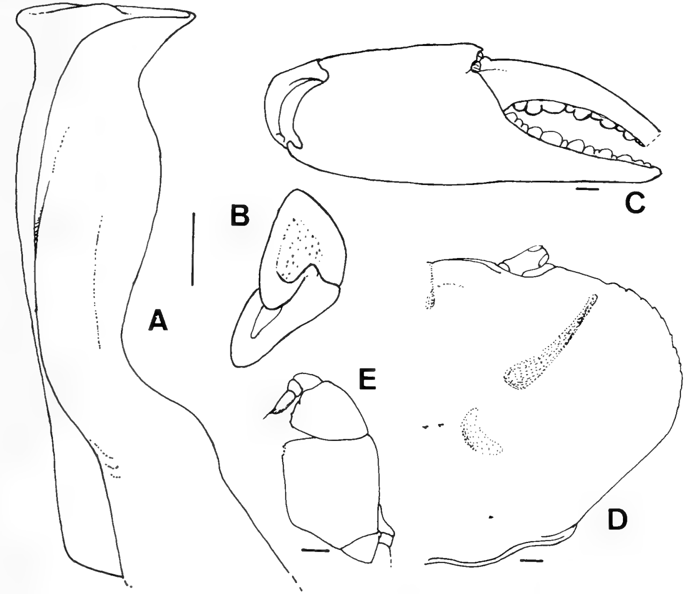

Fig. 6. *Hypolobocera konstanzae*, new species, holotype male from Río Banchal, Manabi Province, Ecuador (IVIC 593): A, first left gonopod, caudal; B, apex, distal; C, chela of largest cheliped, external view; D, dorsal view of right side of carapace; E, third maxilliped. Scales = 3 mm.

Exognath of third maxilliped 0.30 length of ischium of endognath. Chelipeds elongated. Fingers gapping, covered by punctae and few inconspicuous papillae.

First male gonopods with caudal ridge proximally strong and curved to follow strangled shape of basal portion; distally progressively indistinct; lateral lobe reduced, subtriangular, more expanded distally; apex in caudal view funnel-shaped, moderately elongated laterally, not ending in defined spine; in distal view roughly obtuse-angled, lateral expansion rounded; papilla on caudal side of gonopore replaced by semicircular ridge.

Remarks.—The paratypes display the following differences in regard to holotype: The carapace surface has small pores and papillae not visible to naked eye; the antero-lateral margins possess 10–12 small well defined teeth behind level of cervical grooves, which are progressively less prominent posteriorly; the cervical grooves are straight, and reach the margins of carapace; the upper frontal margin is covered with rudimentary papillae; the lower margin is moderately sinuous.

Etymology.—The species is dedicated to Miss Konstanza von Sternberg, for her assistance in the collection of crabs in Ecuador.

Hypolobocera mindonensis, new species
Fig. 7

Material.—Ecuador: Confluence of Río Salaya and Río Mindo, Pichincha Prov-

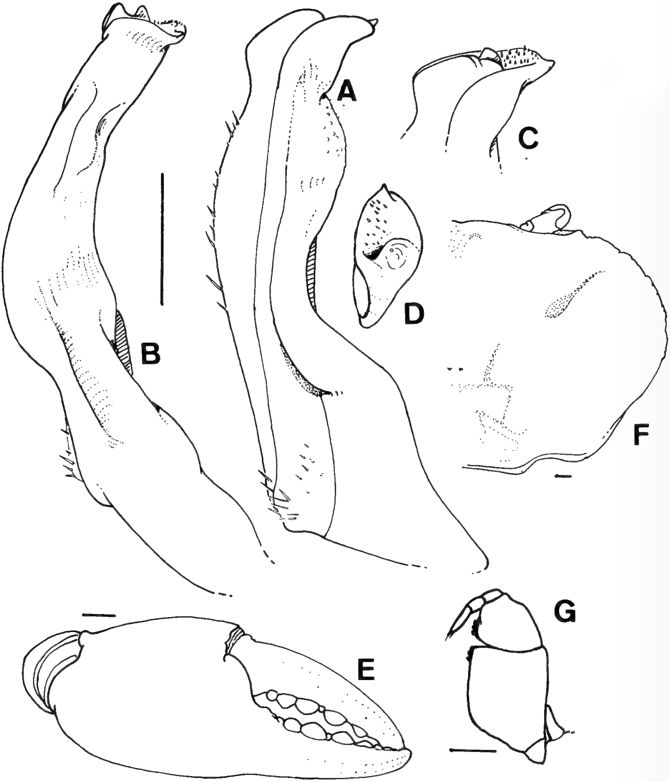

Fig. 7. *Hypolobocera mindonensis*, new species, holotype male from the confluence of Río Salaya and Río Mindo, Ecuador (TU 94-100-4): A, first left gonopod, caudal; B, lateral; C, apex, caudo-distal; D, apex, distal; E, chela of largest cheliped, external view; F, dorsal view of right side of carapace; G, third maxilliped. Scales = 3 mm.

ince, between 1000 and 1200 m altitude, Sep 1968, leg. M. Olalla, 1 male holotype cl. 11.3 mm, cb. 27.1 mm, 14 male paratypes cl. 16.9, 14.7, 14.7, 14.4, 14.4, 14.2, 14.2, 13.7, 13.6, 12.9, 12.0, 11.5, 11.0, and 10.9 mm, cb. 25.2, 23.9, 23.2, 22.2, 23.7, 23.3, 23.1, 21.4, 21.0, 19.4, 18.1, 17.5, 16.5, and 16.4 mm, 2 ovigerous females cl. 15.5 and 15.1 mm, cb. 24.9 and 23.0 mm, with 13 and 18 eggs respectively, 10 mature female paratypes cl. 13.6–22.3 mm, cb. 20.5–33.4 mm, 6 immature females, the largest cl. 17.0 mm, cb. 26.2 mm (TU 94-100-4).

Diagnosis.—Carapace with upper frontal margin rounded, with small papillae and deep notch at middle. First male gonopods with lateral lobe narrow and regularly rounded in outline, covered with minute flattened papillae; apex in caudal view funnel-shaped; elongated in distal view, strong triangular tooth on lateral corner and conical elevated tubercle on caudal side of gonopore.

Description of holotype.—Cervical grooves deep and wide proximally, shallow and straight distally, not reaching margins of carapace. Antero-lateral margins with well defined incision behind outer orbital angle and several ill-defined papillae behind it; tooth at level of cervical grooves and 8–10 very small teeth over rest of margin. Postfrontal lobes almost obsolete, its place indicated by 2 slight swellings; median groove shallow, wide. Upper margin of front rounded, slightly bilobed in dorsal view, with small papillae which are obsolescent towards sides, and deep notch at middle; lower margin moderately sinuous in frontal view; space between upper and lower margins narrow.

Exognath of third maxilliped 0.30 length of ischium of endognath. Larger cheliped with palm inflated, smooth; fingers slightly gapping, with brown-black punctae arranged in parallel lines.

First male gonopods strongly constricted at middle; caudal ridge curved, strongly contoured proximally, becoming indistinct distally; lateral lobe narrow and regularly rounded in outline, with minute flattened papillae; apex funnel shaped in caudal view; elongated along latero-mesial axis, with strong triangular tooth on lateral corner in distal view; conical elevated papilla on caudal side of gonopore.

Etymology.—The species is named after Río Mindo, where it was collected.

Hypolobocera muisnensis, new species.
Fig. 8

Material.—Ecuador: Estero Lojca More, Muisne Salima, Esmeraldas Province, 21 Oct 1988, leg. J. C. Vieira, 1 male holotype cl. 31.1 mm, cb. 51.6 mm (IVIC 952).—Estero El Cañero, La Concordia, Esmeraldas Province, 1 Oct 1988, leg. J. C. Vieira, 1 male cl. 20.7 mm, cb. 31.9 mm (IVIC 953).—Same data, 8 Oct 1988, 1 male cl. 24.2 mm, cb. 39.5 mm (IVIC 954).—Estero Moncauve, Recinto Moncauve, Esmeraldas Province, 5 Jan 1988, leg. J. C. Vieira, 1 male cl. 24.2 mm, cb. 39.5 mm (IVIC 955).

Diagnosis.—Carapace with upper frontal margin well defined, angled, without conspicuous papillae, with deep notch at middle. First male gonopods with lateral lobe triangular, increasing in width distally, with distal margin excavated; apex elongate along meso-lateral axis in distal view, cephalic margin rounded, horseshoe shaped.

Description of holotype.—Lateral border of carapace with shallow notch behind outer orbital angle, followed by short undulated segment; 12–16 very small triangular teeth behind level of cervical grooves, regularly-spaced, subequal in size except for last 3–4 which are squamiform. Cervical grooves deep and wide, slightly arched, reaching margin of carapace. Postfrontal lobes well marked, with distal margin transverse; median groove well defined, forming deep incision at upper border of front; this border well defined, angled, without conspicuous papillae; lower margin thick, strongly sinuous, advanced in relation to upper margin; space between upper and lower margins narrow.

Exognath of third maxilliped 0.35 length of ischium of endognath. Chelipeds heavy, fingers gaping, with rows of minute dark points over outer surface.

First male gonopods strongly arcuate in lateral view; caudal ridge prominent, curving proximally, straight distally; lateral lobe triangular, increasing in width distally, with distal margin excavated; apex in distal view elongated along mesolateral axis, cephalic margin rounded, horseshoe shaped.

Etymology.—The specific epiteth is de-

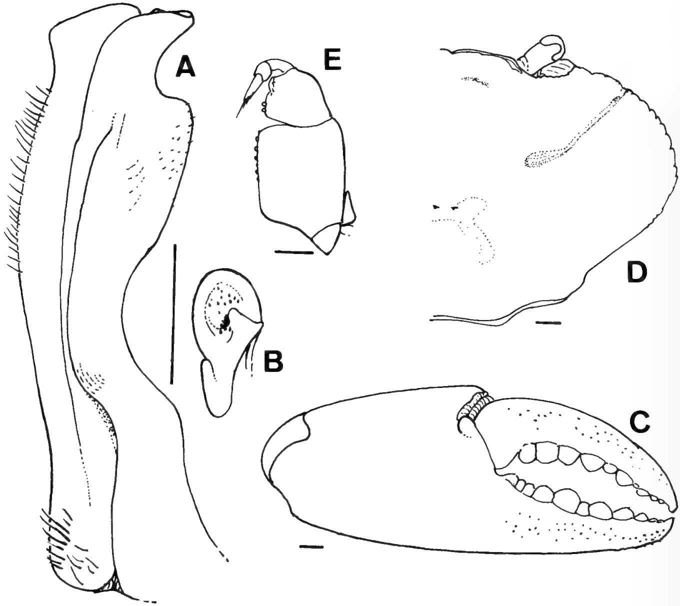

Fig. 8. *Hypolobocera muisnensis*, new species, holotype male from Muisne Salima, Ecuador (IVIC 952): A, first left gonopod; B, apex, distal; C, chela of largest cheliped, external view; D, dorsal view of right side of carapace; E, third maxilliped. Scales = 3 mm.

rived from part of the locality's name where the species was collected.

Hypolobocera orcesi Pretzmann, 1978
Fig. 9

Hypolobocera (*Lindacatalina*) [*plana*] *orcesi* Pretzmann, 1978:166, fig. 6; 1983b: 361.

Hypolobocera (*Lindacatalina*) *orcesi*.—Pretzmann, 1983a:303, pl. 7, 8.

Material.—Ecuador: Valley of Río Mindo, 5 km from Mindo, Pichincha Province, 28 May 1996, leg. R. von Sternberg, 1 male cl. 14.2 mm, cb. 23.5 mm, 1 male soft shell cl. 11.1 mm, 1 juvenile male, 1 mature female cl. 14.8 mm, cb. 24.3 mm (IVIC 956).

Diagnosis.—Carapace with upper frontal margin rounded, devoid of defined papillae. First male gonopods with caudal ridge strongly geniculated proximally, indistinct distally; lateral lobe undifferentiated in caudal view, forming thin ridge in lateral view; apex funnel-shaped in caudal view, projected cephalically in lateral view, subtriangular in distal view, with lateral margin rounded; 2 prominent papillae near gonopore and on cephalic expansion.

Remarks.—The distal angle of the lateral lobe of the gonopod is more squarish in Pretzmann's (1978, fig. 6). Otherwise our material closely corresponds with the original description and with the supplementary characters given by Pretzmann (1983a, b). The

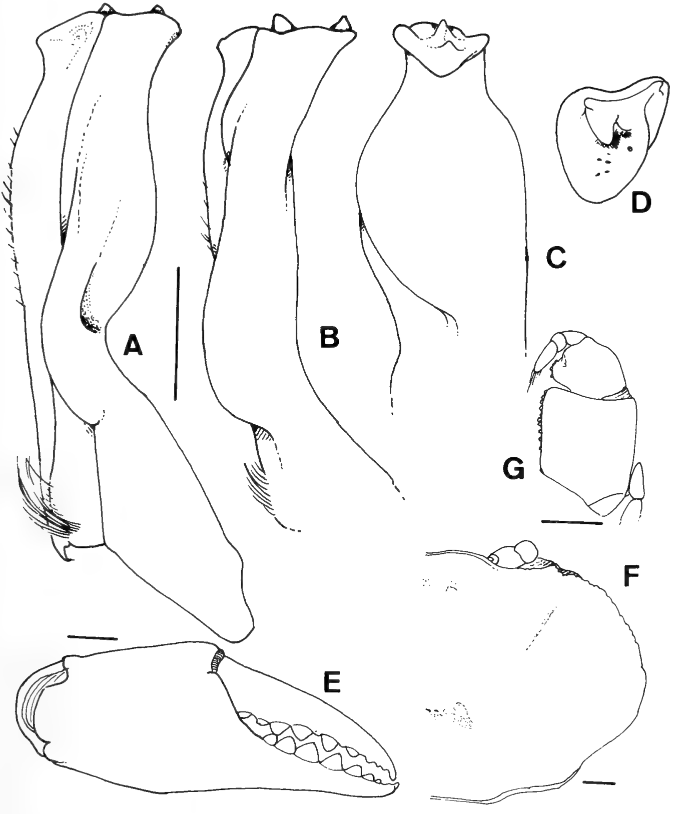

Fig. 9. *Hypolobocera orcesi* Pretzmann, 1978, male from valley of Río Mindo, Ecuador (IVIC 956): A, first left gonopod, caudal; B, lateral; C, cephalic; D, apex, distal; E, chela of largest cheliped, external view; F, dorsal view of right side of carapace, G, third maxilliped. Scales = 3 mm.

two prominent papillae, one near the gonopore and another on the cephalic expansion of the apex, are characteristic of this species.

Hypolobocera rathbuni Pretzmann, 1968
Fig. 1E–F

Hypolobocera (*Hypolobocera*) *rathbuni* Pretzmann, 1968:5.

Hypolobocera (*Hypolobocera*) *guayaquilensis rathbuni*.—Pretzmann, 1972:42, figs. 287–289.

Hypolobocera (*Hypolobocera*) *caputii rathbuni*.—Pretzmann, 1983b:354, figs. 1, 23, 30, 40, 51, 60, 64.

Hypolobocera rathbuni.—Rodríguez, 1982: 63, fig. 19p; 22b, g; 23e; 34a–c.

Material.—Ecuador: Santo Domingo, Pichincha Province, 490 m alt., 1 male neotype (Rodríguez 1982) cl. 23.7 mm, cb. 37.5 mm (BM 1918. 1.31.12).—Río Peripa, between Aurora and Puerto Limón, SW of Santo Domingo de los Colorados, Pichincha Province, 29 Nov 1980, leg. H. Díaz, 18 males, the largest cl. 27.7 mm, cb. 45.0 mm, 1 mature female cl. 22.2 mm, cb. 35.9 mm, 12 immature females, the largest cl. 19.6 mm, cb. 31.1 mm (IVIC 631).—Río Peripa, Puerto Limón, SW of Santo Domingo de los Colorados, Pichincha Province, 200 m alt., 29 Nov 1980, leg. H. Díaz, 1 male cl. 18.2 mm, cb. 28.6 mm, 1 spent female cl. 29.3 mm, cb. 46.4 mm, 1 immature female cl. 17.0 mm, cb. 26.7 mm, 2 juveniles (IVIC 629).—Río Peripa, San Miguel, 5 km from Aurora, SW of Santo Domingo de los Colorados, Pichincha Province, 29 Nov 1980, leg. H. Díaz, 1 immature male cl. 14.3 mm, cb. 22.1 mm, 1 immature female, 3 juveniles (IVIC 630).

Additional illustrations.—Rodríguez (1982, figs. 19p; 22b, g; 23e; 34a–c).

Diagnosis.—Carapace with upper frontal margin well defined by row of distinct papillae on each side and deep notch at middle. First male gonopods with caudal ridge prominent and curved proximally, obsolescent on distal half; lateral lobe long, narrow, slightly expanded distally, with outer border sinuous; apex in caudal view transverse, ending laterally in long spine; in distal view narrow, very elongated laterally, ending laterally in long acuminate spine; flat digitiform papilla on caudal side of gonopore.

Remarks.—There are slight differences between the neotype from Santo Domingo de los Colorados (Rodríguez 1982) and the specimens from Río Peripa. The relationship between the length of the exognath and the ischium of endognath in the third maxilliped of the neotype is 0.28, whereas in the others specimens range between 0.37 and 0.39. The flat papilla on the apex of gonopods has a minute denticle in the neotype which was not observed in the rest of the material listed above.

Lindacatalina Pretzmann, 1977b

Diagnosis.—Exognath of third maxilliped usually more than 0.45 length of ischium of endognath (Table 1). First male gonopods with strong longitudinal ridge on caudal surface; well developed lateral and supplementary cephalic lobes (this last rarely absent), both covered by minute spinules; apex truncated, circular in distal view, with two flat papillae near spermatic channel (Fig. 1K, L, M).

Type species.—*Hypolobocera* (*Lindacatalina*) *hauserae* Pretzmann, 1977b.

Distribution.—Southern Colombia and Ecuador.

Remarks.—We use Pretzmann's genus to group all Hypolobocerini with the lateral lobe of gonopods densely covered by spinules and frequently possessing a supplementary lobe, equally spinulous, on the cephalic side. We exclude from this genus two species that were included by Pretzmann (1977b), *Hypolobocera orcesi* which has a few sparse spinules on the lateral lobe, but not a continuous covering of this process, and *H. nobili* whose holotype is a female, and consequently their gonopods are not known. We place in this genus *Hypolobocera brevipenis* Rodríguez & Díaz, 1981, and a new species, *L. sumacensis*. Thus defined, the genus consist of an homogeneous group of species restricted to a small area on the Amazonian drainage of Southern Colombia and Ecuador.

Key to Species of *Lindacatalina*

1. Lateral lobe of first gonopods with supplementary cephalic lobe 2
–. Lateral lobe without supplementary lobe 5
2. Lateral and supplementary lobes fused distally 3
–. Lateral and supplementary lobes distinct 4
3. Supplementary lobe in cephalic view al-

most pyramidal or strongly excavated on the mesial side . . . . *L. puyensis*
–. Supplementary lobe in cephalic view globular . . . . *L. latipenis*
4. Lateral lobe wide, rounded, distinct; supplementary lobe triangular, not expanded distally . . . .*L. brevipenis*
–. Lateral lobe narrow, partially fused to caudal ridge; supplementary lobe rounded, expanded distally . . . . *L. sumacensis*
5. Lateral lobe square; wide apical portion almost reaching apex . . . .*L. hauserae*
–. Lateral lobe rounded, not reaching apex . . . . *L. orientalis*

Lindacatalina brevipenis (Rodríguez & Díaz 1981)
Figs. 1K–M; 12F, G

Hypolobocera brevipenis Rodríguez & Díaz, 1981:309, figs. 3, 8, 9.

Material.—Ecuador: without other data, leg. M. Olalla, 1 male holotype cl. 15.9 mm, cb. 27.7 (SMF 9140), 1 male paratype cl. 12.0 mm, cb. 20.3 mm (IVIC 606).

Additional illustrations.—Rodríguez & Díaz (1981, figs. 3, 8, 9).

Diagnosis.—Carapace with upper frontal margin rounded, devoid of tubercles. First male gonopods very short and stout; caudal ridge strong, geniculated and wrinkled at middle; lateral lobe auriculariform, wrinkled; supplementary cephalic lobe forming winged triangular expansion, distinct from lateral lobe, both lobes covered by minute spinules; apex oval and expanded laterally in distal view.

Remarks.—This species can be easily distinguished from other within the genus because the lateral and supplementary lobes are distinct and resemble each other in shape (Fig. 12f).

Lindacatalina hauserae Pretzmann, 1977b

Hypolobocera (Lindacatalina) hauserae Pretzmann, 1977b:437, fig. 10; 1983a: 301, pls. 1,2.

Hypolobocera (Lindacatalina) [*nobili*] *hauserae.*—Pretzmann, 1983b:358, fig. 10.

Diagnosis.—Carapace without upper frontal margin. First male gonopods slender, widening progressively proximally; apex oval-elongated in distal view, wider laterally than mesially; lateral lobe wide, placed in line with main axis of appendage; caudal ridge slightly rounded.

Remarks.—We have not seen material of this species, which is the type species of the genus *Lindacatalina*. The diagnosis given above was derived from Pretzmann's (1977b, 1983a, b) diagnoses and keys. The only specimens known, six males, three females, and six juveniles came from 2 km East of Mendez, Morona-Santiago Province.

Lindacatalina latipenis (Pretzmann 1968)
Figs. 1N–P; 12A–C

Hypolobocera (*Hypolobocera*) *latipenis* Pretzmann, 1968:8.

Hypolobocera (*Hypolobocera*) *conradi latipenis.*—Pretzmann, 1971:17; 1972:41, figs. 281–283.

Hypolobocera (*Lindacatalina*) *latipenis latipenis.*—Pretzmann, 1977b:432, figs. 5, 6, 11.

Hypolobocera (*Lindacatalina*) [*latipenis*] *latipenis latipenis.*—Pretzmann, 1983b: 357, figs. 12, 21, 34, 45, 49, 63, 68, 77, 78, 90.

Hypolobocera latipenis.—Rodríguez, 1982: 54, figs. 19n; 20a, f; 23a; 8a–e.

Material.—Ecuador: Faldas del Monte Sumaco, Loreto, Napo Province, 450 m alt., Jun 1968, leg. M. Olalla, 2 males, 1 female (TU 94-100-5).—Ecuador, leg. M. Olalla, 1 male cl. 33.8, cb. 55.7 mm (IVIC 621).

Additional illustrations.—Rodríguez (1982:54, figs. 19n; 20a, f; 23a; 8a–e).

Diagnosis.—Carapace with upper frontal margin well marked, with scattered tubercles. First male gonopods with caudal ridge distinct and strongly geniculated; lateral lobe large, wide, rounded; supplementary cephalic lobe forms large digitiform process transversely directed and fused distally to lateral lobe; both lobes covered by wrinkles and spinules, apex in distal view circular, with wide flat papilla near gonopore.

Remarks.—Pretzmann (1972, 1983b) gives as the original citation of this species *Strengeria* (*Strengeria*) *latipenis* Pretzmann, 1965. However, the specific name did not appear for the first time in Pretzmann (1965), but latter, in Pretzmann (1968) as *Hypolobocera* (*Hypolobocera*) *latipenis*.

Lindacatalina orientalis (Pretzmann 1968)
Fig. 10

Hypolobocera (*Hypolobocera*) *plana orientalis* Pretzmann, 1968:2; 1971:17; 1972: 60, figs. 162–164, 214–221.

Hypolobocera (*Lindacatalina*) [*plana*] *plana orientalis.*—Pretzmann, 1983b: 360, figs. 8, 15, 33, 36, 46, 73.

Hypolobocera orientalis.—Rodríguez, 1982:52, figs. 19d, 20c, h, 26a–c.

Hypolobocera (*Hypolobocera*) *plana plana* Pretzmann, 1972:49, figs. 275–277, 304–307. Not *Pseudothelphusa plana* Smith, 1870:146, 147.—Pocock, 1889:10.—Nobili, 1897:3, 5—Rathbun, 1898:535, 537—Young, 1900:211—Rathbun, 1905: 278—Coifmann, 1939:109—Rodríguez, 1982:192. Not *Potamocarcinus planus.*—Ortmann, 1897:318 (see Remarks).

Hypolobocera (*Lindacatalina*) [*plana*] *plana plana.*—Pretzmann, 1983b:359, figs. 9, 14, 31, 41, 70.

Material.—Ecuador: Oriental Cordillera, Ecuador, 1874, leg. Reiss, 1 male holotype cl. 14.3 mm, cb. 22.3 mm, 7 males paratypes cl. 12.8, 12.6, 12.1, 11.9, 11.5, 10.1 and 9.9 mm, cb. 20.7, 19.6, 19.2, 18.9, 17.3, 15.4 and 15.0 mm, 2 immature females cl. 9.9 and 9.7 mm, cb. 14.7 and 14.3 mm (SM).—Roadside ditch between Calacali and Mindo exit, aprox. 20 km S of Mindo, Pichincha Province, 27 May 1996, leg. R. von Sternberg, 3 males cl. 15.0, 11.1 and 8.1 mm, cb. 26.5, 17.7 and 12.0 mm, 3 mature females cl. 16.3, 15.1 and 13.4 mm, cb. 27.8, 24.6 and 21.6 mm (IVIC 958).—Mindo, Pichincha Province, Jan 1994, leg. J. Garcés, 1 male cl. 16.2 mm, cb. 28.0 mm (IVIC 957).

Diagnosis.—Carapace with upper frontal margin rounded, devoid of defined papillae. First male gonopods with caudal ridge strongly geniculated at middle, progressively tapering to end near apex; lateral lobe very broad, extending from middle of appendage to near apex, rounded, covered by minute spinules on lateral surface; apex truncated in caudal view, oblong, expanded laterally into rounded projection in distal view.

Remarks.—The type material of *Pseudothelphusa plana* Smith, 1870, consisted of 2 females (cl 16.6 and 13.6 mm, cb. 27.7 and 22.4 mm) from Paita, Perú, in the Museum of Yale College, collected by Prof. James Orton. Smith (1870) description of carapace and appendages, although detailed, are generic for many species of Pseudothelphusidae and he did not include illustrations of the gonopods. The species was latter cited in the literature by Pocock (1889), Nobili (1897), Rathbun (1898, 1905), Young (1900), Coifmann (1939), and Ortmann (1897), but any of these authors examined materials of the species.

The types that, according to Smith (1870), were "rather badly preserved specimens," deteriorated further, and latter, Pretzmann (1972) stated that they were no longer available. Consequently he renamed the species as *Hypolobocera* (*Hypolobocera*) *plana plana*, proposed as neotype a male from Ecuador in the USNM (labelled as follows: Mindo, Pichincha Province, Ecuador, 1919 Irwing Expedition, leg. C. N. Eigenmann, cl. 7.9 mm, cb. 13.9 mm, USNM 68558), and also included under this species 10 males and 11 females from Cotocallao (1919 Irwing Expedition, USNM 68564). Latter he (Pretzmann 1983b) omitted these additional specimens and gave a new plurinominal name to the taxon, *Hypolobocera* (*Lindacatalina*) [*plana*] *plana plana*.

Rodríguez (1982) objected to Pretzmann (1972) neotype, and considered *Pseudo-*

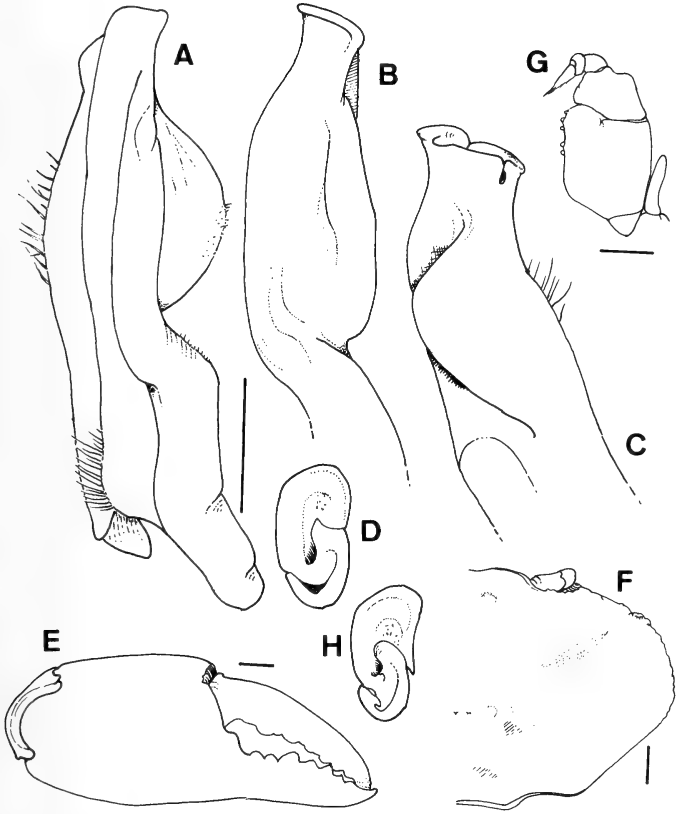

Fig. 10. *Lindacatalina orientalis* (Pretzmann, 1968): A–G, male from 20 km S of Mindo, Ecuador (IVIC 958): A, first left gonopod, caudal; B, lateral; C, cephalic; D, apex, distal; E, chela of largest cheliped, external view; F, dorsal view of right side of carapace; G, third maxilliped. H, male from Mindo (IVIC 957), apex of first gonopod, distal. Scales = 3 mm.

thelphusa plana as incertae sedis on the grounds that the original type locality (Paita) was isolated by a desert (Tumbez), and the neotype locality (Mindo) was 600 km to the north, on an entirely different river basin. Furthermore, there is no diagnostic character in Smith's original description to tie his species to the material examined by Pretzmann in the USNM.

The gonopods of our specimens from Mindo recorded above, and those of Pretzmann's (1972) neotype (USNM 68558) are identical to the illustrations of the gonopods of *Hypolobocera* (*Hypolobocera*) *plana or-*

ientalis Pretzmann, 1968 (see Pretzmann 1972, 1983b).

Another related taxon erected by Pretzmann (1977), *Hypolobocera* (*Lindacatalina*) [*plana*] *plana olallai*, cannot be differentiated from *Hypolobocera* (*Hypolobocera*) [*plana*] *plana plana* (=*Lindacatalina orientalis*) from the diagnosis or the sketchy illustration of the gonopod given by Pretzmann (1978, 1983b). We have found no specimens that could be attributed to *Hypolobocera* (*Lindacatalina*) [*plana*] *plana olallai* in our collections from the type locality (Aurora, Río Peripa) of this taxon.

Lindacatalina puyensis Pretzmann, 1978

Fig. 12 D, E

Hypolobocera (*Lindacatalina*) *latipenis puyensis* Pretzmann, 1977b:438 (nomen nudum); 1978:165, fig. 7; 1983a:302, pl. 5, 6.

Hypolobocera (*Lindacatalina*) [*latipenis*] *latipenis puyensis*.—Pretzmann, 1983b: 358, fig. 11.

Material.—Ecuador: Teniente Ortiz, 10 km N of Puyo, Río Rebadeneira, affluent of Río Arajuno, Pastaza Province, 980 m alt., 5 Nov 1980, leg. H. Díaz, 1 male cl. 19.8 mm, cb. 32.3 mm (IVIC 626).—Archidona, Cuevas de San Bernardo, Napo Province, 12 Jun 1986, leg. P. Villamar, 3 males cl. 16.8, 10.8 and 9.9 mm, cb. 29.0, 17.4 and 16.5 mm, 1 juvenile female, carapace broken, cb. aprox. 9 mm (IVIC 947).—Village of Talac, Napo Province, 1500 m, 28 Dec 1993, leg. S. Baez, 1 male cl. 18.0 mm, cb. 30.4 mm (IVIC 962).

Diagnosis.—Carapace with upper frontal margin well marked. First male gonopods with caudal ridge distinct and strongly geniculated; lateral lobe large, wide, rounded; supplementary cephalic lobe forms large conical process transversely directed and fused distally to lateral lobe; both lobes covered by wrinkles and spinules; apex in distal view circular, with wide flat papilla near gonopore.

Remarks.—The materials of this species and of *L. latipenis* come from localities within a small area between Puyo and Tena, and north of Tena. The specimens reported above are from localities 22 km and 35 km from the type locality of *L. puyensis*. The type locality of *L. latipenis* is 40 km ENE from Archidona. All these localities are located in a few small river basins draining to the upper reaches of the Napo River.

The first gonopods of the two species closely resemble each other, but in *L. puyensis* the supplementary lobe in cephalic view is oblong, almost pyramidal, and strongly excavated on the mesial side (Fig. 12D, E), whereas in *L. latipenis* it is clearly globular (Fig. 12A, B, C). The carapace breadth of all male specimens attributed to *L. puyensis* (3 type specimens and present records) is less than 35 mm, while *L. latipenis* attains a carapace breadth of at least 58 mm. It is possible that the male specimens attributed to *L. puyensis* are younger specimens of *L. latipenis*, or populations of dwarf individuals, a phenomenon that has been described in other Brachyura (Conde et al. 1989). This situation could be solved only by the discovery of mature females of small size. Pretzmann (1983a, b) recorded small females, but did not state whether they were mature. We are keeping both species distinct until more information is forthcoming.

Lindacatalina sumacensis, new species

Figs. 11, 12H, I

Material.—Ecuador: Faldas del Monte Sumaco, Loreto, Napo Province, 450 m alt., Jun 1968, leg. M. Olalla, 1 male holotype cl. 21.9 mm, cb. 35.6 mm, 10 males paratypes, 27 females, 7 of the largest mature females as follows: cl. 22.8, 20.9, 20.6, 20.5, 19.1, 19.1, and 18.4 mm, cb. 35.3, 32.9, 33.8, 34.9, 30.5, 29.3, and 29.1 mm (TU 94-100-6).—Same data, 11 males, 1 female with young under the abdomen cl. 19.5 mm, cb. 35.8 mm (IVIC 948).

Diagnosis.—Carapace with upper frontal

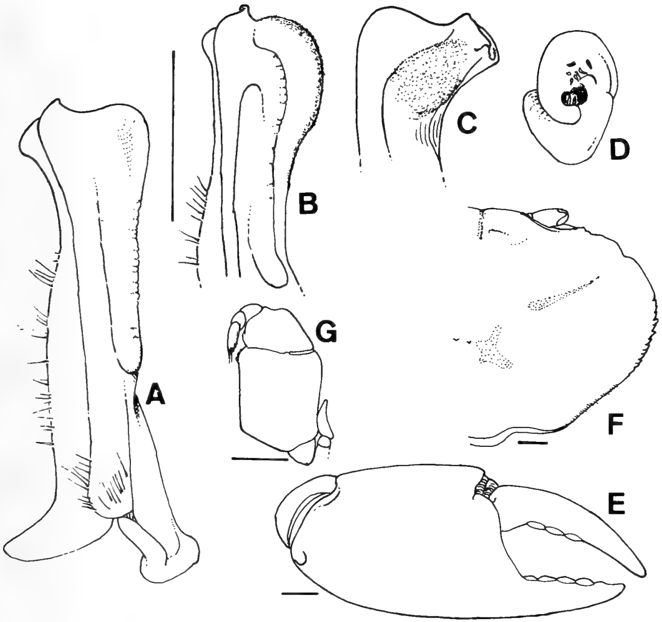

Fig. 11. *Lindacatalina sumacensis*, new species, holotype male from Monte Sumaco, Napo Province, Ecuador (TU 94-100-6): A, first left gonopod, caudal; B, lateral; C, apex, cephalic; D, apex, distal; E, chela of largest cheliped, external view; F, dorsal view of right side of carapace; G, third maxilliped. Scales = 3 mm.

margin angled, without conspicuous papillae, with inconspicuous notch at middle. First gonopods with caudal ridge straight, fused to lateral lobe, covered by minute transverse wrinkles; lateral lobe rounded, expanded distally; supplementary cephalic lobe rounded, thick, covered by minute spinules; apex oval in distal view.

Description of holotype.—Antero-lateral margins with wide notch after external orbital angles and another at level of cervical grooves; between these two notches and for short space behind second one, border devoid of teeth or papillae; towards the middle of border begins series of approximately 15 small but well defined triangular teeth. Cervical grooves wide and shallow, becoming indistinct toward margins of carapace. Postfrontal lobes small, but well defined, placed transversely in relation to middle axis of carapace; median groove wide and shallow. Upper margin of front rounded in dorsal view, with inconspicuous notch at middle, angled in frontal view, without conspicuous papillae; the lower margin strongly sinuous; space between both margins very narrow. Upper surface of carapace smooth and polished, covered by closely placed papillae not visible to naked eye.

Chelipeds strongly unequal; palm of larger one (right) inflated; fingers strongly gaping; movable finger strongly arched. Ex-

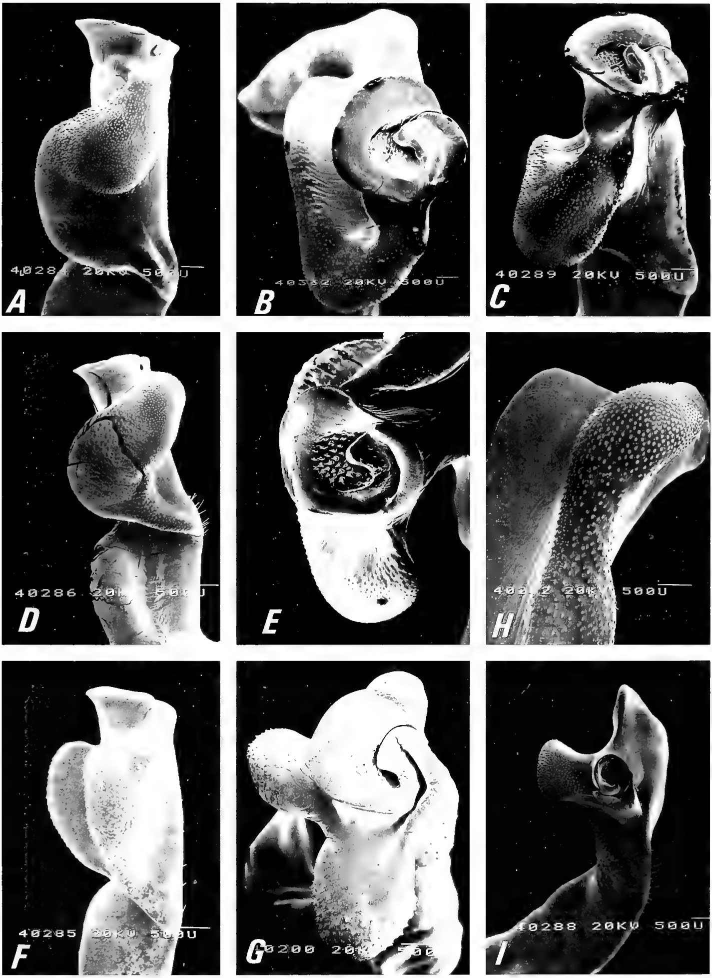

Fig. 12. First male gonopods of *Lindacatalina*. A, B, C, *L. latipenis* (Pretzmann, 1968), from Ecuador (IVIC 621); D,E, *L. puyensis* Pretzmann, 1978, from Teniente Ortiz (IVIC 626); F,G, *L. brevipenis* (Rodríguez & Diaz, 1981), from Ecuador (IVIC 606); H, I, *L. sumacensis* new species, holotype male from Monte Sumaco (TU 94-100-6). (A,D,F,H, cephalic; C, disto-cephalic; B,E,G,I, distal).

ognath of third maxilliped 0.46 length of ischium of endognath.

First male gonopods slender, strongly arched dorso-ventrally; caudal ridge straight, fused with lateral lobe, covered by minute transverse wrinkles; lateral lobe rounded, expanded distally; supplementary cephalic lobe rounded, thick, covered by minute spines; outline of apex oval in distal view.

Etymology.—This species is named after Monte Sumaco, where it was collected.

Moritschus Pretzmann, 1965

Diagnosis.—Exognath of third maxilliped usually more than 0.30 length of ischium of endognath (Table 1). First male gonopods with strong longitudinal ridge on caudal surface; lateral expansion continuos with apex of appendage; apex truncated, very elongated in distal view, with two flat papillae on side or in front of spermatic channel (Fig. 1I, J).

Type species.—Pseudothelphusa ecuadorensis Rathbun, 1897.

Distribution.—Southern Colombia, Ecuador and northern Peru.

Remarks.—Pseudothelphusa ecuadorensis Rathbun, 1897, *P. henrici* Nobili, 1897, and *Moritschus narinnesis* Campos & Rodríguez, 1988 (from southern Colombia) display the same lateral elongation of the gonopods that results in the distal migration of the lateral lobe and the consequent narrowing and elongation of the apex. These characters show that the three species are closely related, although their sizes are extremely different.

Key to Species of *Moritschus*

1. Lateral margin of first gonopod's apex without spinules; caudal end produced in short beak; elongate process over field of spines with 2 rudimentary papillae directed laterally, placed near opening of spermatic channel or displaced towards lateral expansion, its distal margin entire 2

–. Lateral margin of apex covered with small closely set spinules; caudal end produced in strong finger-like process directed proximally; elongate process over field of spines formed by one papilla, displaced towards lateral expansion, its distal margin bordered by minute spinules . . . . *M. narinnensis* (Colombia)

2. Elongated process over field of spines placed near opening of spermatic channel. Adult specimens very large (more than 6 cm cb.) . . . . *M. henrici*

–. Elongated process over field of spines displaced towards lateral expansion. Adult specimens very small (cb less than 3 cm) . . . . *M. ecuadorensis*

Moritschus ecuadorensis (Rathbun 1897)
Fig. 1G, H

Pseudothelphusa ecuadorensis Rathbun, 1897:59; 1898:534, 537; 1905:279, fig. 7, pl. 13, fig. 8.—Young, 1900:210—Nobili, 1901:38.—Colosi, 1920:17.—Coifmann, 1939:107.

Guinotia (*Moritschus*) *ecuadorensis*.—Pretzmann, 1965:3.

Potamocarcinus (*Hypolobocera*) *ecuadorensis*.—Bott, 1967:370, fig. 5a–c.

Hypolobocera (*Moritschus*) *ecuadorensis*.—Pretzmann, 1971:18; 1983b:348, 363

Hypolobocera (*Moritschus*) *ecuadoriensis* (sic).—Pretzmann, 1972:52, figs. 249, 250, 316–318.

Moritschus ecuadorensis.—Rodríguez, 1982:68, fig. 37a–d.

Material.—Ecuador: Alluriquin, affluent of Río Toachi, SE of Santo Domingo de los Colorados, Pichincha Province, 31 Nov 1980, leg. H. Díaz, 12 males, the largest cl. 13.9 mm, cb. 22.0 mm (IVIC 651).—West of Gualea, 880 m alt., leg. O. Thomas, 1 male cl. 13.2 mm, cb. 25.5 mm (BM 1918.1.331.11).

Additional illustrations.—Rodríguez (1982, fig. 37a–d).

Diagnosis.—Carapace with upper frontal margin absent. First male gonopods long and slender, with lateral margin widening progressively towards apex, this extending considerably laterally and produced in short beak; elongate process over field of spines displaced towards lateral expansion.

Moritschus henrici (Nobili 1897)
Fig. 1I, J

Pseudothelphusa henrici Nobili, 1897:1; 1901:40.—Rathbun, 1898:534, 537; 1905:302.—Young, 1900:219.—Colosi, 1920:40.—Coifmann, 1939:108.

Strengeria (*Strengeria*) *henrici*.—Pretzmann, 1965:7.

Hypolobocera (*Hypolobocera*) *henrici henrici*.—Pretzmann, 1971:17; 1972:39, figs. 260, 261, 294, 296.

Hypolobocera henrici.—Pretzmann & Mayta, 1980:139, figs. 5, 6.—Rodríguez, 1982:66, figs. 19o; 22a, f; 23d; 36a, d.

Hypolobocera (*Hypolobocera*) [*peruviana*] *henrici henrici*.—Pretzmann, 1983b:355, figs. 7, 19, 34, 42, 50, 62, 66, 75.

Hypolobocera (*Hypolobocera*) [*henrici*] *henrici nora* Pretzmann, 1977b:436 (nomen nudum); 1978:164, fig. 3.

Hypolobocera (*Hypolobocera*) [*peruviana*] *henrici nora*.—Pretzmann, 1983b:356, figs. 6, 20, 32, 43, 47, 61, 67, 84–88.

Material.—Ecuador: Leg. M. Olalla, 38 males, the largest cl. 54.8, cb. 91.1 mm, 59 females, the largest cl. 35.4 mm, cb. 56.7 mm (IVIC 615).—Monte Sumaco, Loreto, Napo Province, 450 m, Jun 1968, leg. M. Olalla, 1 male, 1 immature female (TU 94 100-7).—Río Latas, affluent of Río Napo, between Tena and Puerto Misuahalli, Napo Province, 3 Nov 1980, leg. H. Díaz, 3 males cl. 24.5, 16.2 and 8.3 mm, cb. 38.6, 24.8 and 12.9 mm (IVIC 616).—Cuevas de Jumundí, 5 km N of Archidona, near Tena, in affluent of Río Napo, Napo Province, 3 Nov 1980, 1 immature male (IVIC 968).—Río Rebadeneira, affluent of Río Arajuno, Río Napo basin, Teniente Ortíz, 18 km N of Puyo, Pastaza Province, 980 m alt., 5 Nov 1980, leg. H. Díaz, 1 male cl. 21.3 mm, cb. 35.5 mm (IVIC 619).—Puyo, Pastaza Province, 820 m alt., 10 Jan 1986, leg. Lilian Real, 1 male (IVIC 939).—Río Pladia, affluent of Río Ansú, Río Napo basin, Santa Clara, Pastaza Province, 550 m alt., 4 Nov 1980, leg. H. Díaz, 3 males cl. 18.5, 12.5 and 9.9 mm, cb. 28.7, 19.5 and 13.4 mm, 1 immature female cl. 10.2 mm, cb. 15.3 mm (IVIC 618).—Road Mera-Baños, 4 km from Mera, Río Pastaza basin, Pastaza Province, 1100 m alt., 6 Nov 1980, leg. H. Díaz, 1 mature female cl. 48.4 mm, cb. 76.5 mm (IVIC 617).

Additional illustrations.—Rodríguez (1982:66, figs. 19o; 22a, f; 23d; 36a, d).

Diagnosis.—Carapace with upper frontal margin angled, advanced, with ill-defined papillae and deep notch at middle. Third abdominal tergites with unusually deep cavities to receive apex of first gonopods, already present in juveniles. Propodous of fifth pereiopods wide, with row of plumose setae on infero-posterior margin. First male gonopods extraordinarily large, lateral margin widening progressively towards apex which extends considerably laterally, giving apex in caudal view triangular-elongated appearance; elongate process over field of spines with 2 rudimentary papillae directed laterally, placed near opening of spermatic channel.

Remarks.—The material of *Hypolobocera* (*Hypolobocera*) [*henrici*] *henrici nora* Pretzmann, 1978, consist of two male specimens, collected by Pretzmann at two localities, Mendez and Río Arajuno respectively, widely separated from each other, in the basins of Río Napo and Río Santiago. Pretzmann also collected specimens of the typical form of *H. henrici* from the same localities (Pretzmann 1978). The wide distribution of both subspecies, and their overlap at two localities, suggest that they cannot be separated as distinct subspecies. On the other hand it is not possible to give specific rank to *Hypolobocera* (*Hypolobocera*) *henrici* [*henrici*] *nora*, since the characters are part of the variability of *H. henrici*. The round distal margin of the apex in the first gonopods, mentioned by Pretzmann (1978) for *H. nora* ("Oberrand der Krönchens, in seitlicher Ansicht, stärker geknickt"), is observed in all our immature specimens. The lateral lobe of first gonopods ("Außenrand der Laterallobe lateral stark ausgebaucht") displays a similar variation in our series.

Another character mentioned by Pretzmann (1978) is the relative wideness of carapace in both subspecies. The relationship cb/cl in *H. henrici* is stated to be more than 1.64 ("Cpx. breit, Index über 1.64," Pretzmann 1977b), whereas in the subspecies *nora* it is described as wider, with the radius of curvature of lateral borders larger ("VSR-Krümmungradius groß . . . Cpx breiter," Pretzmann 1978). The length of the radius mentioned is of course a function of the carapace width. In a series of 26 specimens from one locality we examined, the relationship cb/cl varies between 1.51 and 1.66 according to the size of the specimens.

Biogeography

The section of the Andes comprised within the territory of Ecuador (Fig. 13) is divided into five major basins draining to the Pacific, and three basins to the Amazon. From North to South the Pacific basins begins with the valleys of the rivers Mira and Esmeraldas, followed by several littoral valleys isolated from the Daule basin by the low mountains of the Manabí Province; after the estuary of Guayas lies the basin of the Rio Jubones and a few minor littoral streams. The basin of the Daule–Vinces rivers, enclosed between the Andes and the Manabí mountains, is the most extensive valley on the Pacific drainage. The Amazonian drainage comprises to the North, the basin of the Napo River, and to the South the basins of the Pastaza and Santiago rivers. These last two drain the internal valleys of the Oriental and Central Cordilleras, and discharge into the Marañon River.

The distribution of species among these eight basins is unequal. The largest numbers occur in the Esmeraldas and Napo basins, with ten and seven species respectively. This abundance is related mainly to the extension and topographic complexity of these basins, but possibly also to a more intensive collecting effort due to the vicinity of large cities. Several species are known from single localities, underlining our imperfect knowledge of the fauna; these are: *Hypolobocera orcesi*, *H. muisnensis*, *H. mindonensis*, *Lindacatalina hauserae*, *L. sumacensis*. The most interesting cases are those of trans-basin distribution. Two extreme examples are *Hypolobocera aequatorialis* and *Lindacatalina. orientalis*, which involve distribution across the main Andean water divide. *H. esmeraldensis*, *H. guayaquilensis*, *H. rathbuni*, *H. exuca*, and *Moritschus henrici*, exhibit similar trans-basin distributions. According to the present records and others available in the literature, the area of distribution of *H. henrici* covers the basins of four of the largest effluents of the Amazon: Río Napo (Pretzmann 1978), Río Pastaza (Pretzmann 1972), Río Santiago (Nobili 1897, holotype; Pretzmann 1972, 1978) in Ecuador, and Río Ucayali in Perú (Pretzmann & Mayta 1980, Rodríguez 1982). This is one of the largest ranges for a species of Pseudothelphusidae.

The vertical distribution of the species (Table 2) on the Pacific side ranges from 50 m to 2000 m. *Hypolobocera delsolari* extends from 50 to 1 500 m along the Río Jubones; *H. esmeraldensis*, *H. guayaquilensis*, *H. konstanzae* and *H. muisnensis*, have been found along the coastal plain of the Esmeraldas and Manabi provinces, between 150 and 200 m, but *H. guayaquilensis* has been also recorded inland in the Daule valley (Fig. 13). The other species on the Pacific side are inland dwellers: *H. caputii* and *H. rathbuni*, found at 200 m and between 200 and 450 m, respectively; *H. mindonensis*, *H. orcesi*, and *Moritschus ecuadorensis* between 950 and 1200 m; and *H. exuca* at 100 and 2000 m. On the Amazonian side the species range from 400 to 1500 m: *H. conradi* between 900 and 1500 m; *Lindacatalina orientalis* and *L. puyensis* between 1000 and 1200 m; and *L. hauserae*, *L. latipenis* and *L. sumacensis*, between 400 and

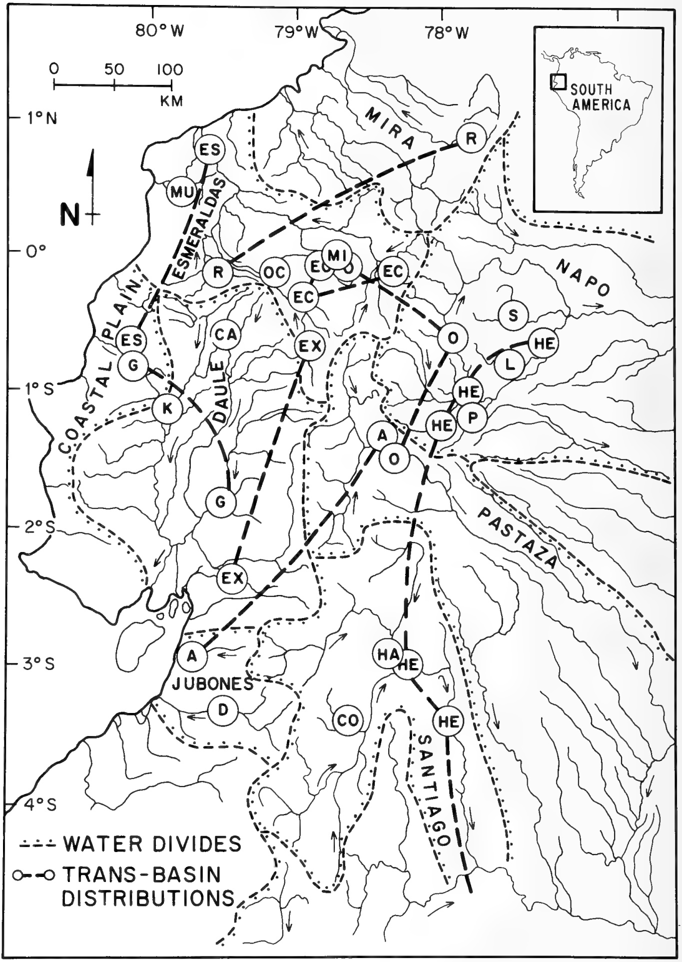

Fig. 13. Geographical distributions of Ecuadorean Pseudothelphusidae. A = *Hypolobocera aequatorialis*; CO = *H. conradi;* CA = *H. caputii*; D = *H. delsolari*; ES = *H. esmeraldensis*; EX = *H. exuca*; G = *H. guayaquilensis*; K = *H. konstanzae*; MI = *H. mindonensis*; MU = *H. muisnensis*; OC = *H. orcesi*; R = *H. rathbuni*; O = *Lindacatalina orientalis*; HA = *L. hauserae*; P = *L. puyensis*; S = *L. sumacensis*; L = *L. latipenis*; EC = *Moritschus ecuadorensis*; HE = *M. henrici*

Table 2.—Altitudes reported for Ecuadorian Pseudothelphusids (m above sea level).

Hypolobocera aequatorialis	50–1750
H. caputii	200
H. conradi	900–1500
H. delsolari	50–1500
H. esmeraldensis	150
H. exuca	100–2000
H. guayaquilensis	200
H. konstanzae	200
H. mindonensis	1000–1200
H. muisnensis	200
H. orcesi	1200
H. rathbuni	200–450
Lindacatalina hauserae	500
L. latipenis	400
L. orientalis	1200
L. puyensis	1000
L. sumacensis	450
Moritschus ecuadorensis	950–1200
M. henrici	450–1100

500 m; *Moritschus henrici* between 450 and 1100 m.

Hypolobocera aequatorialis has been collected at 50 m on the Pacific side, and from 700 to 1750 m on the Amazonian side. This vertical distribution, together with the trans-basin distribution mentioned above, is rather peculiar for a species of Pseudothelphusidae. However, we were unable to find differences among the specimens from the area of the Jubones River and those from the vicinity of Baños, recorded under our materials of this species.

Moritschus henrici and the species of *Lindacatalina* reach the lowest altitudes recorded for the Andean species on the Amazonian side. Further on the lower course of the Amazonian tributaries, in Colombia and Brazil, the Andean Hypolobocerini are replaced by other species taxonomically very distant, belonging to the tribe Kingsleyini, mainly species of the genus *Fredius* (Magalhaes 1986; Rodríguez & Pereira 1992; Rodríguez & Campos, 1998).

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Chelomalpheus koreanus, a new genus and species of snapping shrimp from Korea (Crustacea: Decapoda: Alpheidae)

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Abstract.—*Chelomalpheus koreanus*, a new genus and species, is described on the basis of three specimens collected from the Yellow Sea, Korea. The new genus differs from all other genera of Alpheidae by the combination of the following characteristics: the presence of a notch on the inferior margin of carapace, the presence of an articulated movable plate on the posteroventral margin of the sixth abdominal somite, and the presence of roundly elongate immovable teeth on the transverse suture of the uropodal exopod.

During recent collections in a mud-sandy beach in the Yellow Sea, Korea, specimens of a new genus and species of the family Alpheidae were found. The new genus and species is described herein. Holotype and ovigerous female paratype are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Chelomalpheus, new genus

Definition.—General body form as usual for members of the family Alpheidae.

Body slightly compressed, surfaces smooth and glabrous.

Rostrum very small and acute. Orbital hoods absent. Carapace with anteroventral margin bluntly rounded, not produced anteriorly; inferior margin with a broad notch at middle part; cardiac notch well developed.

Eyes well developed, cornea fully exposed dorsally and laterally.

Antennules slender. Stylocerite falling slightly short of middle of second segment. Scaphocerite normal, with distal spine and inner blade. Carpocerite slightly overreaching distal end of antennular peduncle. Basicerite with sharp lateral spine.

Mouthparts similar to those in *Alpheus* Fabricius, 1798 (Kim & Abele 1988). Third maxilliped with coxa bearing one arthrobranch.

First pereopods similar in shape and size, lacking sexual dimorphism. Chela elongate, deflexed below near base of immovable finger. Movable finger shallowly arched along superior margin, bearing 2 blunt teeth on inferior margin. Immovable finger with 1 blunt tooth at middle of superior margin and another small tooth proximally.

Second pereopods equal, similar, and slender. Carpus 5-segmented: first segment as long as fifth, about 2 times as long as second; second, third, and fourth almost equal in size.

Ambulatory pereopods slender, dactyli simple. Third pereopod rather slender; dactylus acute, slender; ischium with 1 movable spine.

Abdomen with pleura of first four segments broadly rounded in both sexes. Sixth segment with posteroventral margin with articulated, movable triangular plate. Appendix masculina far overreaching distal end of appendix interna.

Telson slender, with 2 pairs of dorsal spines located laterally.

Uropodal exopod bearing 1 slender movable spine laterally; transverse suture (diaeresis) with about 10 immovable teeth and ending in small immovable spine on lateral margin.

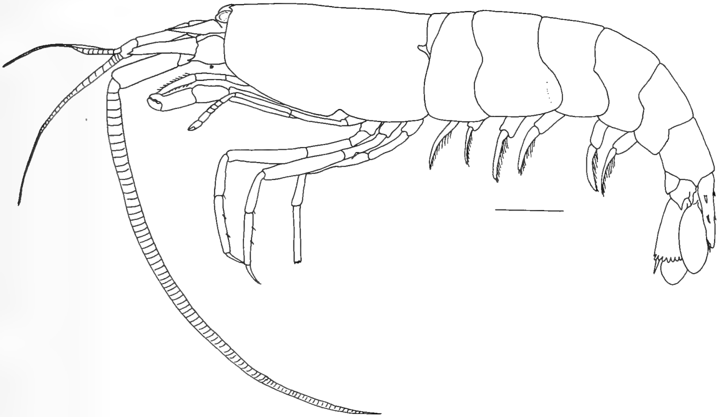

Fig. 1. *Chelomalpheus koreanus*, new species, holotype male, USNM 285514, cl 4.7 mm, lateral view. Scale, 2.0 mm.

Epipods present on first three pereopods.

Type species.—*Chelomalpheus koreanus*, new species.

Etymology.—The generic name is derived from the Greek word "cheloma," meaning "notch," indicating the presence of a notch on the inferior margin of the carapace.

Chelomalpheus koreanus, new species
Figs. 1–3

Material examined.—Holotype (USNM 285514): Male, cl 4.7 mm, Daecheon, the Yellow Sea, Korea (36°19′05″N, 126°30′25″ E), from pool dug in mud-sandy beach, coll. Sa Heung Kim, 6 Jun 1996. Paratypes: 1 male (cl 4.0 mm), 1 ovigerous female (cl 4.5 mm, USNM 285515), same locality as holotype.

Description.—Body (Fig. 1) slightly compressed, surfaces smooth and glabrous.

Rostrum (Figs. 1, 3A) very small, acute, and triangular in dorsal view, and clearly carinate for short distance posteriorly.

Carapace (Fig. 1) with anterior margin shallowly concave near base of rostrum and then almost straight; anteroventral margin bluntly rounded, not produced anteriorly; inferior margin of carapace with a broad notch at middle part near basis of second peropod; cardiac notch well developed.

Eyes well developed, cornea fully exposed dorsally and laterally.

Antennules (Fig. 3A) slender. First segment longer than wide, with shallow carina extending from ventral inner margin. Second segment elongate, about 3.3 times as long as broad, 1.9 times as long as visible part of first segment and 3 times as long as third segment. Stylocerite narrowing to long sharp point, falling slightly short of middle of second segment.

Scaphocerite slightly more than 3 times as long as broad. Lateral margin almost straight. Distal spine directing forward, overreaching distal margin of second antennular segment. Inner blade broadly rounded distally, with no cleft between inner blade and distal spine.

Carpocerite slightly overreaching distal end of antennular peduncle. Basicerite with broadly based, sharp, lateral spine.

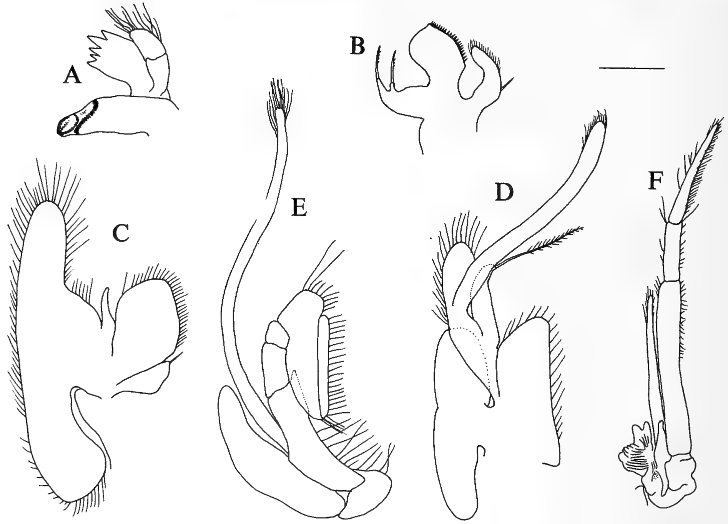

Fig. 2. *Chelomalpheus koreanus*, new species, holotype male, USNM 285514, cl 4.7 mm: A, mandible; B, first maxilla; C, second maxilla; D, first maxilliped; E, second maxilliped; F, third maxilliped. Scale = 1 mm; F, 0.5 mm: A, B, C, D, E.

Mandible (Fig. 2A) with incisor process rather broad and bearing 5 teeth on distal margin; molar process bearing some ridges provided with beds of soft hairs; palp consisting of 2 distinct segments. First maxilla (Fig. 2B) with upper endite broad, bearing spinules on distolateral margin; endopod bilobed, each lobe bearing single strong seta. Second maxilla (Fig. 2C) with upper endite entire, provided with setae; lower endite small, bearing 1 seta; endopod narrow and simple; scaphognathite large, anterior lobe narrow, posterior lobe large. First maxilliped (Fig. 2D) with endites entire, bearing row of setae on marginal region; exopod with exopodal (caridean) lobe narrow but distinct; endopod slender with single, long, simple seta on distal margin; epipod large, elongated oval shape with lateral margin broadly concave. Second maxilliped (Fig. 2E) with ultimate segment of endopod narrow, attached as strip to penultimate segment; exopod well developed; epipod fairly large and elongate. Third maxilliped (Fig. 2F) slender, extending to almost distal end of carpocerite; ultimate segment tapering distally with 3–4 small spinules distally, about 1.8 times as long as penultimate; penultimate segment rather elongate, about 4 times as long as broad near distal end; antepenultimate segment rather elongate, about 7.8 times as long as broad; exopod reaching to far short of distal end of antepenultimate segment; coxa with 1 arthrobranch.

First pereopods (Fig. 3B, C) similar in shape and size and no sexual dimorphism, almost reaching to tip of lateral spine of scaphocerite. Chela (Fig. 3D) elongate, 3.6 times as long as broad, deflexed below near base of immovable finger; fingers slightly deflexed internally, occupying less than dis-

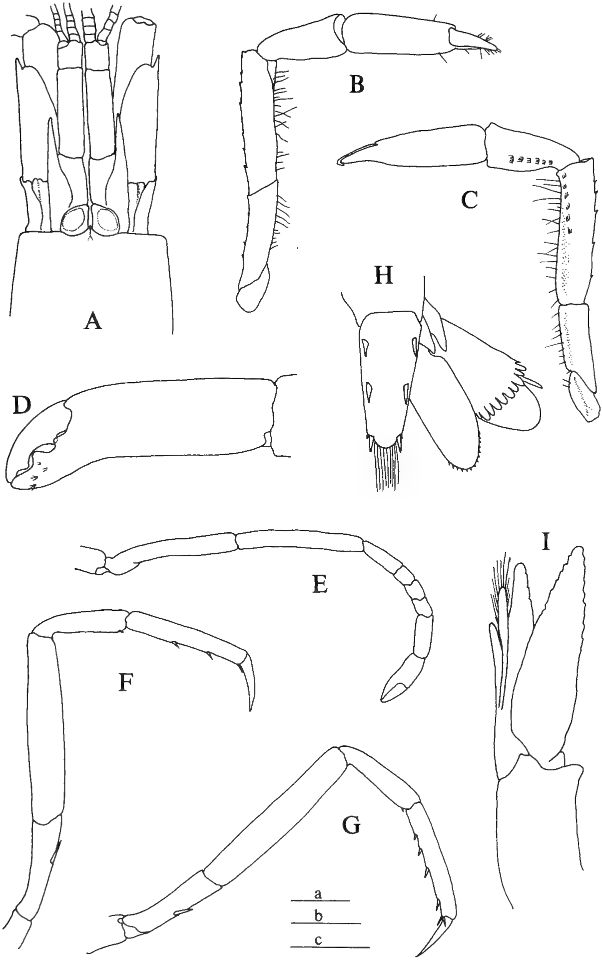

Fig. 3. *Chelomalpheus koreanus*, new species, holotype male, USNM 285514, cl 4.7 mm: A, anterior region, dorsal view; B, right first pereopod, outer view; C, same, inner view; D, same, chela, outer view; E, right second pereopod; F, right third pereopod; G, right fourth pereopod; H, telson and right uropod; I, right second pleopod. Scale a = 1 mm: A; scale b = 1 mm: E, H, 0.5 mm: D, I; scale c = 1 mm: B, C, F, G.

tal 0.3 of chela; palm entire, subcylindrical, about 2.6 times as long as broad; movable finger shallowly arched along superior margin, bearing 2 blunt teeth on inferior margin; immovable finger with 1 blunt tooth at middle of superior margin fitting space between 2 immovable teeth of movable finger and another small tooth proximally. Carpus more than 2 times as long as broad near distal end with about 6 short tufts of setae along inferior margin. Merus about 4 times as long as broad; superior margin with about 6 immovable small spinules along superior margin and with about 6 short tufts of setae along inferior margin. Ischium about 2.5 times as long as broad, with 5–6 very small spinules along superior margin.

Second pereopods (Fig. 3E) equal, similar, and slender, not reaching to lateral spine of scaphocerite. Fingers of chela about as long as palm. Carpus 5-segmented: first segment about 2 times as long as second; second, third, fourth almost equal in size; fifth segment almost as long as first.

Third pereopod (Fig. 3F) rather slender. Dactylus acute, slender. Propodus about 6.1 times as long as broad, about 2.4 times as long as dactylus and 1.3 times as long as carpus, with 2 small movable spines on inferior margin and a pair at distal end. Carpus with 1 small movable spine at distal end of inferior margin, 4 times as long as broad. Merus about 5.3 times as long as broad, 2 times as long as carpus, unarmed. Ischium with 1 rather strong movable spine.

Fourth pereopod (Fig. 3G) almost same as third pereopod. Propodus with 4 movable spines on inferior margin and a pair at distal end. Ischium with 1 rather strong movable spine.

Fifth pereopod similar to fourth pereopod, but much more slender. Ischium with no movable spine.

Abdomen (Fig. 1) with pleura of first four segments broadly rounded in both sexes. Pleuron of fifth somite subrectangular on posteroventral margin. Sixth segment almost as long as fifth, posterolateral margin acute, posteroventral margin with articulated, fairly large, movable, triangular plate. Appendix masculina (Fig. 3I) far overreaching distal end of appendix interna.

Telson (Fig. 3H) slender, about 2.3 times as long as broad at anterior end, lateral margins almost straight; posterior margin convex; 2 pairs of dorsal spines located rather laterally, at about 0.2 and 0.5 of telson length; posterior margin with 2 pairs of movable spines located laterally, lateral spine very small, equal to 0.2 of length of medial.

Uropodal endopod (Fig. 3H) bearing small spinules on distal margin. Uropodal exopod bearing 1 slender movable spine laterally; transverse suture (diaeresis) with about 10 roundly elongate immovable teeth and ending in small immovable spine on lateral margin.

Variation.—Little variation exists among the three specimens. In males, the notch of the inferior margin of the carapace is deeper compared to the female. In the female, the carpocerite almost reaches to the distal end of antennular peduncle. The number of movable spines on the inferior margin of the propodus in the third and fourth pereopods varies from 2–4 in males.

Etymology.—The specific name is after the Republic of Korea.

Discussion.—The specimens referred to this new genus key out to *Potamalpheops* and *Pseudathanas* in Holthuis' (1993) generic key, though they are easily distinguished from members of any known genus in the family Alpheidae by having a notch on the inferior margin of the carapace. The present specimens obviously do not belong to *Potamalpheops* Powell, 1979 (Bruce 1993, Yeo & Ng 1997) because they lack a tooth behind the eye, nor to *Pseudathanas* Bruce, 1983 because they have immovable teeth instead of a row of movable spines on the transverse suture (diaeresis) of the uropodal exopod. The present new species is easily distinguished from the species of *Athanas* Leach, 1814 by having very short rostrum and by having no supracorneal, extracorneal, and infracorneal spines usually present with varying degrees of development in *Athanas*. The present new species is also different from the species of *Automate* de Man, 1888 (Chace 1988, Holthuis 1993) in having an articulated movable plate on the posteroventral margin of the sixth abdominal segment. Therefore this shrimp species is easily distinguished from any of the known species of the family Alpheidae by the combination of the following characteristics: the presence of a notch on the inferior margin of carapace; the presence of an articulated plate on the posteroventral margin of sixth abdominal somite; and the presence of roundly elongate immovable teeth on the transverse suture of uropodal exopod.

Acknowledgments

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A new crawfish of the genus *Procambarus* (Crustacea: Decapoda: Cambaridae) from central Texas

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Abstract.—*Procambarus* (*Girardiella*) *ceruleus* is a new burrowing crawfish known from two localities in the Brazos River drainage of Brazos County, Texas. Although it shares many key characters with the members of the Gracilis Group of the subgenus, the following combination of characters will distinguish the species: presence of cephalic process in the male; prominent caudal knob surmounted by conspicuous caudal process in the male; unbearded palm; narrow areola; rostrum lacking marginal spines or tubercles; and female annulus ventralis that is subcircular in outline.

After a period of comparative neglect, the crawfish fauna of Texas has recently received the attention it deserves. Of the 20 crawfishes described since Hobbs' (1989) checklist, six were from type localities in Texas, more than from any other state. Other, longer studies have since been based on Texas materials (Hobbs 1990, Hobbs & Whiteman 1991, Fitzpatrick & Suttkus 1992). In addition, recent collections by David Hillis and his associates have indicated the presence of several undescribed species, especially among the burrowing forms (Keith A. Crandall, in litt.), and students of one of us (MKW) have provided records of other previously unknown crawfishes. The description that follows represents one of the latter.

The following abbreviations are employed: TCL, Total Carapace Length; PCL, Postorbital Carapace Length; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; TU, Tulane University Museum of Natural History, Belle Chasse, Louisiana.

Procambarus (Girardiella) ceruleus, new species

Fig. 1

Diagnosis.—Body pigmented; eyes well developed, faceted and pigmented. Rostrum slightly depressed; margins not conspicuously thickened and without marginal spines, somewhat rounded cephalically and tapering to small rounded acumen; lacking median carina. Carapace without cervical spines. Areola 10.3 to 14.8 (average 12.4) times longer than wide, constituting 37.9% to 43.1% (average 40.1%) of TCL and 44.3% to 46.6% (average 45.8%) of PCL. Suborbital angle small but obvious; hepatic region of carapace sparsely granulate; branchiostegal spine small but acute. Antennal scale about 1.8 times longer than broad, widest distal to mid-length, with thickened lateral portion ending in stout spine. Mesial surface of chela not bearded, with row of 6 to 8 spiniform tubercles, which are flanked dorsally and ventrally by row of smaller and less numerous tubercles; ventral surface slightly tuberculate; dorsal surface with scattered setiferous punctations; shallow notchlike excavation in proximal third of opposable margin of dactyl. Ischium of third pereiopod of male with simple hook overreaching basioischial articulation and not opposed by tubercle on basis; coxa of fourth pereiopod without caudomesial boss. First pleopods of first form male reaching coxae of third pereiopods when abdomen

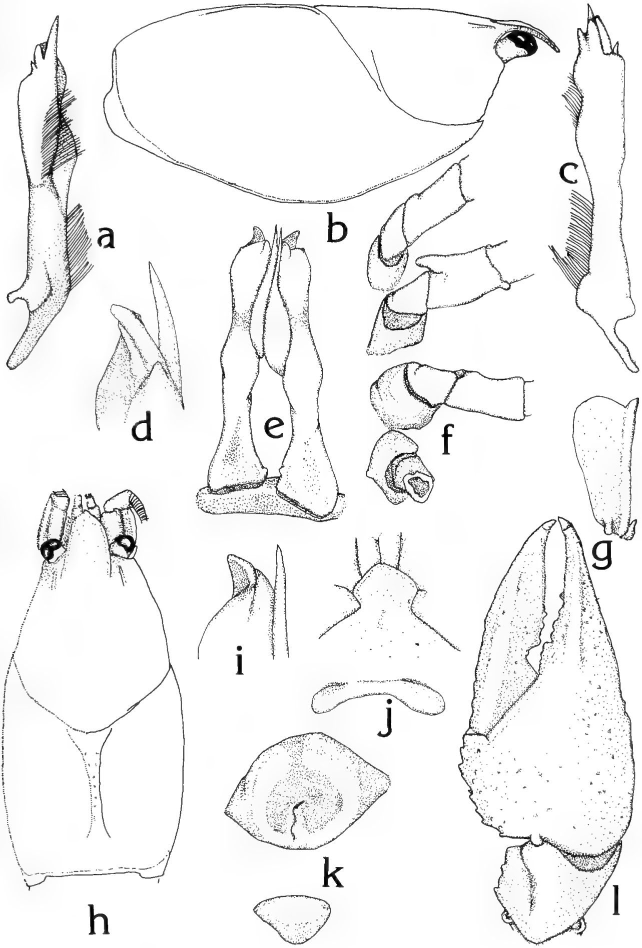

Fig. 1. *Procambarus* (*Girardiella*) *ceruleus*, new species (all figures of holotype, except *k* of allotype.): *a*, Mesial aspect of first pleopod; *b*, Lateral aspect of carapace; *c*, Lateral aspect of first pleopod; *d*, Cephalic aspect of apex of first pleopod; *e*, Caudal view of first pleopods; *f*, Basal podomeres of left third through fifth pereiopods; *g*, Antennal scale; *h*, Dorsal aspect of carapace; *i*, Cephalic aspect of apex of first pleopod; *j*, Epistome; *k*, Annulus ventralis and postannular sclerite; *l*, Dorsal aspect of distal podomeres of right cheliped.

flexed, asymmetrical, bases not contiguous and with proximomesial spine; strong shoulder at cephalic base of terminal elements; lacking subterminal setae; terminal elements all sclerotized at least distally, consisting of straight, tapering, subacute, distally directed mesial process extending well beyond other elements; short, cephalodistally directed cephalic process somewhat separated from central projection; strong, flattened, caudodistally arched central projection, which strongly deflected laterally and barely overreaching prominent, distally directed, apically rounded caudal process. Annulus ventralis of female freely movable, about 1.4 times wider than long, with central depression surrounded by rounded smooth ridges; sinus originating slightly lateral to midpoint of annulus, then moving to midline where curving caudad and tracing gently sinuous path before terminating near caudal margin. Postannular sclerite small (annulus about 2.2 times longer and wider); preannular plate poorly developed; first pleopods present.

Measurements of types.—See Table 1.

Holotypic male, form I.—Cephalothorax (Fig. 1b, h) subcylindrical. Second segment of abdomen distinctly narrower than thorax (12.5 and 18.0 mm, respectively). Areola 12.1 times longer than wide, with single punctuation across narrowest part. Cephalic section of carapace 2.5 times as long as areola, latter constituting 39.2% of TCL (44.3% of PCL). Surface of carapace punctuate dorsally, having low tubercles in hepatic region, and with tiny granulations in extreme cephalolateral portion of branchiostegite. Rostrum slightly excavate dorsally, with converging margins (right side inflated, apparently by premortem injury) not ending in distinct shoulders or spines; median carina absent; acumen reduced to small tubercle. Subrostral ridges weak, scarcely visible in dorsal aspect. Suborbital angle small but distinct. Branchiostegal spine small but acute; cervical spine absent.

Abdomen shorter than carapace: Cephalic section of telson with single fixed spine in each caudolateral corner. Uropod with both lobes of basal podomere bearing stout subacute spine, mesial ramus with premarginal distomedian spine not overreaching margin and strong lateral spine; dorsal surfaces of both rami with submedian ridge proximally. Cephalic lobe of epistome (Fig. 1j) subovate in outline and without markedly elevated margins; fovea of main body of epistome scarcely visible; zygoma only mildly arched. Ventral surface of proximal podomere of antennular peduncle without spine near midlength. Antennal peduncle lacking spines on both basis and ischium; flagellum when flexed reaching to caudal margin of carapace. Antennal scale (Fig. 1g) 1.6 times as long as broad, widest distal to midlength; greatest width of lamellar part 3.9 times width of thickened lateral part.

Palpus of third maxilliped reaching almost to distal margin of proximal podomere of antennule; ventromesial and opposable surfaces of ischium and merus provided

Table 1.—Measurements (mm) of type specimens of *Procambarus* (*Girardiella*) *ceruleus,* new species.

	Holotypic male, Form I	Allotypic female
Carapace		
Height	16.4	13.4
Width	18.0	14.9
Total length	33.9	30.6
Postorbital length	30.0	26.6
Areola		
Width	1.0	1.0
Length	13.3	12.1
Rostrum		
Width	5.5	6.6
Length	7.4	6.9
Chela		
Length of mesial margin of palm	9.8	6.2
Width of palm	13.4	7.3
Length of lateral margin	26.8	17.2
Length of dactyl	17.9	11.6
Abdomen		
Width	12.5	damaged
Length	29.1	damaged

with dense mat of plumose setae that totally obscure dentate opposable margins and mesial half of podomeres.

Right chela (Fig. 1l) subovate in cross section, moderately depressed, palm 1.4 times wider than length of inner margin, dorsal surface studded with shallow, sparsely setiferous punctations; mesial margin with row of 8 strong spiniform tubercles, flanked dorsally by row of 6 smaller ones, and single small but stout tubercle ventral to mesial row. Both fingers with submedian longitudinal ridges dorsally and ventrally, dorsal ones flanked by numerous setiferous punctuations. Opposable margin of fixed finger with row of 3 prominent tubercles in proximal third, distalmost largest, and band of minute denticles extending along distal half almost to corneous tip; large apically rounded tubercle ventral to denticle band near midlength of band. Opposable margin of movable finger with row of 5 tubercles in shallow excision in basal half, distalmost markedly larger; distal half with band of minute denticles extending almost to corneous tip.

Carpus of cheliped 1.4 times longer than wide, with conspicuous longitudinal furrow flanked by few punctuations on dorsal surface; mesial surface with 4 small tubercles proximally and large spiniform tubercle near midlength; ventral surface with strong spiniform tubercle in mesiodistal corner and row of 3 such tubercles on laterodistal half of margin; conspicuous oblique, shallow furrow between row and mesiodistal tubercle, extending to near midpoint of podomere.

Merus with dorsal row of 10 tubercles, distalmost large and subspiniform, flanked laterally by row of 4 small tubercles; ventrolateral margin with row of 11 small spiniform tubercles and ventromesial margin with row of 16, tubercles in both rows increasing in size distally. Ischium with single tubercle dorsally just distal to midlength and row of 2 ventrally. Margins of basis and coxa entire.

Hook on ischium of third pereiopod only (Fig. 1f), simple, overreaching distal margin of basis but not opposed by tubercle. Coxae of third and fourth pereiopods lacking boss.

Sternum of third through fifth thoracic segments deeply excavate and with long dense mats of plumose setae on ventrolateral margins, which setae masking most of length of first pleopods when abdomen flexed.

First pleopods (Figs. 1a, c, d, e, i) as described in "Diagnosis."

Allotypic female.—Differing from holotype, except in secondary sexual characters, as follows: Areola 39.5% of TCL (45.5% of PCL), with 1 or 2 punctations across narrowest part. Length of mesial margin of chela 1.2 times width of palm; mesial margin with median row of 6 tubercles, with only single tubercle flanking dorsally and none ventrally; ultimate tubercle on opposable margin of fixed finger of right side markedly larger than that of holotype. Annulus ventralis (Fig. 1k) with subcircular central elevations; deep cephalomedian trough dividing ridges and central depression making elevations imperfect ring; barest hint of tuberculation on cephalolateral crests of elevations. Otherwise, as described in "Diagnosis."

Paratypic male, form II.—Differing from holotype as follows: Areola 37.9% of TCL (46.4% of PCL) and 13.1 times as long as wide. Tubercles of mesial margin of chela more spiniform and with medianmost row of 7 tubercles, flanked dorsally by row of 5 and ventrally by row of 5. Acumen of rostrum much reduced by comparison, possibly broken and healed.

First pleopods with severe premortem damage; right scarcely reaching beyond base, left apparently about half typical length and with attenuate apex devoid of indication of terminal elements. Pleopods apparently similar to holotype in proximal parts.

Color notes.—Ground color basically light beige, mottled everywhere by fine blue-black to black spots. Spots coalescing into larger ones on lateral branchiostegites, those in dorsal gastric region often conspicuously large. Light dorsomedian stripe on abdominal segments flanked by punctate stripe, and it flanked more ventrolaterally by angled dark stripe formed of close-set spots; pendulant parts of pleuron delimited by stripe intermediate in density between two aforementioned stripes. Telson and uropods uniformly mottled by fine spots. Chelae with dorsal surfaces of podomeres suffused with intense cerulean blue, and tubercles outstanding with blue-black coloration; large tubercles of opposable margins of fingers creamy white; tips of both fingers with encircling subdued dark red stripe. Coxae and bases of other pereiopods paler cerulean color; more distal podomeres not strikingly different in patterns from body.

Type locality.—Burrows in a wet area of a horse pasture on Riley Road, Reliance community, 0.7 mi (1.4 km) east of Farm to Market (FM on maps) Road 1179, east of Bryan, Brazos County, Texas; latitude and longitude approximately 30°45′N, 96°14′W. Here the habitat is grassy pasture on a sand and clay soil. It has been used as a pasture for horses and cattle for at least 10 years. The area contains depressions that can hold rain water for weeks, but the entire area dries out in summer. The depressions contain taller grasses and sedges (family Cyperaceae).

Disposition of types.—The holotypic male Form I, and allotypic female are deposited in the National Museum of Natural History as USNM nos. 260824 and 260825, respectively; paratypes are in the Tulane University Museum of Natural History (TU 6814, 1 ♂I; TU 6815, 1 ♀; TU 6816, 2 ♂I; TU 6817, 1 ♂II [exuvium]; TU 6818, 1 ♂I, 1 ♂II).

Specimens examined.—With one exception, noted below, all specimens came from the type locality; Brazos County, Texas: (1) type locality, 24 Jun 1993, 1 ♂I, coll. M. K. Wicksten; 12 Jun 1994, 1 ♀, MKW; 25 Jun 1994, 1 ♂I [carapace and chela only] MKW; 12 Jun 1995, 3 ♂I, 1 ♀, MKW; (2) Wolf Pen Creek at Gilchrist Avenue and Francis Street, College Station, 12 Jun 1995, 1 ♂II [broken exuvium only], MKW; 1 Jan 1995, 1 ♂I, 1 ♂II, James Self.

Variations.—There is little recorded variation other than slight differences in the numbers and comparative sizes of the tubercular and spinose ornamentation, especially of the chelipeds. Considering the sample size and geographic restriction of the type series, this is not surprising.

Relationships.—The presence of a cephalic process on the gonopod of the male places *Procambarus* (*Girardiella*) *ceruleus* in the Gracilis Section of the subgenus *Girardiella* as designated by Fitzpatrick (1978a). Within the group it has its closest affinities with *P.* (*G.*) *kensleyi* Hobbs (1990), *P.* (*G.*) *liberorum* Fitzpatrick (1978b) *P.* (*G.*) *nigrocinctus* Hobbs (1990), *P.* (*G.*) *curdi* Reimer (1975), *P.* (*G.*) *reimeri* Hobbs (1979), and *P.* (*G.*) *tulanei* Penn (1953). It shares with these a broad cephalodistally directed caudal knob surmounted by a corneous conspicuous caudal process, and a more or less straight mesial process that extends beyond the other elements by at least their length. The narrow areola of *P.* (*G.*) *ceruleus* is approached only in *P. curdi* and *P. reimeri*; in *P. liberorum* the areola is obliterated. The annulus ventralis of the female, which is subcircular in outline, is most like that of *P. tulanei*, but the latter species has a bearded mesial margin of the palm, as does *P. kensleyi*. The following combination of 6 characters will distinguish this species: presence of a cephalic process in the male; a prominent caudal knob surmounted by a conspicuous caudal process in the male; an unbearded palm; a narrow areola; a rostrum lacking marginal spines or tubercles; and a female annulus ventralis that is subcircular in outline. The characters that this new species shares with a large number of members of the Gracilis Group that were previously thought not so closely related suggests that a reevaluation of the phylogeny of this cluster of species is in order, perhaps using molecular techniques.

Ecological notes.—The species apparently is a primary burrower, but the collections from the second site indicate that it, like many of its relatives, will venture into a stream or puddle, perhaps to breed or to feed. No data exist to indicate its breeding habits, but first form males were collected in June and January; no ovigerous females, no juveniles, and no females with a sperm plug were encountered. The largest animal, the form II male from Wolf Creek, is 44.8 mm TCL (36.6 mm PCL), and the largest and smallest form I males are 35.1 and 24.3 mm TCL (31.8 and 20.3 mm PCL, respectively) (the figures for the smallest are a close approximation because of damage to the caudal region of the cephalothorax). At the type locality, a juvenile male *Fallicambarus*, probably *F.* (*Creaserinus*) *fodiens* (Cottle, 1863) was collected on 12 June 1995.

Remarks.—One other feature merits mention. All specimens examined by us exhibited damage. Some was extensive and involved loss of a sizeable body part, others were slightly damaged; none of the specimens was missing chelae. Those from the type locality were collected on the surface of the soil after heavy rainfall, and it seems likely that the damage was due to the hazards of exposure on the surface. One of us (MKW) observed cattle egrets, *Bubulcus ibis*, foraging in the pasture on the same day that the crawfish were collected. Cattle egrets often eat crawfish. The pasture also contains numerous colonies of fire ants, *Solenopsis invicta*, which will attack any larger invertebrate that cannot escape quickly.

Some comment is necessary on the paucity of specimens and localities. Both are related to a social phenomenon of this section of the country. Almost all the land is fenced, posted and zealously defended against encroachment. Owners deny access to everyone and it is virtually impossible to obtain license to collect, much less to dig holes that potentially could injure livestock. What is reported here is the limit of what we could secure between the first collection and the Fall of 1997.

Etymology.—L., *caeruleus*, sky blue; an allusion to the coloration characteristic of the cheliped of this species.

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We would like to thank W. Tyler and Mary Moore, owners of the property where the crawfishes were collected, for their interest in the natural habitat and for permission to collect on their land. James Self donated the animals noted above. We also are indebted to John E. Cooper, North Carolina State Museum of Natural Sciences, who reviewed the manuscript.

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Pagurus retrorsimanus (Crustacea: Decapoda: Paguridae), a new and distinctive hermit crab from the eastern Pacific

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Abstract.—*Pagurus retrorsimanus*, a new and distinctive hermit crab species from the eastern Pacific of the genus *Pagurus* Fabricius, is described and illustrated. It is immediately distinguished from other representatives of the genus in the region by its extremely massive right cheliped.

While sorting and identifying specimens of hermit crabs from the collections of the Allan Hancock Foundation, now transferred to the Los Angeles County Museum of Natural History (LACM), we discovered a very unusual and undescribed hermit crab. One of us (MKW) and other divers observed and photographed the crab in life on rocky reefs of California. The hermit crab is described herein.

The material used for this study is deposited in the collections of the Los Angeles County Museum of Natural History. The shield length, abbreviated as SL, has been measured in millimeters from the tip of the rostrum to the midpoint of the posterior margin of the shield, and is indicated in parenthesis in the material examined; ov. indicates ovigerous female.

Pagurus retrorsimanus, new species
Figs. 1, 2

Pagurus sp. 2: Jensen 1995: 67, fig. 126.

Holotype.—Male (SL 4.8), LACM number 40-113.13. Off Redondo Beach, Los Angeles County, California (33°49′55″N, 118°23′50″W), 20–37 m, gravel, 6 May 1940, *Velero III* sta. 1139–40.

Paratypes.—California, U.S.A.: Off Cannery Row, Monterey, 11 m, on reef, 25 Jan 1975, coll. M.K. Wicksten, 1 male (SL 3.8). Naples Reef, ca. 18 mi. N. of Santa Barbara, 11–15 m, Jun–Jul 1976, coll. Gary Robinson, female ov. (SL 3.1), male (SL 3.6), male (SL 4.0). Becher's Bay, Santa Rosa Is., 18 m, sand, 2 Aug 1938, *Velero III* sta. 881-38, female ov. (SL 3.2), female (SL 4.3). Becher's Bay, 18 m, sand and corallines, 10 Aug 1939, *Velero III* sta. 995-39, female ov. (SL 2.8), male (SL 2.5), female (SL 2.8), female (SL 2.4), female (SL 1.4), male (SL 1.5). Becher's Bay, 26 m, sand and shell, 18 Aug 1939, *Velero III* sta. 1003-39, male (SL 2.6). 2.6 mi. 360° True to E. Point, Santa Rosa Is., 50 m, 7 Nov 1975, *Velero IV* sta. 23206, female ov. (SL 2.8). 2.6 mi. 230° True to Diablo Pt., Santa Cruz Is., 85–90 m, 27 Apr 1976, *Velero IV* sta. 24867, male (SL 2.9). 2.6 mi. 105° True to Fraser Pt., Santa Cruz Is., 44–66 m, 28 Apr 1976, *Velero IV* sta. 24873, male (SL 2.5). Off Redondo Beach, 20–37 m, gravel, 6 May 1940, *Velero III* sta. 1139–40, female (SL 3.3), female (SL 3.8). Off Redondo Beach, 46 m, gravel, May 1941, coll. J. Burch, female (SL 3.2). Off Redondo Beach, 18–36 m, 31 Aug 1940, coll. T. Burch, female (SL 4.7), male (SL 5.5). Off Redondo Beach, 16 Jul 1939, Burch sta. 3919, male (SL 3.1). Point Loma, San Diego, 12 m, "Grid 15," 23 Oct 1975, male (SL 6.2), with parasitic rhizocephalan. Baja California Norte, Mexico: Los Coronados

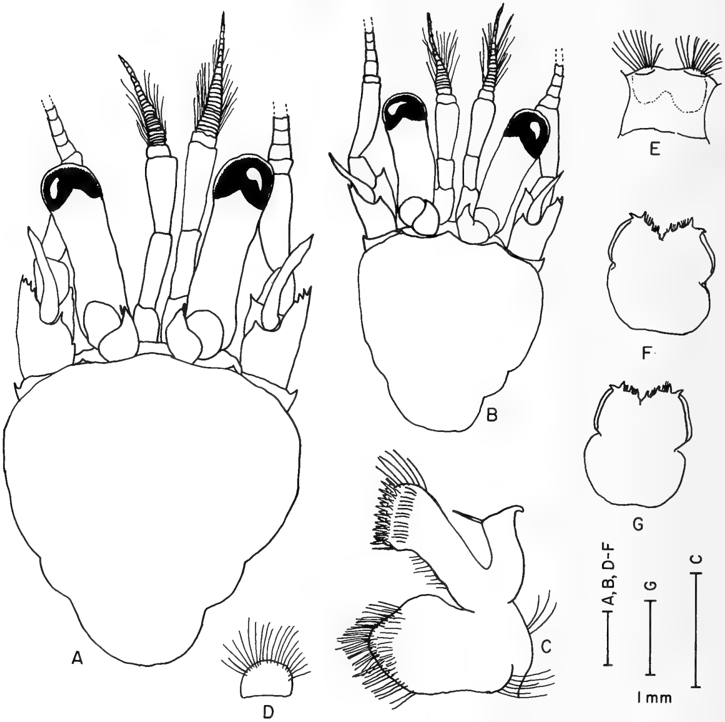

Fig. 1. *Pagurus retrorsimanus*, new species. A, shield and cephalic appendages of male; B, shield and cephalic appendages of female; C, maxillule of male; D, anterior lobe of sternite of third pereopods of male; E, sternite of fifth pereopods of male; F, telson of male; G, telson of female. Scales equal 1.0 mm.

Islands, 28 m, 19 Jul 1901, *Elsie* sta. LIX-H1, female ov. (SL 3.6), male (SL 3.4), male (SL 3.8), male (SL 5.7).

Description.—Shield (Fig. 1A, B) longer than broad (females) to slightly broader than long (males); anterior margin between rostrum and lateral projections usually slightly concave; posterior margin truncate or rounded. Dorsal surface of shield with scattered setae, anterior half granulate. Rostrum triangular, broadly rounded, or obsolete. Lateral projections obsolete or weakly produced, and with small marginal or submarginal spine. Interocular lobes weakly developed. Ocular peduncles approximately ⅔ length of shield, but overreached by both antennular and antennal peduncles; corneae slightly dilated. Ocular acicles triangular or subovate, with moderate to strong submarginal spine; separated basally by less than basal width of 1 acicle.

Antennular peduncles overreaching corneae by ⅓ to ½ length of ultimate segment; unarmed.

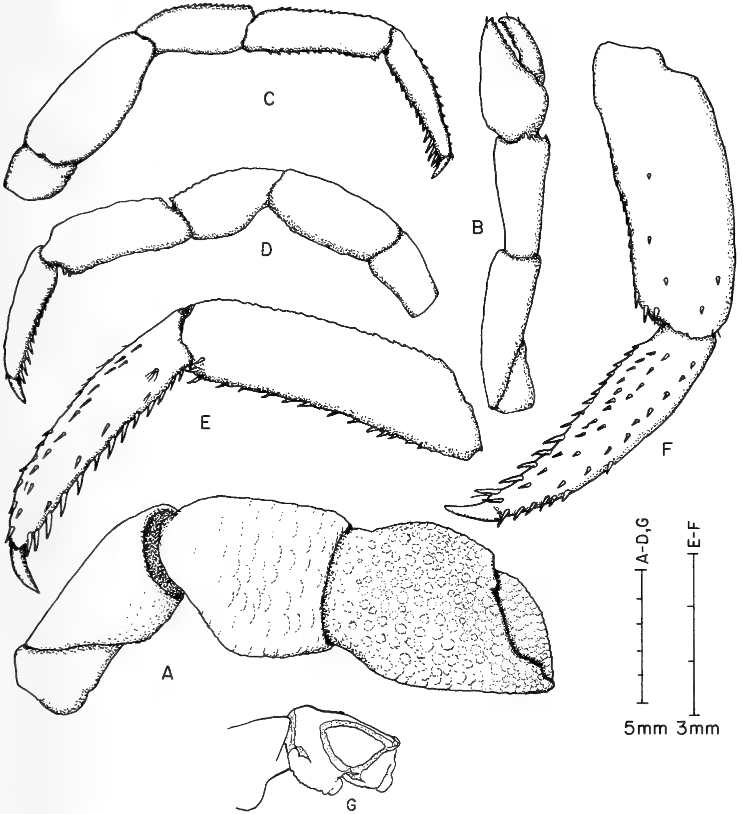

Fig. 2. *Pagurus retrorsimanus*, new species. A, right cheliped (dorsolateral view); B, left cheliped (dorsal view); C, right second pereopod (lateral view); D, left third pereopod (lateral view); E, dactyl and propodus of left second pereopod (mesial view); F, dactyl and propodus of left third pereopod (mesial view); G, merus of right cheliped (mesial view). Scales equal 3.0 mm (E, F) and 5.0 mm (A–D, G). Note: 2G was drawn from a different specimen than that illustrated in A–F.

Antennal peduncle overreaching corneae by ⅛ to ¼ length of ultimate segment. Fifth and fourth segments unarmed. Third segment with spine at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in simple or bifid spine and often with 2 or 3 accessory spinules on mesial margin; dorsomesial distal angle with small spine. First segment with small spine on dorsolateral distal margin; ventral margin produced and with 3 or 4 small spines laterally. Antennal acicle moderately short, terminating in small spine, and with row of tufts of setae on mesial margin. Antennal flagellum with very few scattered setae.

Palp of mandible 3-segmented. Maxillule (Fig. 1C) with external lobe of endopod somewhat produced, slightly recurved. Maxilla with endopod slightly overreaching scaphognathite. First maxilliped with moderately slender exopod; endopod approximately ⅔ length of exopod. Third maxilliped with well developed crista dentata and 1 accessory tooth; merus and carpus unarmed. Sternite of third maxillipeds with small spine on either side of midline.

Right cheliped (Fig. 2A) extremely massive; dactyl ⅓ to ½ length of palm; articulating obliquely with very short fixed finger; cutting edge of dactyl with 1 very broad calcareous tooth proximally and 3 smaller calcareous teeth distally, terminating in strong calcareous claw; cutting edge of fixed finger with broad calcareous tooth proximally and few smaller calcareous teeth distally, terminating in strong calcareous claw. Palm very broad and dorsoventrally compressed, dorsomesial and dorsolateral margins not delimited. Dorsal and ventral surfaces of dactyl, fixed finger, and palm all with flattened, plate-like tubercles, particularly densely packed marginally. Carpus short and broad, with lateral face strongly produced ventrally, dorsolateral and dorsomesial margins not delimited, distal margin tuberculate; all surfaces covered with densely packed flattened tubercles at least in distal halves. Meral-carpal articulation twisted at approximately 75° counterclockwise. Merus approximately as long as carpus, with few blunt spinules on dorsodistal margin and row of small spinules on distomesial margin; ventrolateral margin with row of small acute or blunt spinules distally; ventromesial margin with strong, broad, blunt tubercle. Ischium with row of blunt or acute tubercles on ventromesial margin.

Left cheliped (Fig. 2B) reaching only to proximal half of right palm. Dactyl nearly 1 ⅓ times longer than palm; cutting edge with row of closely-spaced corneous teeth, terminating in small corneous claw; dorsal surface unarmed, but with few scattered setae distally, ventral surface with row of tufts of stiff setae. Fixed finger with 2 or more rows of tufts of stiff setae on ventral surface, dorsal surface with few tufts adjacent to cutting edge, latter with row of small calcareous teeth interspersed with corneous teeth and terminating in small corneous claw. Palm and fixed finger roundly triangular in cross section, margins not delimited; dorsal surface sometimes with few minute spinules or tubercles on mesial half. Carpus approximately twice length of palm and equal to length of merus; subtriangular; dorsal surface with irregular single or double row of very small spines, extending onto mesiodistal margin; ventrolateral margin with few spines distally. Merus subtriangular; ventromesial and ventrolateral margins each with row of small to minute spinules. Ischium unarmed.

Second left and right pereopods (Fig. 2C, E) and third right pereopod similar; third left with distinctly different dactyl and propodus from these (Fig. 2D, F). Dactyls of second and right third approximately as long and broad as propodi; ventral margins with 10–14 corneous spines on ventral margins; dorsal margins with irregular row of small corneous spinules or bristles, mesial faces each with dorsal and ventral rows of corneous spinules. Propodi each with 2 or 3 corneous spines at ventrodistal angle and row of small corneous spines on ventral margins. Carpi with row of very small spinules on dorsal margins, strongest on second. Meri with 1 or 2 rows of minute spinules on ventral margins. Ischia unarmed. Third left pereopod with dactyl slightly longer than propodus, broader (in lateral view) proximally and tapering to claw; ventral margin with 13 or 14 corneous spines; mesial face with single row (dorsally) and double row (ventrally) of small corneous spines. Propodus also broad (in lateral view), ventral margin with row of minute corneous spinules, 3 or 4 stronger spinules at distal angle. Carpus, merus, and ischium as in third right.

Sternite of third pereopods with subsemicircular, setose anterior lobe (Fig. 1D). Sternite of fifth pereopods (Fig. 1E) with 2 broadly separated, setose lobes.

Fourth pereopods without definitive preungual process at base of claw. Proposal rasp consisting of several rows of corneous scales.

Uropods markedly asymmetrical. Telson (Fig. 1F, G) with distinct transverse suture; posterior lobes separated by shallow median cleft; terminal margins oblique, each armed with 3–5 strong spines and several smaller spines, outermost, and sometimes also innermost, strongest; lateral margins weakly chitinized.

Color in life.—Ocular peduncles and antennules dark, translucent blue. Dark blue ring at base of ocular peduncles. Antennal flagellum translucent reddish. Third maxillipeds orange-red. Shield flesh-colored, with two large and few smaller brown spots. Walking legs, entire minor cheliped and major cheliped except for propodus and dactyl covered with dark red specks, giving crab a reddish color when seen from a distance. Palm and fingers of major chela usually bone white, rarely also covered with red specks.

Distribution.—Monterey, California to Los Coronados Islands, Baja California Norte, Mexico; 11–90 m.

Etymology.—The specific name is derived from the Latin *retrorsus* meaning bent or turned backward, and *manus* meaning hand. The name is a noun in apposition. In life, the major chela is bent underneath the body and appears to be turned backwards.

Remarks.—*Pagurus retrorsimanus* is distinguished not only by its massive right chela but also by the very broad, blunt tubercle on the ventromesial margin of the merus of the right cheliped. At first glance, the shape, structure and positioning of the right chela with the dorsal surface in a lateral position are reminiscent of the left chelipeds of some *Calcinus* species. However, in *Calcinus*, as well as in other diogenid genera such as *Dardanus*, it is the carpal-propodal articulation that is twisted from the perpendicular. In *P. retrorsimanus*, it is in the meral-carpal articulation that the twisting occurs.

This species exhibits sexual dimorphism, but in a manner different from other *Pagurus* species. Rather than the right cheliped exhibiting dimorphic attributes, in *P. retrorsimanus* large males (SL > 5.0 mm) are characterized by an obsolete or markedly reduced rostrum, a shield that is broader than long and having a nearly straight or only very weakly concave anterior margin, and a telson with only the outermost spines appreciably larger. In contrast, females have triangular, acute rostra, shields that are appreciably longer than broad, with distinctly concave anterior margins, and telson with strong spines in the innermost as well as outermost positions.

Pagurus retrorsimanus does not appear to have any close relatives among eastern Pacific *Pagurus* species. It shares with *Pagurus hemphilli* (Benedict 1892) the ventrally produced carpus of the right cheliped and the slightly recurved external endopodal lobe of the maxillule (cf. McLaughlin, 1974), but there the similarity ends.

Acknowledgments

The late Janet Haig of the University of Southern California was the first to recognize this hermit crab as an undescribed species, and located specimens of it among the collections of the Allan Hancock Foundation. The figures were drawn by G. Fain Hubbard. This is a scientific contribution from the Shannon Point Marine Center.

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A new genus for four species of hermit crabs formerly assigned to the genus *Pagurus* Fabricius (Decapoda: Anomura: Paguridae)

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Abstract.—A new genus, *Propagurus*, is described for four species formerly assigned to the hermit crab genus *Pagurus* Fabricius. The species, all very *Pagurus*-like in overall appearance, are characterized by having gills of a quadriserial nature and rudimentary pleurobranchs on the fifth and sixth thoracic somites (above the second and third pereopods).

During a review of South African species assigned to the hermit crab genus *Pagurus* Fabricius, 1775 (McLaughlin & Forest 1998), the holotype of *Pagurus deprofundis* (Stebbing 1924) was reexamined for the first time. Two characters immediately set Stebbing's species apart from other members of the genus, i.e., its asymmetrical, quadriserial gill structure, and a longitudinal keel on the mesial face of the propodus of each second pereopod. The general body morphology and telson structure reminded one of the authors (JF) of the South American *Pagurus gaudichaudii* H. Milne Edwards, 1836. In a report by Forest & de Saint Laurent (1968) on species of *Pagurus* collected during the voyage of the *Calypso* to the Atlantic coast of South America, these authors established four distinct species groups for South American species within this heterogeneous genus. *Pagurus gaudichaudii* (as *P. gaudichaudi*) was recognized as distinct from all other described *Pagurus* species and assigned to a monotypic group ("groupe *gaudichaudi*"), characterized by having rudimentary pleurobranchs on the fifth and sixth thoracic somites (above the second and third pereopods) and a quadriserial gill structure. When *P. deprofundis* was closely examined, it too was found to have pleurobranchs on the fifth and sixth thoracic somites; however, in Stebbing's (1924) unique specimen, only the pleurobranch of the sixth thoracic somite was rudimentary; that of the fifth was moderately well developed.

At the time the *gaudichaudi* group was established, Forest & de Saint Laurent (1968) indicated that they had examined several Indo-Pacific specimens, then still unidentified, that shared the gill number and structure of *P. gaudichaudii*, but differed from the South American species in several important characters. They considered that *P. gaudichaudii* was probably an unique species for which a new genus should be considered. We have now reexamined the referred-to Indo-Pacific specimens and have found most to represent *P. deprofundis* that had previously gone unrecognized because of Stebbing's (1924) inadequate and inaccurate original description and figures.

When McLaughlin (1997) described *Pagurus haigae* from the French-Indonesian KARUBAR expedition to Indonesia, she failed to detect the quadriserial nature of the gills in that species, or the presence of rudimentary pleurobranchs on the fifth and sixth thoracic somites. Like *P. gaudichaudii*, *P. haigae* lacks the propodal keel of *P. deprofundis*. A few of the Indo-Pacific specimens examined earlier by Forest & de

Saint Laurent also proved to be conspecific with *P. haigae*. McLaughlin (1997) contrasted *P. haigae* with *P. yokoyai* Makarov, 1938 and *P. brachiomastus* (Thallwitz 1892). Reexamination of specimens of these latter two species has shown that *P. yokoyai*, but not *P. brachiomastus*, has the same gill structure and number as the above mentioned taxa. For these four species we now propose a new genus. It must be noted that *Pagurus* remains a very heterogeneous taxon. As better knowledge of the species currently assigned to *Pagurus* becomes available, there will certainly be further apportionment.

With the exception of one specimen in the personal collection of one of the authors (PMcL), materials for this study have come from the following institutions: Museums and Art Galleries of the Northern Territories, Darwin, Australia (NTM), Muséum national d'Histoire naturelle, Paris, France (MNHN), Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (NMNZ) (formerly the National Museum of New Zealand), Museum of Victoria, Melbourne, Australia (NMV), National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (USNM), Natural History Museum and Institute, Chiba, Japan (CBM-ZC), New Zealand Oceanographic Institute, Wellington, New Zealand (NZOI) (now part of the National Institute of Water and Atmospheric Research), Osaka Museum of Natural History, Osaka, Japan (OMNH), Swedish Natural History Museum, Stockholm, Sweden (SNHM), The Natural History Museum, London, U.K. (NHM), and Zoological Museum, University of Copenhagen, Denmark (ZMUC). These specimens have been returned to their institutions of origin. Shield length (sl), measured from the tip of the rostrum or midpoint of the rostral lobe to the midpoint of the posterior margin of the shield, or carapace length (cl), measured from the tip of the rostrum or midpoint of the rostral lobe to the midpoint of the posterior margin of the carapace provides an indication of animal size. The abbreviation ovig. indicates ovigerous female. The following abbreviations indentify campaignes, expeditions, vessels, sample type, or gear: SMIB, Substances Marines d'Intérêt Biologique; KARUBAR, acronym for the French-Indonesian campaign to the Islands of Kai, Aru and Tanimbar; MUSORSTOM, acronym for the joint expeditions by the Muséum national d'Histoire naturelle, Paris, and Office de la Recherche Scientifique et Technique Outre-Mer; FR, Fisheries Research; CM, *Chiyo Maru*; JO, *James Cook*; SM, *Shinkai Maru*; So, *Soela*; BS, bottom sample; DW, Warén dredge; CP, beam trawl; CC, shrimp trawl.

Propagurus, new genus

Eupagurus.—Barnard, 1950:458 (in part); not *Eupagurus* Brandt, 1851.

Pagurus.—Makarov, 1938:169; 1962: 181 (in part).—Miyake, 1978:78 (in part).—McLaughlin, 1997:525 (in part); not *Pagurus* Fabricius, 1775.

Type species.—*Pagurus gaudichaudii* H. Milne Edwards, 1836.

Diagnosis.—Thirteen pairs of symmetrical or asymmetrical, generally quadriserial gills (Fig. 1): 2 arthrobranchs on each third maxilliped, cheliped and second through fourth pereopods; single moderately well developed or rudimentary pleurobranch on fifth thoracic somite, rudimentary pleurobranch on sixth thoracic somite, and well developed pleurobranch on seventh thoracic somite (above fourth pereopod). Ocular acicles subacutely to roundly triangular. Basal segment of antennular peduncle with strong lateral spine (Fig. 2A). Antennal peduncles with laterodistal projection of second segment well developed, mesial margin spinose. Maxillule (Fig. 2B–E)) with external lobe of endopod varying from vestigial or rudimentary to well developed, arched, but not strongly recurved. Third maxilliped (Fig. 2F, G) with basis-ischium fusion incomplete; crista dentata well developed and with strong accessory tooth. Sternite of

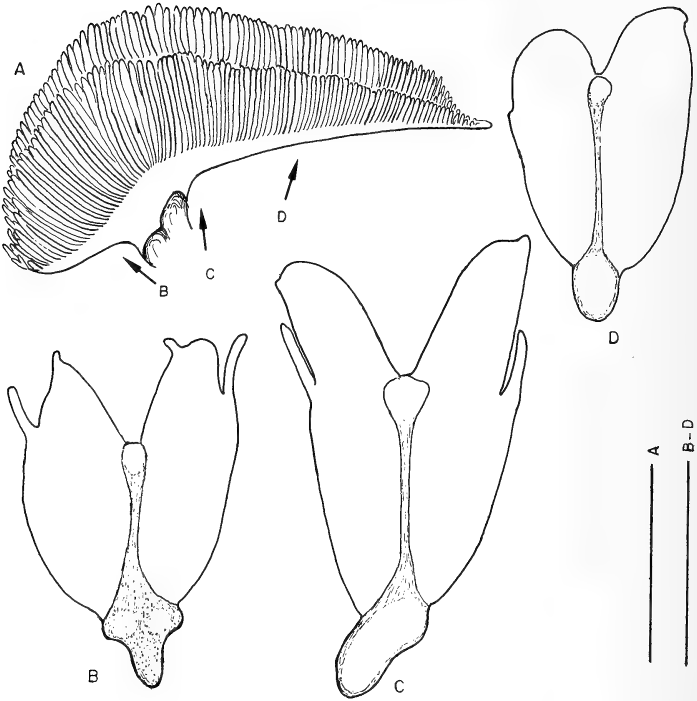

Fig. 1. Right anterior arthrobranch of third pereopod of *Propagurus gaudichaudii* (H. Milne Edwards, 1836), new combination, ♂ (cl = 21 mm) MNHN-Pg 2550. A, entire gill; B–D, sections at indicated levels showing lamellar shapes. Scales equal 2 mm (B–D) and 5 mm (A).

third maxillipeds (third thoracic sternite) with spine on each side of median concavity. Left second and third pereopods shorter than right; propodus and dactyl of left third with more prominent setation. Fourth pereopods with propodal rasp consisting of 2 to several rows of corneous scales. Eight thoracic sternite (sternite of fifth pereopods) (Fig. 3A) with broadly and ovately subrectangular lobes, each with horizontal or transverse tuft of long setae.

Abdomen well developed, somites often delineated dorsally by strong transverse fibrils; tergite of sixth somite strongly calcified, with deep submedian transverse furrow dividing tergite into subquadrate anterior and subrectangular posterior lobes. Uropods markedly asymmetrical. Telson with deep submedian transverse indentation providing indication of division into anterior and posterior portions; asymmetrical posterior lobes separated by median cleft.

Males with paired gonopores, each partially masked by adjacent tuft of stiff setae; no sexual tubes; no paired pleopods, usually three unpaired left pleopods, third (Fig. 3B)

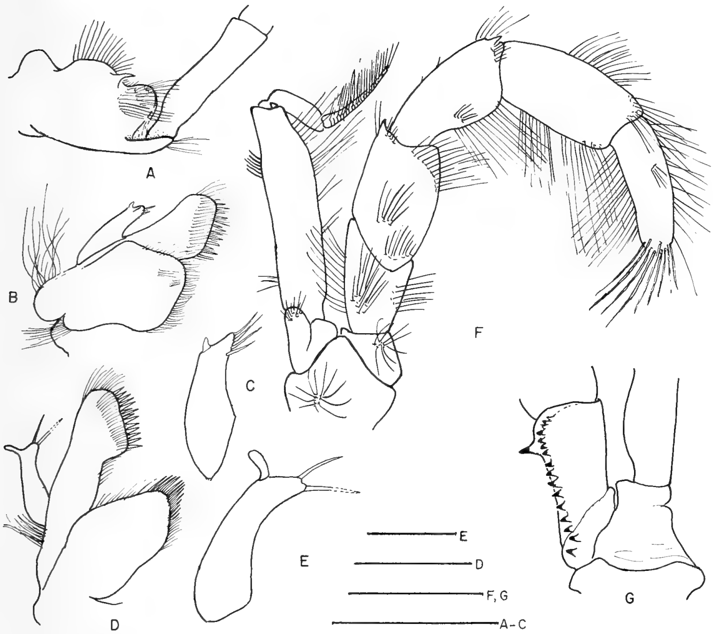

Fig. 2. Cephalic appendages. A–C, F, G, *Propagurus gaudichaudii* (H. Milne Edwards, 1836), new combination, ♂ (cl 21 = mm), MNHN-Pg 2550; D, E, *Propagurus deprofundis* (Stebbing, 1924), n. comb, ♂ (sl = 11.2 mm), NZOI sta. E719: A, antennule (lateral view); B, D, maxillule (lateral view); C, E, endopod of maxillule, enlarged; F, third maxilliped, lateral view; G, basis-ischium of third maxilliped showing development of crista dentata. Scales equal 1 mm (E), 2 mm (D), and 5 mm (A–C, F, G).

to fifth each with somewhat foliaceous elongate endopod and rudimentary exopod. Females with paired gonopores; no paired pleopods, 4 unpaired left pleopods, second (Fig. 3C) with subequal rami, both short, somewhat paddle-shaped, third (Fig. 3D) and fourth each with elongate somewhat foliaceous endopod and short paddle or blade-shaped exopod; fifth as in male.

Etymology.—From the Greek *pro* meaning before, and *pagouros* meaning crab and referring to the more primitive characters of this very *Pagurus*-appearing genus. Genus masculine.

Remarks.—We have chosen to use the term "quadriserial" in reference to gill structure equivalent to Lemaitre's (1989) trichobranchiate and intermediate conditions. Studies by one of us (MST) have shown that it is not the shape of the gill elements, so much as their insertion on the rachis of the gill that determines the gill type. In true trichobranchiate gills the tubular elements are equal or unequal, but inserted in order or disorder, around the axis, or in regular transverse rows along the axis. In contrast, the elements of phyllobranchiate gills almost always are inserted biserially

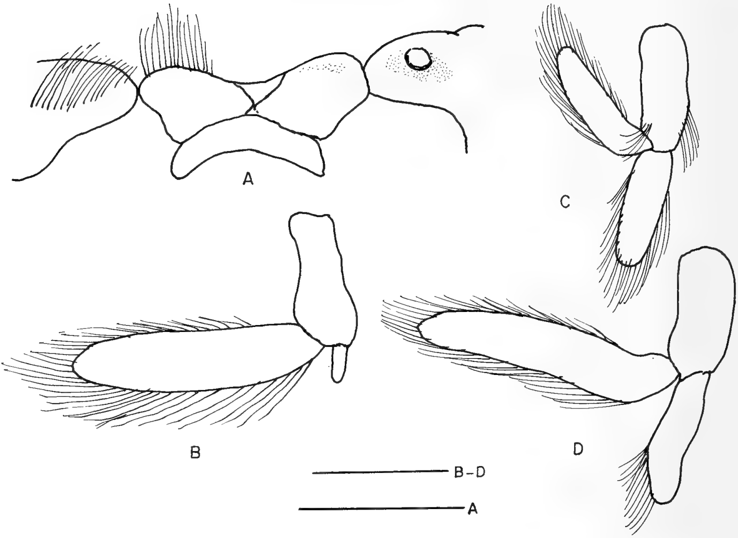

Fig. 3. *Propagurus gaudichaudii* (H. Milne Edwards, 1836), new combination. A, ♂ (cl = 25 mm), MNHN-Pg 2550; B, ♂ syntype (sl = 18.6 mm) of *P. patagoniensis* (Benedict, 1892), USNM 16772; C, D, ♀ syntype (sl = 16.0 mm) of *P. patagoniensis* (Benedict, 1892), USNM 16772. A, sternite and coxae of fifth pereopods (ventral view, setae omitted from left side); B, C, second left pleopod; D, third left pleopod. Scales equal 5 mm.

in regular pairs along the rachis. There are many types of true trichobranch gills, just as there are phyllobranch gills. The quadriserial appearing gills of *Propagurus*, like those of pylochelids and some parapagurids, are inserted biserially on the rachis; it is the lamella of each pair that is divided, equally or unequally, giving a "trichobranch" or "intermediate" appearance. However, as may be seen in Fig. 1, the lamellar structure varies from one level of the rachis to another. Similarly, the degree of asymmetry may vary from one arthrobranch to another.

In certain morphological characters, species of *Propagurus* seems to be undergoing evolutionary transformations from those seen in the typical *Pylopaguropsis* group of pagurid genera (cf. de Saint Laurent-Dechancé 1966) to those seen in *Pagurus*-like genera. Three important variations seen among the species of this new genus offer support to this hypothesis: the overall development of the gill lamellae, which varies, even within a single species from deeply quadriserial to only weakly so; reduction of the pleurobranch of the fifth thoracic somite, which varies from moderately well developed to rudimentary; and development of the external endopodal lobe of the maxillule that is quite well developed in two species, rudimentary in another, and variable in the fourth.

A key to the species is provided, however exclusive reliance on it for species identifications is not recommended. Only in the case of *P. deprofundis* will a single character distinguish the species with certainty. Differentiation between *P. haigae* and *P. yokoyai* is particularly difficult, because of their considerable morphological similarities and magnitudes of intraspecific variation.

Key to the species of *Propagurus*, new genus

1. Left chela with dorsal surface uniformly covered with strong, tuberculate spines; dactyls of ambulatory legs each with only few distal strong spines on ventral margin, followed by row of tiny widely-spaced spinules; propodi of second pereopods each with dorsal row of corneous-tipped spines (southern South America) .... *P. gaudichaudii*, new combination

–. Left chela with distinct median row of spines, separating dorsal surface into strongly armed lateral portion and more tuberculate mesial portion; dactyls of ambulatory legs each with complete row of strong corneous spines on ventral margin; propodi of second pereopods without dorsal row of corneous-tipped spines 2

2. Propodi of second pereopods each with longitudinal keel on mesial face; lateral faces of palms of chelipeds each with few to several rows of closely-spaced tubercles or blunt spines (South Africa, southern Australia, New Zealand, Philippine and Hawaiian Islands) .... *P. deprofundis*, new combination

–. Propodi of second pereopods without longitudinal keel on mesial face; lateral faces of palms of chelipeds without few to several rows of closely-spaced tubercles or blunt spines 3

3. Distal margins of corneas usually not reaching to mid-length of fully extended ultimate segments of antennular peduncles; dorsomesial surface of palm of left cheliped with tufts of setae accompanied by several small spines; telson without, or with row of accessory spinules on dorsal surfaces adjacent to terminal margin (Indonesia, New Caledonia, Coral and Tasman Seas) .... *P. haigae*, new combination

–. Distal margins of corneas reaching to or beyond mid-length of fully extended ultimate segments of antennular peduncles; dorsomesial surface of palm of left cheliped with tufts of setae sometimes accompanied by low protuberances; telson with 2 to several rows of accessory spinules on dorsal surfaces adjacent to terminal margin (Japan) .... *P. yokoyai*, new combination

Propagurus gaudichaudii (H. Milne Edwards 1836), new combination

Figs. 1A–D, 2A–C,F,G, 3A–D, 4A, 5A–F, 6A–D, 7A, 11A, B

Pagurus Gaudichaudii H. Milne Edwards, 1836:269.—Nicolet, 1849:188.

Pagurus Gaudichaudi.—H. Milne Edwards, 1837:217.—Porter, 1935:137.

Bernhardus barbiger A. Milne Edwards, 1891:28, pl. 3, figs 1, 1a–c.

Eupagurus patagoniensis Benedict, 1892: 3.—Alcock, 1905:181 (list).–Barattini & Ureta, 1960:52, unnumbered fig.

Pagurus patagoniensis.—Benedict, 1901: 465, unnumbered fig.

Pagurus barbiger.—Benedict, 1901:466.—Rathbun, 1910:598.—Porter, 1935:137.

Eupagurus barbiger.—Lenz, 1902:737.—Lagerberg, 1905:4.—Alcock, 1905:180 (list).—Doflein & Balss, 1912:31.

Pagurus gaudichaudii.—Rathbun, 1910: 598.

Pagurus gaudichaudi.—Haig, 1955:24.—Gordan, 1956:330 (lit).—Forest & de Saint Laurent, 1968:142, fig. 112.—Scelzo & Boschi, 1973:208.—Scelzo, 1973: 166; 1976:43.—McLaughlin, 1974:43.—Boschi et al., 1981:244.—Boschi et al., 1992:53, fig. 51.

Holotype of *Pagurus gaudichaudii*.—♂ (sl = 13 mm), Valparaiso, MNHN Pg 221 (damaged).

Holotype of *Pagurus barbiger*.—♀ (sl = 6.9 mm), Orange Bay, Patagonia, 22 m, 29 Dec 1882, MNHN Pg 2401.

Syntypes of *Pagurus patagoniensis*.—1 ♂, 1 ♀ (sl = 15.5, 11.8 mm), *Albatross* sta. 2768, east coast of Patagonia, 79 m, 1888, USNM 16772.

Other material examined.—Argentina:

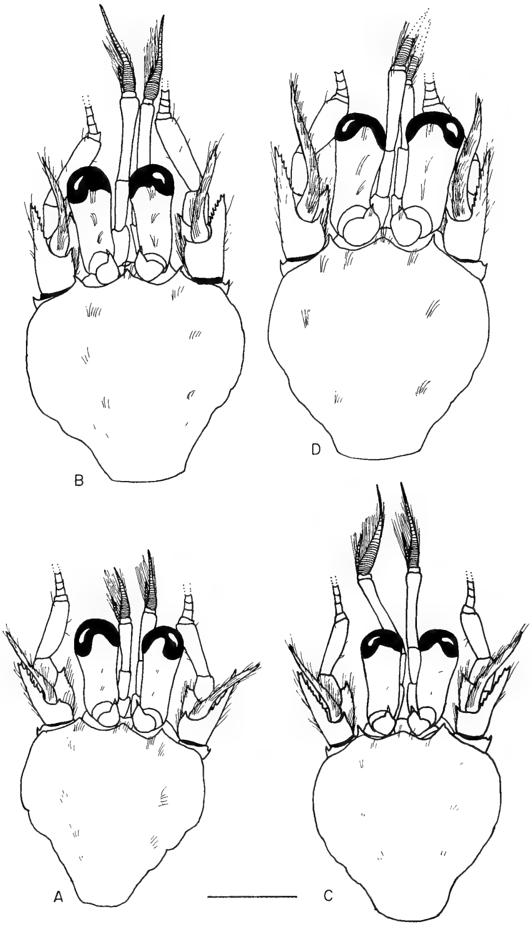

Fig. 4. Shield and cephalic appendages. A, *Propagurus gaudichaudii* (H. Milne Edwards, 1836) new combination, ♀ (sl = 16.0 mm), MNHN-Pg 2852; B, *Propagurus deprofundis* (Stebbing, 1924) new combination, ♂ (sl = 11.2 mm), NZOI; C, *Propagurus haigae* (McLaughlin, 1997) new combination, ♂ (sl = 17.1 mm) NTM Cr 6864; *Propagurus yokoyai* (Makarov, 1938) new combination, ♂ (sl = 11.5 mm), OMNH Ar 1941. Scale equal 5 mm (B, D) and 7.5 mm (A, C).

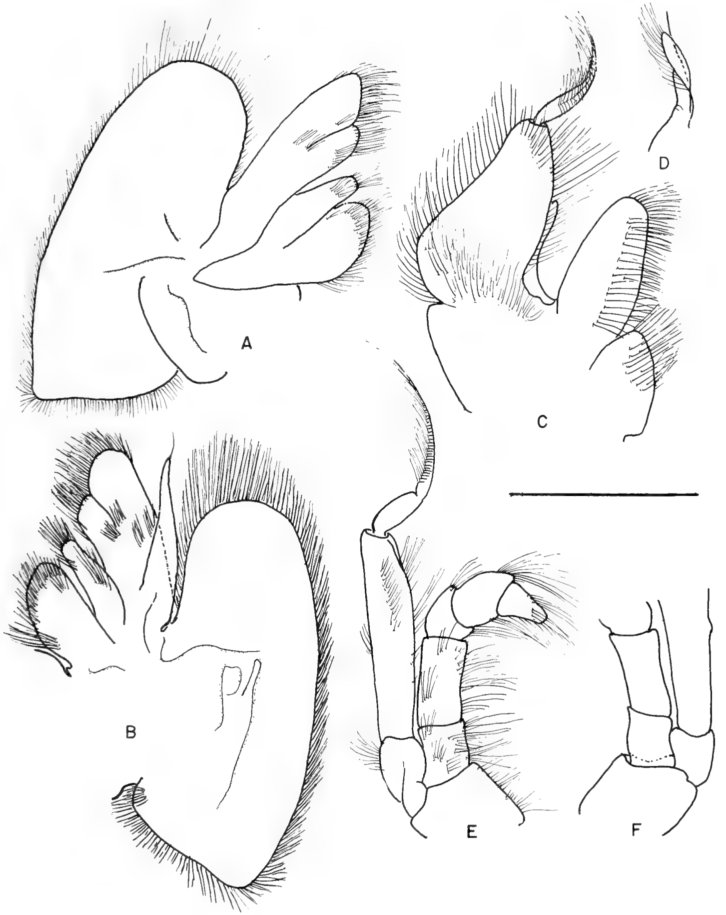

Fig. 5. *Propagurus gaudichaudii* (H. Milne Edwards, 1836), ♂ (cl = 21 mm), MNHN-Pg 2550, mouthparts. A, maxilla (lateral view); B, maxilla (mesial view); C, first maxilliped (lateral view); D, enlarged distal portion of endopod of first maxilliped; E, second maxilliped (lateral view); F, basis-ischium of second maxilliped (mesial view). Scale equals 5 mm.

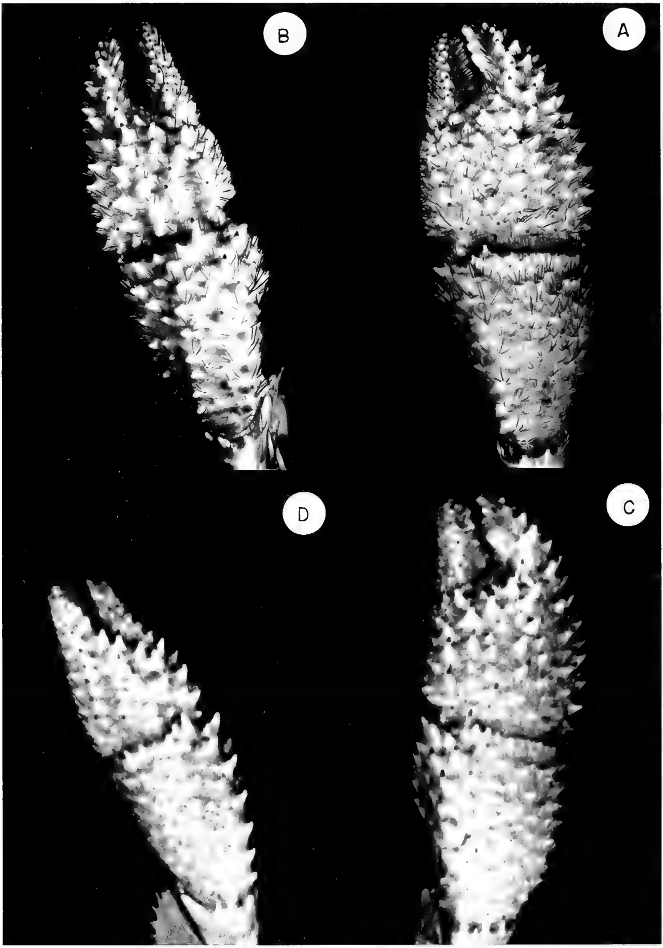

Fig. 6. *Propagurus gaudichaudii* (H. Milne Edwards, 1836) new combination. A, C, chela and carpus of right cheliped; B, D, chela and carpus of left cheliped. A, B, ♀ (sl = 16.0 mm), MNHN-Pg 2852; C, D, syntype of *Pagurus patagoniensis* (Benedict, 1982), ♀ (sl = 11.8 mm), USNM 16772. Magnifications equal 1.6× (A), 1.9× (B), 2.6× (C), and 2.1× (D).

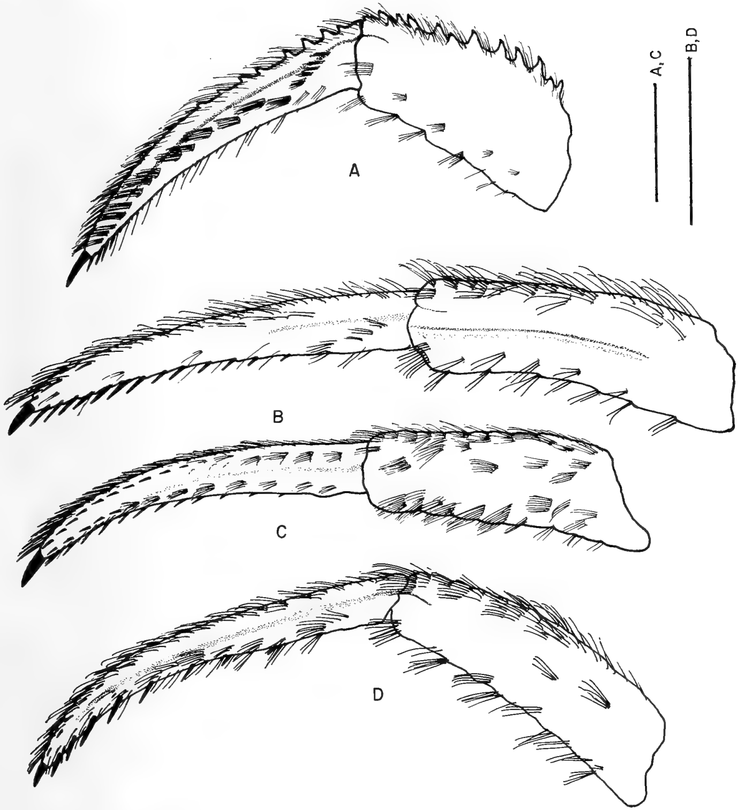

Fig. 7. Dactyl and propodus of second right pereopod (mesial view). A, *Propagurus gaudichaudii* (H. Milne Edwards, 1836) new combination, ♀ (sl = 16.0 mm), MNHN-Pg 2852; B, *Propagurus deprofundis* (Stebbing, 1924) new combination, ♂ (sl = 11.2 mm), NZOI; C, *Propagurus haigae* (McLaughlin, 1997) new combination, ♂ (sl = 17.1 mm) NTM Cr 6864; D, *Propagurus yokoyai* (Makarov, 1938) new combination, ♂ (sl = 11.5 mm), OMNH Ar 1941. Scales equal 5mm.

2♂ (cl = 33.0, 41.0 mm), 36°30′S, 54°00′W, 9 Jul 1961, coll. L. Rossi MNHN Pg 2550. *Calypso*, eastern South America (1961–1962): 4 ♂ (cl = 22.0–45.0 mm), 2 ovig. ♀ (cl = 27.0, 37.0 mm), sta. 169 off Rio de la Plata, 37°00′S, 55°21′W, 69 m, 29 Dec 1961, MNHN Pg 2852.—3 ♂ (cl = 41.0–48.0 mm), 1 ♀ (cl = 35.0 mm), sta. 170, 37°24.5′S, 54°56′W, 126–132 m, 9 Dec 1961, MNHN Pg 2851.—1 ♂ (cl = 37.0 mm), sta. 173, 38°25.54′S, 56°14′W, 81 m, 30 Dec 1961, MNHN Pg 2853.

Diagnosis.—Shield (Fig. 4A) varying from slightly broader than long to slightly longer than broad. Rostrum roundly subtriangular, subacute, sometimes produced beyond level of lateral projections; with or without terminal spine. Lateral projections broadly triangular or rounded, with or without submarginal spine. Ocular peduncles slightly more than half to approximately 0.75 length of shield; broader at base of corneas than proximally; corneas slightly dilated. Ocular acicles ovately or roundly triangular, dorsal surfaces somewhat concave, each with strong, sometimes corneous-tipped submarginal spine. Antennular peduncles overreach distal margins of corneas by 0.50–0.65 length of ultimate segment; basal segment with strong spine on lateral surface in distal half. Antennal peduncles overreach distal margins of corneas by 0.15–0.35 length of ultimate segment; second segment with laterodistal angle reaching to or beyond distal margin of fourth peduncular segment, with simple or bifid terminal spine, mesial margin with 4–7 corneous-tipped spines, lateral margin with few tufts of setae, dorsomesial distal angle with small corneous-tipped spine; first segment sometimes with spine on distolateral margin dorsally; ventrolateral margin with 1 small spine. Antennal acicles reaching to or beyond distal margins of corneas, each with strong terminal spine and numerous tufts of long stiff setae on mesial face.

External enopodal lobe of maxillule (Fig. 2B, C) rudimentary. Maxilla (Fig. 5A, B) with broad scaphognathite. First maxilliped (Fig. 5C, D) with short, distally twisted endopod. Second maxilliped (Fig. 5E, F) with basis-ischium fusion incomplete. Meri of third maxillipeds each with dorsodistal spine, ventral margins unarmed.

Right cheliped (Fig. 6A, C) considerably stronger than left, but not appreciably longer; with weak hiatus between dactyl and fixed finger. Dactyl with double row of corneous-tipped spines on dorsal surface laterad of midline, at least proximally and double row of tufts of stiff setae; dorsomesial margin with row of small corneous-tipped spines, becoming more prominent distally. Palm with row of strong corneous-tipped spines on dorsomesial margin, convex dorsal surface with 6 rows of conical corneous-tipped spines; dorsolateral margin not distinctly delimited proximally, but with irregular row of corneous-tipped spines becoming marginal and extending nearly to tip of fixed finger; lateral face of palm with few spines or tubercles dorsally; mesial face with transverse rows of tubercles. Carpus with irregular row of strong corneous-tipped spines on dorsomesial margin, dorsal surface with irregular rows of corneous-tipped spines accompanied by sparse tufts of stiff setae; dorsolateral margin not distinctly delimited, but with row of corneous-tipped spines; lateral face primarily with tufts of stiff setae. Merus with 2–4 strong and 1 or 2 smaller spines on dorsodistal margin, dorsal margin with short transverse ridges and quite short stiff setae, distal-most ridge spinose; ventromesial margin with row of small spines distally replaced by short transverse row of tuberculate spines proximally; ventrolateral margin with row of corneous-tipped spines distally replaced by low protuberances proximally; ventral surface with 2 transverse rows of conical spines, largest proximally.

Left cheliped (Fig. 6B, D) with two irregular rows of corneous-tipped spines on dorsal surface of dactyl proximally becoming single row distally, dorsomesial margin and mesial face with irregular rows of tuberculate corneous-tipped spines, more numerous in proximal half. Palm with irregular row of strong corneous-tipped spines on dorsomesial margin, dorsal surface generally somewhat flattened, with 4 irregular rows of tuberculate corneous-tipped spines decreasing to 2 rows on fixed finger; dorsolateral margin not clearly delimited but with double row of tuberculate or corneous-tipped spines. Carpus with 1 prominent spine on dorsodistal margin; dorsomesial margin with strong corneous-tipped spines and tufts of stiff setae, dorsal surface with adjacent and median rows of corneous-tipped spines, interspersed with few smaller spines; dorsal surface laterad of midline with irregular rows of corneous-tipped spines extending onto lateral face dorsally. Merus with 1–3 large and 1 or 2 smaller spines on dorsodistal margin, dorsal margin with transverse ridges and setae, distal-most spinose; ventromesial margin usually with short row of corneous-tipped spines in distal half, becoming low tubercles proximally and extending onto ventral surface; ventrolateral margin with row of prominent spines in distal half, shifting onto ventral surface proximally, 1 larger tuberculate spine at proximal angle.

Ambulatory legs overreaching chelipeds by approximately half length of dactyls. Dactyls of left and right (Fig. 7A, second) similar; moderately long and stout, 1.65–2.0 length of propodi; in dorsal view slightly twisted; in lateral view slightly curved; dorsal surfaces somewhat flattened, each with double row of corneous-tipped spines and row of stiff setae, inner-most row becoming simple corneous spines distally; lateral and mesial surfaces each with longitudinal sulcus, strongest on second; lateral faces each also with row of tufts of stiff setae, and arc of 4 or 5 stiff setae proximally, mesial faces each also with row of stiff setae proximally and arc of stiff setae distally; ventral margins each with row of 4 or 5 prominent corneous spines distally, becoming very small widely-spaced spinules in proximal 0.75. Propodi each with 2–4 rows of strong corneous-tipped spines accompanied by tufts of stiff setae extending onto lateral face dorsally; mesial faces each with 1 or 2 blunt or subacute spines dorsally and tufts of stiff setae; ventrodistal margin with row of small corneous spinules or short stiff bristles. Carpi each with row of strong corneous-tipped spines on dorsal surface; lateral faces spinulose (second) or with low protuberances and tufts of stiff setae (third). Meri all with transverse rows of short stiff setae dorsally, ventral margins of second pereopods each with 1 or 2 spines; ventral margins of third unarmed. Sternite of third pereopods with row of setae on roundly subrectangular to subquadrate anterior lobe.

Telson (Figs. 11A, B) with asymmetrical posterior lobes separated by slender median cleft; terminal margins often considerably produced laterally, each with row of small calcareous spines on inner half, calcified but unarmed on outer half.

Color.—Beautiful violet (Boschi et al. 1992).

Distribution.—Chile, Strait of Magellan, Argentina, Uruguay; littoral to 150 m.

Remarks.—The holotype of *Pagurus gaudichaudii* has the abdomen and all appendages disarticulated; the fourth and fifth pereopods, including their coxae, are missing. The specimen is determined to be a male since no gonopores are present on the coxae of the third pereopods. The bottle contains two labels, an old printed one reading "*Pagurus Gaudichaudii* Edw., M. Gaudichaud, Valparaiso," and a second hand written by Bouvier indicating the reference to Milne Edwards' publication and the mention of "type." The holotype of *Pagurus barbiger*, as noted by Forest & de Saint Laurent (1968) is a young female. Its label indicates "*Eupagurus* (*Bernhardus*) *barbiger* M. Edw. et Mocquet, 1891, Mission du Cap Horn, baie Orange, 22m." The bottle, MNHN Pg 2401, also contains a second smaller female (sl = 5 mm), which is not mentioned in the original publication, and therefore cannot be considered a type specimen.

Benedict (1901) noted that A. Milne Edwards' (1891) description of *Pagurus barbiger* had come to his attention only after his own description of *Pagurus patagoniensis* (as *Eupagurus*) had been published (Benedict 1892). Based on A. Milne Edwards (1891) description and figures, Benedict (1901) pointed out several differences between *P. barbiger* and *P. patagoniensis*, but acknowledged that these differences might well be related to size and that the two might prove to be conspecific. Lagerberg (1905) formally placed *P. patagoniensis* in synonymy. Haig (1955) recognized the similarities between *P. barbiger* as described by Lagerberg (1905) and *P. gaudichaudii* (as *P. gaudichaudi*) from Chile. At Haig's request, J. Forest examined the types of both species and confirmed her suspicions. *Pagurus barbiger*, together with *P. patagoniensis* were then placed in synonymy with *P. gaudichaudii*; however, neither Lagerberg (1905) nor Haig (1955) actually examined Benedict's (1892) *P. patagoniensis*. We have now compared Benedict's syntypes with the holotypes of *P. gaudichaudii* and *P. barbiger*, as well as with specimens of *P. gaudichaudii* from *Calypso* station 170 off Rio de la Plata, and can reaffirm the conspecificity of the three taxa.

Forest & de Saint Laurent (1968) discussed the size-related variations observed in small specimens of *P. gaudichaudii*. These include longer ocular peduncles, narrower ocular acicles, shorter antennular and antennal peduncles, and stouter ambulatory legs. *Propagurus gaudichaudii* differs from the other species of the genus in several morphological attributes: the dorsal surface of the chela of the left cheliped is flattened, lacking the elevated median row(s) of spines of the other species; the carpus of the left cheliped is appreciably broader and, while armed with numerous spines, these do not form the two distinctive longitudinal rows seen in the other species; the ambulatory dactyls have only a few strong corneous spines distally, followed by widely-spaced very tiny spinules, whereas the dactyls of all three other species are each armed with a complete row of strong spines; the dorsal surfaces of the propodi of the ambulatory legs are generally flattened and each is armed with a double row of spines. In these characters, *P. gaudichaudii* approaches species of the *bernhardus* group of *Pagurus* (cf. McLaughlin 1974), which is undoubtedly why Benedict (1901) aligned *P. patagoniensis* with species like *Pagurus bernhardus* (Linnaeus 1758).

In addition to the differentiating characters of the gills, the short ocular peduncles, spinose laterodistal projections of the second segment of the antennal peduncle, and spatulate pleopodal endopods clearly unite *Propagurus gaudichaudii* with the other species assigned to the genus. The distinctive subquadrate shield and general shape of the posterior telsonal lobes of *P. gaudichaudii* appear to indicate a closer relationship to *P. deprofundis* than to either *P. haigae* or *P. yokoyai*. Although the shield is more angular in *P. gaudichaudii* than in *P. deprofundis*, both are somewhat dissimilar to the more rounded shields of *P. haigae* and *P. yokoyai*. In both *P. gaudichaudii* and *P. deprofundis* there is a tendency for the terminal margins of the telson to be produced laterally; however, while in *P. gaudichaudii* the lateral half of each lobe usually consists of a pectinate, faintly denticulate, or entire plate, this portion in *P. deprofundis*, like the median portions in both species, is often provided with spines. In *P. gaudichaudii*, the mesial faces of the palms of the chelipeds are armed with transverse rows of tubercles, not identical with, but similar to the rows of tubercles or small spines seen on the lateral surfaces of the palms of *P. deprofundis*. No comparable armature is seen on either surface of the palms of *P. haigae* or *P. yokoyai*.

Propagurus deprofundis (Stebbing 1924), new combination

Figs. 2D, E, 4B, 7B, 8A–D, 9, 11C, D

Eupagurus deprofundis Stebbing, 1924: 243, pl. 70.—Barnard, 1950: 164.—Forest, 1955: 107.

Pagurus deprofundis.—Gordan, 1956:329 (lit).

Pagurus deprofundus.—Kensley, 1981:33 (list) (misspelling).

Propagurus deprofundis.—McLaughlin & Forest, 1998, figs. 7A–K.

Holotype.—♀ (sl = 9.3 mm); 13 miles

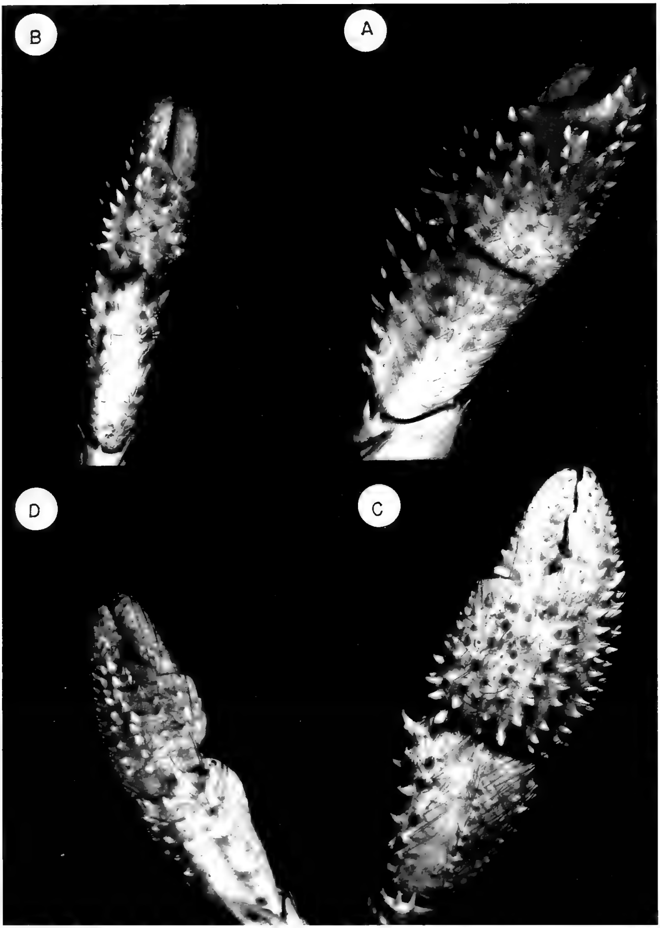

Fig. 8. *Propagurus deprofundis* (Stebbing, 1924) new combination. A, C, chela and carpus of right cheliped; B, D, chela and carpus of left cheliped. A, B, ♂ (sl = 11.2 mm), NZOI; C, D, holotype ♀ (sl = 9.3 mm), NHM 1928.12.1.245. Magnifications equal 2.8× (A), 3.0× (B), 3.8× (C), and 3.1× (D).

Fig. 9. *Propagurus deprofundis* (Stebbing, 1924) new combination, ♂ (sl = 11.2 mm), NZOI. Chela and carpus of left cheliped (lateral view). Magnification equal 3.0×.

northwest of Cape Morgan, South Africa, 32°42.6′S, 28°21.8′E, 457–585 m, NHM 1928.12.1.245.

Other material examined.—Philippine Islands. MUSORSTOM Philippine Expeditions: 1 ♂, 1 ♀ (sl = 9.3, 9.5 mm) sta. 44, 13°46.9′N, 120°29.5′E, 610–592 m, 24 Mar 1976, MNHN Pg 5545.—1 ♂ (sl = 7.6 mm), sta. 77, 13°48.8′N, 120°30.1′E, 552–529 m, 1 Dec 1980, MNHN Pg 5546.—1 ♂ (sl = 11.5 mm), sta. 106, 13°47′N, 120°30′E, 640–668 m, 2 Jun 1985, MNHN Pg 5547.

Indonesia. Corindon: 1 ♂, 1 ♀ (sl = 10.5, 11.5 mm), *Corindon II* Makassar Strait sta. 276, 1°54.6′S, 119°13,8′E, 456–395 m, 8 Nov 1980, MNHN Pg 5548.

Australia. Th. Mortensen's Pacific Expedition: 1 ovig. ♀ (sl = 10.2 mm), 38°05′S, 150°00′E, 366–475 m, 12 Nov 1914, ZMUC.—1 ovig. ♀ (sl = 5.8 mm), 39°10′S, 149°55′E, 366–457 m, 15 Nov 1914, ZMUC.—Museum of Victoria: 1 ♀, 3 ovig. ♀ (sl = 6.8–10.8 mm), sta. FR5/86, 38°14.9′S, 149°26.1′E, 800 m, 23 Jul 1986, J 21015.—1 ♂, 3 ovig. ♀ (sl = 5.9–8.9 mm), sta. Slope 40, 38°17.7′S, 149°11.3′E, 400 m, 24 Jul 1986, J 40397.—1 ♀ (sl = 5.9 mm), sta. Slope 46, 42°00.2′S, 148°37.7′E, 720 m, 27 Jul 1986, J 17422.—2 ♂, 1 ♀ (sl = 3.6–5.2 mm), sta. Slope 49, 41°56.5′S, 148°37.9′E, 200 m, 27 Jul 1986, J 17431.—1 ♂, 1 ♀ (sl = 5.2, 8.0 mm), sta. Slope 67, 34°43.6′S, 151°13.2′E, 450 m, 22 Oct 1988, J 40390.—3 ♀, 1 ovig. ♀ (sl = 6.2–7.4 mm), sta. Slope 84, 41°53.5′S, 148°39.1′E, 732 m, 30 Oct 1988, J 40389.—1 ♂, 2 ♀ (sl = 6.9–13.7 mm), 33°46′S, 151°49′E, 414 m, 9 Sep 1981, J 40386.—1 ♂ (sl = 12.7 mm), sta. So5/84-27, 37°59.4′S, 150°05.4′E, 452 m, 14 Oct 1984, J 40385.—2 ♂ (sl = 13.3, 10.4 mm), sta. So6/84-13, 37°45.2′S, 150°13.4′E, 426 m, 28 Nov 1984, J 21012, J 40388.—1 ♂ (sl = 11.0 mm), sta. So6/84-18, 39°17.1′S, 148°44.4′E, 580 m, 30 Nov 1984, J 40387.—1 ♂, 2 ♀ (sl = 7.3–17.1 mm), sta. So1/85-45, 37°41.5′S, 150°14′E, 458 m, 4 Feb 1985, J 40391.

New Zealand. NMNZ: 1 ♀, 2 ovig. ♀ (sl = 12.0–14.0 mm), sta. CM 149, 46°30′S, 165°14.4′E, 545–573 m, 10 Sep 1987, NMNZ Cr 8066.—1 ♂ (sl = 14.5 mm), sta. JO6/008/81, 39°29.8′S, 178°10.8′E, 529–568, 15 Apr 1981, NMNZ Cr 8097.—1 ♂ (sl = 17.0 mm), sta. SM 2/50, 42°50.5′S, 177°42.5′E, 540–499 m, 9 Nov 1975, NMNZ Cr 8099.—1 ♂, 1 ♀ (sl = 15.2, 10.9 mm), sta. BS844, 37°10.9′S, 176°38.7′E, 685–705 m, 23 Jan 1981, NMNZ Cr 7592, Cr 8211.—Northern Prawn Survey: 1 ♀ (sl = 9.7 mm), haul 14, 8 mi E White I., 640–548 m, 10 Sep 1962.—NZOI: 1 ♂ (sl = 12.4 mm), sta. C619, 43°52′S, 174°48′E, 802 m, 2 May 1961.—1 ♂ (sl = 14.7 mm), sta. D233, 38°50′S, 169°20′E, 530 m, 29 Sep 1964.—1 ♂ (sl = 12.9 mm), sta. E711, 39°18.8′S, 178°13.8′E, 490–428 m, 23 Mar 1967.—5 ♂, 1 ovig ♀ (sl = 9.0–11.8 mm), sta. E719, 38°46′S, 178°48′E, 913–750 m, 23 Mar 1967.—1 ♀ (sl = 11.8 mm), sta. E747, 40°43.2′S, 176°48.4′E, 554–569 m, 29 Mar 1967.—1 ♂ (sl = 9.9 mm), sta. E797, 45°20′S, 166°44.7′E, 471 m, 20 Oct 1967.—1 ♀ (sl = 7.8 mm), sta. E822, 46°50.6′S, 165°36′E, 682–786 m, 23 Oct 1967.—1 ♂, 1 ♀ (sl = 14.4, 12.6 mm) sta. E827, 46°35.5′S, 166°44.5′E, 532 m.—1 ovig ♀ (sl = 11.8 mm) sta. E831, 47°50.6′S, 167°03.8′E, 479 m, 25 Oct 1967.—1 ♀ (sl = 10.0 mm), sta. E876, 37°32.5°S, 177°34′E, 529–492 m, 10 Mar 1968.—1 ♀ (sl = 7.6 mm), sta. E 879, 35°19′S, 172°25′E, 762–780 m, 22 Mar 1968.—1 ♂ (sl = 10.5 mm), sta. J711, 37°59.4′S, 176°03′E, 366–472 m, 11 Sep 1974.

Hawaiian Islands. U.S. Fish Commission: 1 ♀ (sl = 7.1 mm), *Albatross* sta. 4132, 22°01.5′N, 159°21.2′W, 470–570 m, 1 Aug 1902, USNM 284748.

Diagnosis.—Shield (Fig. 4B) varying from slightly longer than broad to distinctly broader than long. Rostrum commonly triangular, usually produced beyond level of lateral projections, occasionally even developing slight, short rostral keel; usually with prominent terminal spine. Lateral projections obtusely triangular, each with strong submarginal spine. Ocular peduncles slightly less to slightly more than half shield length; moderately stout, broader at base of corneas than proximally, dorsal or dorsomesial surface usually with short transverse rows of sparse tufts of setae; corneas slightly dilated. Ocular acicles ovately or acutely triangular, dorsal surfaces somewhat concave, each with strong submarginal spine. Fully extended antennular peduncles overreach distal margins of corneas by 0.20 length of ultimate segments to 0.25 length of penultimate segments; basal segment with very strong spine on lateral surface in distal half. Antennal peduncles overreach distal margins of corneas by 0.10–0.75 length of ultimate segments, and reach approximately to distal 0.35–0.85 of ultimate segments of antennular peduncles; second segment with laterodistal projection reaching at least to distal half of fourth peduncular segment, with simple or bifid terminal spine, mesial margin with 5–9 small spines, lateral margin with tufts of long setae, dorsomesial distal angle with very strong spine; first segment with prominent spine on distolateral margin dorsally; ventrolateral margin with 1–3 spines. Antennal acicle reaching at least to mid-length of ultimate peduncular segment, usually considerably beyond, with strong terminal spine and numerous tufts of long stiff setae on mesial face. External endopodal lobe of maxillule (Fig. 2D, E) well developed, sometimes arched, but never strongly recurved. Meri and carpi of third maxillipeds each with dorsodistal spine; meri also usually with 1, occasionally with 2 spines on ventral margin, rarely unarmed.

Right cheliped (Fig. 8A, C) considerably stronger than left, but not always appreciably longer; sometimes with hiatus between dactyl and fixed finger. Dactyl with convex dorsal surface marked by transverse rows of tufts of stiff setae and often few spines proximally; dorsomesial margin with single or double row of small spines. Palm varying from moderately slender to moderately broad, with irregular double row of spines on dorsomesial margin, convex dorsal surface sparsely covered with short setae, with 6 somewhat irregular rows of spines, usually accompanied by long stiff setae; dorsolateral margin not distinctly delimited proximally, but with irregular row of spines becoming marginal and extending nearly to tip of fixed finger; lateral face of palm with distinct rows of closely-spaced tubercles or tuberculate spines particularly in ventral half. Carpus with irregular row of strong spines on dorsomesial margin accompanied by adjacent slightly irregular row of spines on dorsal surface, separated by broad nearly naked longitudinal strip from median row of shorter spines, few scattered spines laterally; dorsolateral margin rounded but with row of small spines usually becoming double row distally; lateral face sometimes with forwardly directed spines and spinules or tubercles, occasionally just low protuberances and long setae; ventral surface often with row of spines mesially and laterally. Merus with 0–3 spines on dorsodistal margin, dorsal margin with short transverse ridges; mesial face with scattered protuberances proximally; ventromesial margin usually with row of spines or tubercles, strongest proximally; lateral face with transverse sometimes spinulose ridges at least in ventral half, ventrolateral margin with row of acute or subacute spines; ventral surface often with few small and occasionally 2 large spines.

Left cheliped (Fig. 8B, D) frequently with hiatus between dactyl and fixed finger; with numerous tufts of long setae and also often with few spinules proximally on rounded dorsal surface of dactyl. Palm usually moderately slender, with median single or double row of spines on convex dorsal surface, becoming less regular on proximal half of fixed finger; dorsomesial face usually with central row of spines and nearly double row of slightly smaller spines; dorsolateral face (Fig. 9) with several irregular rows of small closely-spaced tubercles, spines or spinules, appreciably stronger dorsally, but not extending to tip of fixed finger. Carpus with 1 sometimes quite strong spine on dorsodistal margin, and occasionally with second spine directly beneath; dorsomesial margin with irregular row of moderate to strong spines and tufts of long setae, dorsal surface unarmed, slightly depressed; rounded dorsolateral margin with row of spines; lateral surface with semi-perpendicular rows of small tuberculate spines decreasing in size proximally, ventrolateral margin with row of small subacute spines. Merus with 1–3 spines at dorsodistal margin, dorsal margin and mesial face each with transverse ridges and setae, sometimes becoming multispinose ventrally on mesial face; ventromesial margin with row of spines proximally and frequently also small spine distally; lateral face with short transverse ridges becoming flattened multifid tubercles ventrally, ventrolateral margin with row of spines sometimes becoming double row proximally.

Ambulatory legs overreaching left cheliped by at least 0.75 length of dactyls. Dactyls and propodi of left and right (Fig. 7B of second) morphologically similar, but left with greater setation on lateral faces. Dactyls moderately long and stout, 1.10–1.85 as long as propodi; in dorsal view weakly to strongly twisted; in lateral view straight (second) or slightly curved (third); dorsal surfaces with transverse low protuberances and long stiff setae; lateral surfaces each with faint longitudinal sulcus and row(s) of long or moderately long setae; ventral margins each with row of 8–21 strong corneous spines. Propodi each with transverse low ridges and long stiff setae on dorsal and lateral surfaces; mesial faces of second pereopods (Fig. 7B right) each with longitudinal keel in ventral third, extending from near distal margin to mid-length, or more frequently, proximal third. Carpus of second right with row 5–8, second left with row of 3–7 spines and transverse setose ridges on dorsal surfaces; dorsal surfaces of third each with 0–5 smaller spines and transverse setose ridges in additional to strong dorsodistal spine; lateral faces all with short transverse ridges and long setae. Meri all with transverse setose ridges dorsally, ventral margins of second each with ventromesial row of spines, more numerous and stronger on left, ventrolateral distal angles each sometimes with spine; ventral margins of third unarmed or rarely with tiny spinule on ventrolateral margin and stronger spinule on ventromesial margin distally. Sternite of third pereopods with submarginal row of setae on subsemicircular to roundly subrectangular anterior lobe.

Mature females usually with dense setae on coxae of fifth pereopods. Telson (Fig. 11C, D) with asymmetrical posterior lobes separated by slender median cleft; terminal margins often considerably produced laterally, each with row of small calcareous spines becoming stronger toward outer angles, largest spines, particularly on left, somewhat hooked.

Color (in preservative).—Shield mottled white and orange. Ocular peduncles orange; ocular acicles orange basally, white distally. Antennular peduncles whitish with flagella orange. Antennal peduncles faintly orange, darkest on proximal segments. Chelipeds with orange tint, darkest on dactyls. Ambulatory legs each with orange band proximally and distally on meri; carpi, propodi and dactyls all faintly orange, darkest on distal halves of dactyls.

Habitat.—Found in a variety of gastropod shells, sometimes with anemone attached.

Distribution.—Southeastern South Africa; Tasmania and southeastern Australia, Tasman Sea, west and east New Zealand to Chatham Rise; Philippine Islands; Hawaii; 200 to 750–913 m. Bathymetric range over entire geographic range is between 450 and 750 m, with only the capture of young specimens at shallower depths.

Remarks.—As previously indicated, the only published record of rudimentary pleurobranchs on the fifth and sixth thoracic somites is that of Forest & de Saint Laurent (1968) for "*Pagurus*" *gaudichaudii*, a species superficially resembling *bernhardus* group species. Had it not been for the astute observation by Jacques Forest, Muséum national d'Histoire naturelle, (McLaughlin & Forest 1998) of the similarities between *P. gaudichaudii* and *P. deprofundis*, and the recognition in earlier (but as yet unpublished) studies of one of the present authors (MST) of similar characters in certain unidentified Indo-Pacific pagurids, this suite of species could not have been unified in a distinct genus. Following the redescription of the holotype of *P. deprofundis* (McLaughlin & Forest 1998), this enigmatic species is now recognized as having an extremely broad distribution.

The three smallest specimens examined came from the shallowest recorded depth, 200 m off Tasmania. Of these, the tiniest was a male (sl = 3.5 mm) with the gonopores barely visible, suggesting immaturity; however, another male that was only slightly larger (sl = 3.6 mm) had well marked gonopores. Pleopod development in these two males was comparable. Females were ovigerous at shield lengths as short as 5.8 and 5.9 mm.

Not only has marked variation been observed among 25 males, 22 non-ovigerous and 13 ovigerous females, as is indicated in the diagnosis, but a few abnormalities have been also noted. One specimen (sl = 10.0 mm) from the vicinity of the Solander Trough, southwestern New Zealand, has well developed female gonopores and pleopods, but also one male gonopore. Another female from the Solander Trough has a normal left cheliped, but a right that is nearly identical to it. One male specimen (sl = 14.5 mm), collected of Napier on the east side of the North Island of New Zealand has four left pleopods, that of the second somite with subequal rami as seen in females; however, no external evidence of a rhizocephalan infestation could be detected that might have had a feminizing effect. Another male (sl = 11.0 mm), collected in the same general vicinity, has a weakly produced, obtusely triangular, terminally rounded rostral lobe, that is in marked contrast to the prominent, triangular, acute rostrum seen in other specimens. The female specimen from the Makassar Strait, Indonesia, has much shorter ocular peduncles and antennal acicles than does the male from the same station. A similar condition has been observed in one of the Philippine specimens; however in this specimen, the

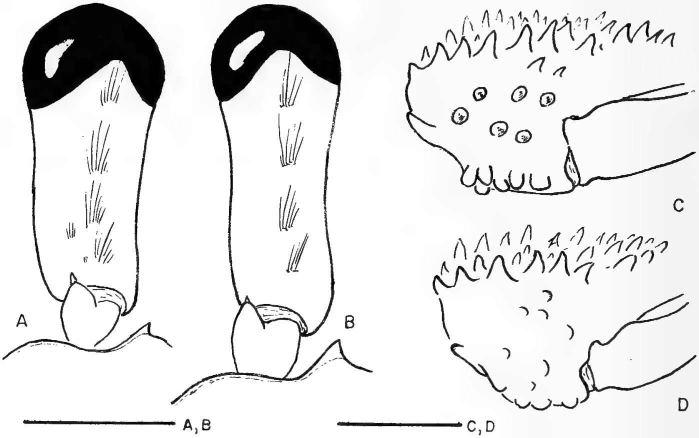

Fig. 10. A, C, *Propagurus haigae* (McLaughlin, 1997) new combination, A, ♂ (sl = 10.1 mm), MNHN-Pg 5311; C, ♀ (sl = 12.1 mm), MNHN-Pg 5310 (bis). B, D, *Propagurus yokoyai* (Makarov, 1938) new combination: B, ♂ (sl = 10.8 mm), MNHN-Pg 2277; D, ♂ (sl = 12.0 mm), MNHN-Pg 3651. A, B, right ocular peduncle portion of anterior margin of shield and right lateral projection; C, D, dorsomesial view of palm of left cheliped. Scales equal 3 mm (A, B) and 5 mm (C, D).

shortened ocular peduncle and antennal acicle are present only on one side of the animal. We do not believe that these latter two specimens represent extremes in variation, but rather abnormalities.

Propagurus haigae (McLaughlin 1997), new combination

Figs. 4C, 7C, 10A, C, 11E, F, 12A, B

Pagurus haigae McLaughlin, 1997:533, figs 27a–h, 43a–d.

Holotype.—♂ (sl = 18.6 mm), KARUBAR sta. CP 16, 05°17′S 132°50′E, 315–349 m, 24 Oct 1991, MNHN Pg 5310.

Paratypes.—1 ♀ (sl = 12.1 mm), KARUBAR sta. CP 16, 05°17′S 132°50′E, 315–349 m, 24 Oct 1991, MNHN Pg 5310.— 1 ♂ (sl = 10.1 mm with branchial bopyrid), sta. CP 26, 05°34′S, 132°52′E, 265–302 m, 26 Oct 1991, MNHN Pg 5311.— 1 ♂ (sl = 7.3 mm), sta. CP 26, 05°34′S, 132°52′E, 265–302 m, 26 Oct 1991, SNHM 4812.—1 ♂ (sl = 11.5 mm), Sta CC 41, 07°45′S, 132°42′E, 401–393 m, 28 Oct 1991, USNM 276014.

Other material examined.—New Caledonia: 2 ♂ (sl = 5.1, 6.3 mm, 1 with branchial bopyrid), SMIB 4, sta. DW 58, 22°59.8′S, 167°24.2′E, 560 m, 9 Mar 1989, MNHN Pg 5549.

Indonesia. Danske Kei Expedition: 1 ♂ (sl = 18.7 mm), 05°28′S, 132°36′E, 385 m, 12 May 1922, ZMUC.—U.S. Fish Commission: 1 ♀ (sl = 11.2 mm), *Albatross* sta. 5623, 7.5 mi. NE of S Makyan Is., 00°16.5′N, 127°30′E, 497 m, 29 Nov 1909, USNM 284749.

Australia. 1 ♂ (sl = 17.1 mm), *Soela* sta. 0685–27, 20°24′S, 152°57.8′E, 511–508 m, 22 Nov 1985, NTM Cr 6864.—Th. Mortensen's Pacific Expedition: 1 ♂ (sl = 15.7 mm), 37°45′S, 150°10′E, 274–475 m, 14 Sep 1914, ZMUC.—1 ♂ (sl = 4.8 mm), 38°05′S, 150°00′E, 347–439 m, 12 Sep 1914, ZMUC.—1 ♂ (sl = 12.9 mm),

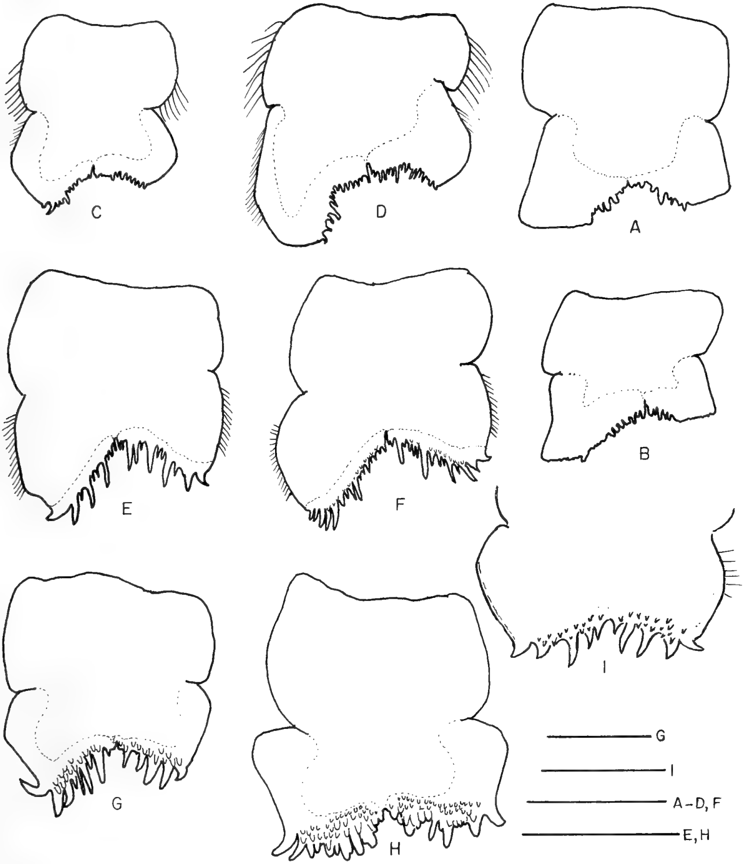

Fig. 11. Telsons. A, B, *Propagurus gaudichaudii* (H. Milne Edwards, 1836) new combination, A, ♀ (sl = 16.0 mm), MNHN-Pg 2852, B, syntype of *Pagurus patagoniensis* (Benedict, 1892), ♀ (sl = 11.8 mm), USNM 16772; C, D, *Propagurus deprofundis* (Stebbing, 1924) new combination, A, ♂ (sl = 11.2 mm), NZOI; D, holotype ♀ (sl = 9.3 mm), NHM 1928.12.1.245; E, F, *Propagurus haigae* (McLaughlin, 1997) new combination, ♂ (sl = 17.1 mm), NTM Cr 6864, F, paratype ♂ (sl = 11.5 mm), USNM 276014; G–I, *Propagurus yokoyai* (Makarov, 1938) new combination, G, ♂ (sl = 11.5 mm), OMNH Ar 1941, H, ovig. ♀ (sl = 9.6 mm), CBM-ZC 3390, I, juvenile ? ♂ (sl = 5.0 mm), MNHN-Pg 2198. Scales equal 1 mm (I), 2 mm (E, H) and 5 mm (A–D, F, G).

Fig. 12. Carpi and chelae of chelipeds. A, B, *Propagurus haigae* (McLaughlin, 1997) new combination, ♂ (sl = 17.1 mm), NTM Cr 6864, A, right, B, left. C, D, *Propagurus yokoyai* (Makarov, 1938) new combination, ♂ (sl = 11.5 mm), OMNH Ar 1941, C, right, D, left. Magnifications equal 1.6× (A, B), and 2.5× (C, D).

38°10′S, 149°55′E, 366–475 m, 11 Sep 1914, ZMUC.—Museum of Victoria: 1 ♂ (sl = 9.6 mm), 38°00′S, 141°00′E, 540 m, Jan 1981, J 40407.—1 ♂ (sl = 5.7 mm), sta. Slope 40, 38°17.7′S, 149°11.3′E, 400 m, 24 Jul 1986, J 40397.—1 ♂ (sl = 10.6 mm), sta. So5/84-27, 37°59.4′S, 150°05.4′E, 452 m, 14 Oct 1984, J 40402.—1 ♀ (sl = 18.7 mm), sta. So5/84-51, 41°03′S, 144°20′E, 520–480 m, 20 Oct 1984, J

21071.—1 ♂, 1 ovig. ♀ (sl = 11.7, 14.1 mm), sta. So6/84-18, 39°17.1′S, 148°44.4′E, 580 m, 14 Sep 1984, J, 40393, J 40404.

Diagnosis.—Shield (Fig. 4C) with length equaling width or longer than broad. Rostrum usually broadly triangular, terminally rounded or acute, with or without terminal spinule. Lateral projections triangular, with strong marginal or submarginal spine. Ocular peduncles (Fig. 10A) 0.50–0.75 length of shield, slightly broader distally; corneas weakly dilated; dorsal surfaces frequently with row of sparse setae. Ocular acicles roundly triangular, terminating subacutely and with strong submarginal spine. Distal margins of corneas usually not reaching to mid-length of fully extended ultimate segment of antennular peduncle. Antennal peduncles overreaching distal margins of corneas by 0.10–0.50 length of ultimate segments; second segment with laterodistal projection reaching to or beyond mid-length of fourth peduncular segment, terminating in simple or bifid spine and usually with 3–6 spines on mesial margin sometimes partially obscured by thick setae; dorsomesial distal angle with acute spine; first segment with spine on lateral margin distally, ventrolateral margin with 3–6 small spines laterally and distally. Antennal acicles reaching distal half of ultimate peduncular segments, and usually considerably beyond distal margin of corneas; terminating in acute spine, mesial margin with row of tufts of stiff setae. Maxillule with external lobe of endopod varying from vestigial to well developed. Meri, and usually also carpi, of third maxillipeds each with small dorsodistal spine.

Chelipeds grossly unequal; spines of chelae and carpi often practically obscured by tufts of long dense setae. Right cheliped (Fig. 12A) with dactyl slightly overlapped by fixed finger; dorsal surface convex, with median row of small spines decreasing in size distally but usually extending nearly to tip; dorsomesial margin with row of moderate to small spines also decreasing in size distally. Palm with dorsomesial margin usually only weakly delimited by quasi-double row of moderate to strong spines, frequently 1 more prominent spine or tubercle at dorsoproximal angle, convex dorsal surface with 8 or 9 irregular rows of moderate to strong spines; dorsolateral margin not distinctly delimited except on fixed finger; dorsal surface of fixed finger with median row of spines decreasing in size distally, mesial face of palm and lateral and ventral surfaces of palm and fixed finger usually all with spines or low, sometimes spinulose protuberances and tufts of long setae, occasionally unarmed. Carpus moderately broad and short (distal margin:dorsomesial margin = 2:3–3:4); with row of usually strong spines on dorsomesial margin, dorsal surface with few to numerous small spines or low sometimes spinulose protuberances and tufts of long setae, distal margin with row of spinules and few slightly larger spines; dorsolateral margin not delimited, lateral face with low sometimes spinulose protuberances and tufts of long setae, laterodistal margin with row of small spines; mesial face with few spines dorsally, scattered low protuberances and setae ventrally, mesiodistal margin sometimes with row of very small blunt spines. Merus with 2–4 spines on dorsodistal margin, dorsal surface with few short transverse rows of setae; ventrolateral margin with row of small spines not extending to proximal margin but frequently terminating proximally in 1 or 2 larger blunt spines or tubercles; ventromesial margin with few small spines, sometimes 1 or 2 larger tubercles at proximal angle.

Left cheliped (Fig. 12B) with ventral surfaces of palm, fixed finger and dactyl all with tufts of long setae; dorsomesial margin of dactyl not delimited or with 2 or 3 small spines proximally, dorsal midline unarmed or with few spinules or spinulose tubercles in proximal half. Palm triangular in cross-section, dorsal surface with row of strong spines decreasing in size distally and usually extending to distal half, occasionally nearly to tip, of fixed finger; dorsolateral margin with single or double row of strong spines, decreasing in size and becoming single row on fixed finger; dorsolateral face with numerous strong spines; dorsomesial face (Fig. 10C) usually with smaller spines or spinulose tubercles partially obscured by tufts of setae, dorsomesial margin with row of 3 or 4 spines or tubercles. Carpus with row of acute spines on dorsolateral margin, dorsodistal margin with 1 strong spine, dorsomesial margin with row of smaller spines, strongest proximally, all partially obscured by long setae; laterodistal margin with few spines dorsally, lateral face with low frequently spinulose protuberances and long setae, ventrolateral margin with row of spines and moderately dense row of long setae; ventromesial margin with 2–4 small, often blunt spines distally. Merus with short transverse rows of long setae on dorsal margin; ventromesial margin with few small spines; ventrolateral margin with row of very strong acute spines sometimes interspersed with shorter spines and row of long setae, frequently 1 or pair of stronger acute or blunt spines on each margin proximally.

Ambulatory legs with dactyls (Fig. 7C of right second) 1.2–1.5 as long as propodi; in dorsal view, slightly to moderately twisted; in lateral view, somewhat curved ventrally; dorsal margins each with rows of long setae, often interspersed with corneous bristles; lateral faces each with weak to prominent longitudinal sulcus and few setae (second and third right), moderately dense but randomly placed long setae on third left; mesial faces often also with faint longitudinal sulcus, second pereopods flanked dorsally and ventrally by long setae, and usually also with dorsal and/or ventral row of corneous spines, third pereopods with row of corneous spines often interspersed with tufts of setae dorsally and medially; ventromesial surfaces each with 8–17 strong corneous spines, increasing in length distally, but partially obscured by long setae. Propodi each with row of low transverse protuberances and tufts of setae dorsally and ventrally; lateral faces each frequently with small tubercle at proximal margin medially or dorsally, second and third right pereopods each with 2 or 3 longitudinal rows of sparse tufts of setae, left third with entire surface covered by (but not extremely dense) short transverse rows of moderately short stiff setae; ventrodistal margins each with 1 or 2 small corneous spinules. Carpi of second pereopods each with row of 4–8 spines partially obscured by long setae on dorsal surface, spines of left often smaller and fewer in number, third pereopods each with dorsodistal spine, dorsal surface unarmed or often with 1 to several much smaller spines partially obscured by row of tufts of setae; lateral faces also with 2 or 3 longitudinal rows of sparse tufts of setae. Meri each with several transverse rows of long setae dorsally and ventrally, second also with single or double row of small spines on each ventral margin. Sternite of third pereopods with few long setae on subsemicircular anterior lobe.

Telson (Fig. 11E, F) with posterior lobes somewhat asymmetrical, separated by small median cleft; terminal margins slightly to strongly oblique, each with row of 2–5 strong calcareous spines often interspersed with smaller calcareous or corneous spines, dorsal surfaces adjacent to terminal margins sometimes with row of accessory calcareous spinules, more frequent and/or abundant in larger specimens; lateral margins usually with few to numerous corneous spinules and occasionally calcareous spines.

Color (in preservative).—General overall orange tint; somewhat mottled on shield. Antennal flagella with alternating series of 8–10 transparent articles followed by similar number of burnt-orange. Meri of chelipeds and ambulatory legs with darker orange, but with white band on distal margin dorsally and laterally.

Habitat.—Variety of gastropod shells, sometimes with accompanying anemone.

Distribution.—Off Makyan, Kai, and Tanimbar Islands, Indonesia; New Caledonia;

Marion Plateau, Queensland, Australia; western Tasman Sea; 265 to 580 m.

Remarks.—The quadriserial gill structure of *P. haigae* is not readily discernible in casual observation, as evidenced by McLaughlin's (1997) initial assignment of the species to *Pagurus*. The external branches of the lamellae of the arthrobranchs of the fourth pereopods are quite short, and deliberate manipulation is necessary to make them apparent. Even more easily overlooked is the presence of rudimentary pleurobranchs on the fifth and sixth thoracic somites in what would appear to be a very typical *Pagurus*-like species. It should also be noted that in McLaughlin's figure (1997, Fig. 27) the lettering for the mesial faces of the dactyls of the second and third pereopods is reversed; fig. 27c corresponds to the legend for 27e and vise versa.

McLaughlin (1997) pointed out the marked similarities between *P. haigae* and *P. yokoyai*, but suggested that color, telson armature, strength of cheliped meral spines, number of spines on the ventral margins of the dactyls of the ambulatory legs, and length–width ratios of the carpus of the right cheliped would readily separate the two species. Now having examined a number of larger specimens of *P. haigae*, and similarly, smaller specimens of *P. yokoyai*, those distinctions are not as reliable as previously presumed. Although the carpus of the right cheliped is definitely longer and more slender in large male specimens of *P. yokoyai*, that is not the case in smaller specimens of either sex. However, in *P. haigae*, the relative proportions do not change appreciably with size, thus the character can be an aid in recognition of large males (sl ≥ 11 mm). The meri of the chelipeds of *P. yokoyai*, like *P. haigae*, may have one or two prominent posterior spines on the ventral margins. While the number of spines on the ventral margins of the dactyls of the ambulatory legs usually is fewer in *P. yokoyai*, there is sufficient variation that their numbers do overlap spine numbers in smaller specimens (sl ≤ 10 mm) of *P. haigae*. The generally shorter and distally slightly broadened ocular peduncles (Fig. 10A), the more spinose dorsomesial face of the palm of the left cheliped (Fig. 10C), and the armature of the telson (Fig. 11E, F) afford the best identifying morphological characters; however, even these are subject to some variation. In the case of the telson, larger specimens of *P. haigae* tend to add accessory spinules, while similarly larger specimens of *P. yokoyai* loose them. Although living color is not known for *P. haigae*, the residual colors in preservative differ appreciably from the coloration reported for *P. yokoyai*, particularly the presence in the latter species of a proximal patch of color on the ocular peduncles that has not been observed in specimens of *P. haigae*.

Specimens of *P. haigae* from the Tasman Sea differed from the Indonesian specimens in usually having a less acute rostrum, and often slightly broader shields. At two stations in the Tasman Sea, Slope 40, and So6/84-18, *P. haigae* and *P. deprofundis* occurred sympatrically; however, *P. haigae* is more restricted, both geographically and bathymetrically than *P. deprofundis*.

Propagurus yokoyai (Makarov 1938), new combination
Figs. 4D, 7D, 10B, D, 11G–I, 12C, D

Eupagurus gracilipes Yokoya, 1933:89, fig. 33; 1939:281 [not *Pagurus gracilipes* (Stimpson, 1858)].

Pagurus yokoyai Makarov, 1938:185; 1962: 175.—Okada et al., 1966:138.—Miyake, 1978:140, figs. 44, 45; 1982:131, pl. 44, fig. 1.—1991:131, pl. 44, fig. 1.—Baba, 1986:209, 305, fig. 154.—McLaughlin, 1997:536, fig. 27i.

Eupagurus yokoyai.—Miyake, 1951:138.

Pagurus gracilipes (Yokoya).—Gordan, 1956:330 (lit.) [not *Pagurus gracilipes* (Stimpson, 1858)].

Material examined.—Japan. 2 ♂ (sl = 14.0, 14.8 mm), southeast of Katsuyama-Ukishima, Boso Peninsula, 140–220 m, 10 May 1995, coll. T. Komai & M. Miya, CBM-ZC 1668.—1 ♂, 1 ovig ♀ (sl = 11.5, 8.4 mm) off Mie Pref., 100–200 m, Jan 1977, coll. S. Habu, OMNH Ar 1941, Ar 1944.—2 ♂, 1 ♀ (sl = 7.6–9.4 mm) off Mie Pref., 100–200 m, Jan 1977, coll. S. Habu, OMNH Ar 1942, Ar 1943, OMNH Ar 1945.—1 ♂ (sl = 8.5 mm), Kushimoto, Wakayama, 150 m, 23 May 1989, PMcL.—2 juveniles, 10 ♂, 1 ♀, 8 ovig. ♀ (sl = 5.0–12.0 mm), Tosa Bay, to-300 m, 1963–1966, coll. K. Sakai, MNHN Pg 2194–2200, Pg 2277, Pg 3650—3651.—1 ovig. ♀ (sl = 9.6 mm) off Kochi, Tosa Bay, Shikoku, 33°17.1′N, 133°40.2E, 150–154 m, 5 Mar 1993, coll. K. Sasaki, CBM-ZC 3390.—2 ♂, 1 ♀ (sl = 7.6–9.4 mm), off Kochi, Tosa Bay, 146–150 m, 7 Oct 1992, coll. K. Sasaki, CBM-ZC 3458.

Diagnosis.—Shield (Fig. 4D) slightly to considerably longer than broad. Rostrum broadly triangular or rounded, not produced to level of lateral projections, with or without terminal spinule frequently obscured by tuft of setae. Lateral projections triangular, very prominent, with strong marginal or submarginal spine. Ocular peduncles 0.55–0.65 length of shield, not noticably broader distally (Fig. 10B); corneas usually not dilated; dorsal surfaces each with sparse row of setae. Ocular acicles roundly triangular, terminating subacutely and with small submarginal spine. Distal margins of corneas usually reaching to or beyond midl-length of fully extended antennular peduncles. Antennal peduncles overreaching distal margins of corneas by 0.25–0.50 length of ultimate segments; second segment with laterodistal projection reaching to or beyond distal half of peduncular fourth segment, terminating in simple or bifid spine and with 2–4 spines on mesial margin; dorsomesial distal angle with prominent spine; first segment with spine on lateral margin distally, ventrolateral margin with 1–3 very small spines laterally and distally. Antennal acicle reaching to or beyond distal half of ultimate peduncular segment, terminating in acute spine, mesial margin with row of tufts of stiff setae. Maxillule with external lobe of endopod well developed. Meri and carpi of third maxillipeds unarmed or each with very small dorsodistal spine.

Chelipeds grossly unequal; spines of chelae and carpi usually with small corneous tips and often practically obscured by tufts of long stiff setae. Right cheliped (Fig. 12C) usually with distinct hiatus between dactyl and fixed finger; tip of dactyl slightly overlapped by fixed finger; dorsal surface convex, with median row of strong spines decreasing in size distally but extending nearly to tip; dorsomesial margin with row of strong spines also decreasing in size distally. Palm with dorsomesial margin usually only weakly delimited by quasi-double row of strong spines, frequently 1 more prominent spine or tubercle at dorsoproximal angle, convex dorsal surface with 7 or 8 irregular rows of moderate to strong spines; dorsolateral margin not distinctly delimited except on fixed finger; dorsal surface of fixed finger with several spines proximally and median row of spines decreasing in size distally, mesial face of palm and lateral and ventral surfaces of palm and fixed finger all with low sometimes spinulose protuberances and tufts of long setae, or occasionally unarmed. Carpus moderately broad and short in females and small males (2:3–3:4), but becoming elongate and slender in males (1:2–3:5) with increasing size; with row of moderate to strong spines on dorsomesial margin, dorsal surface with few to numerous smaller spines or low sometimes spinulose protuberances or bifid tubercles and tufts of long setae, distal margin with row of minute or small spinules and few slightly larger spines; dorsolateral margin not delimited, lateral face with low sometimes spinulose protuberances and tufts of long setae, laterodistal margin with blunt tubercles or prominent spines; mesial face with few spines dorsally, scattered low protuberances or spines and setae ventrally, mesiodistal margin sometimes with row of small blunt or subacute spines. Merus with 2–4 spines on dorsodistal margin, dorsal surface with few short unarmed, spinose, or spinulose transverse ridges with setae; ventrolateral margin with row of small spines not extending to proximal margin, but frequently terminating proximally with 1 or 2 prominent spines; ventromesial margin with few small spines, sometimes 1 or 2 larger spines proximally.

Left cheliped (Fig. 12D) with ventral surfaces of palm, fixed finger and dactyl all with few widely-spaced tufts of long setae; dorsomesial margin of dactyl unarmed or with short row of small spines in proximal half; dorsal midline unarmed, surface with short transverse, sometimes spinulose ridges and tufts of stiff setae. Palm triangular in cross-section, dorsal surface with row of strong spines decreasing in size distally, usually extending nearly to tip of fixed finger; dorsolateral margin with irregular single or double row of strong spines, decreasing in size and becoming single row on fixed finger; dorsolateral face with 2 irregular rows of strong spines; dorsomesial face (Fig. 10D) unarmed or with low protuberances partially obscured by tufts of setae, dorsomesial margin with row of 3–5 blunt spines or tubercles. Carpus moderately long and slender; with row of acute, usually very strong spines on dorsolateral margin, dorsodistal margin with 1 strong spine, dorsomesial margin with row of smaller spines, all partially obscured by long setae; laterodistal margin with 1 to few spines dorsally, lateral face with low frequently spinulose protuberances and long setae, ventrolateral margin with few low tubercles or row of spines accompanied by long setae; ventromesial margin with 2–4 small, often blunt spines. Merus sometimes with prominent dorsodistal spine, short transverse rows of long setae on dorsal margin; ventromesial margin with few small spines, strongest proximally; ventrolateral margin with row of very strong acute spines sometimes interspersed with shorter spines accompanied by long setae, frequently 1 or 2 stronger acute or blunt spines proximally.

Ambulatory legs with dactyls (Fig. 7D of right second) 1.20–1.75 as long as propodi; in dorsal view, moderately to strongly twisted; in lateral view, somewhat curved ventrally; dorsal margins each with transverse rows of long stiff setae; lateral faces each with weak to prominent longitudinal sulcus and few setae (second and third right), moderately dense long setae flanking sulcus on third left; mesial faces each also with faint longitudinal sulcus, flanked dorsally and also occasionally ventrally by row of corneous spines and with ventral row of setae; ventromesial surfaces each with 5–15 strong corneous spines. Propodi each with row of low transverse protuberances and tufts of setae dorsally and ventrally; second and third right pereopods each with 2 or 3 longitudinal rows of sparse tufts of setae, left third with entire surface covered (moderate density) by short transverse rows of moderately short to moderately long stiff setae. Carpi of second pereopods each with row of 5–7 spines partially obscured by long setae on dorsal surface, spines of left occasionally smaller and fewer in number; third pereopods each with dorsodistal spine, dorsal surfaces often unarmed or often 1 to several much smaller spines partially obscured by row of tufts of setae; lateral faces also with 2 or 3 longitudinal rows of sparse tufts of setae. Meri each with several transverse rows of long setae dorsally and ventrally; second also with single or double row of small spines on ventral margin. Sternite of third pereopods with few long setae on subsemicircular or subquadrate anterior lobe.

Telson (Fig. 11G–I) with posterior lobes asymmetrical, separated by small median cleft; terminal margins slightly to strongly oblique, each with row of strong calcareous spines usually interspersed with smaller calcareous spines and with additional rows of much smaller spines on adjacent surfaces; lateral margins usually with chitinous or calcareous, frequently spinose or spinulose plate.

Color.—Ocular peduncles purple with red patch proximally. Antennular and antennal peduncles light red, with scattered

red-brown spots. Antennal flagellum minutely mottled with dark and light red-brown. Shield red-brown; cervical groove and neighboring parts dark red-brown; abdomen light red-brown. Chelipeds and ambulatory legs purplish-red with proximal part of each segment and distal part of meri red (Miyake 1978).

Habitat.—Collected on clay, sand, or muddy and shell bottoms. Shells often carrying one or two anemones.

Distribution.—Sagami and Suruga Bays, Boso Peninsula, Kushimoto, southern Kii Peninsula, Tosa Bay, Bungo Strait, Japan; 38–400 m.

Remarks.—As previously noted, males of *P. yokoyai* exhibit a sexually dimorphic lengthening and narrowing of the carpus right cheliped, with a corresponding narrowing of the chela. Additionally, two of the 18 adult males examined, one from Tosa Bay and one from Kushimoto, had female-like second left pleopods developed, but neither had any external evidence of rhizocephalan infection. The males gonopores of both specimens were smaller than usually observed in normal males, but both were small individuals, with shield length of only 8.3 and 8.5 mm respectively. Neither showed any indication of female gonopores.

Although *P. deprofundis* has now been reported from both the Philippine and Hawaiian Islands, and a specimen of *P. haigae* was collected at a latitude of 00°30.5′N, *P. yokoyai* is the only species of the genus recognized to date that has been reported exclusively from the temperate northern hemisphere. As discussed above, *P. yokoyai* most closely resembles *P. haigae*, and is readily distinguished from the latter species only by color and a combination of morphological characters: the ocular peduncles are usually slightly longer and the antennular peduncles shorter in *P. yokoyai*; the spines on the dorsal surfaces of both chelae are usually larger and less numerous in this species and the mesial face of the palm of the left is commonly unarmed; in large males (sl $\geq$ 10.0 mm) the carpus of the right cheliped becomes distinctly longer and narrower. In small specimens of *P. yokoyai* the telson has two to four rows of small accessory spines and spinules. In larger specimens this number may decrease to only a very small, irregularly double row. In contrast, accessory spinules have been observed forming a single row in some specimens of *P. haigae*. Both species bear a superficial resemblance to the North Pacific *capillatus* group species of *Pagurus* (cf. McLaughlin 1974); however, the quadriserial gill structure and rudimentary pleurobranchs on the fifth and sixth thoracic somites immediately set *Propagurus* species apart.

Discussion

Of the four species now assigned to *Propagurus* new genus, in only one had the gill structure and number previously been documented; all were still assigned to the genus *Pagurus*. The overall morphological similarities of these *Pagurus*-like species with numerous taxa assigned to that genus, together with the ease in which the quadriserial gill structure and rudimentary pleurobranchs can be overlooked, makes it quite possible that *Propagurus* is far more speciose than is currently recognized.

Three of the four recognized species are regionally endemic. *Propagurus yokoyai* has been reported in eastern Japanese waters from Sagami Bay and the Boso Peninsula southward to the Bungo Straits, but over the broad bathymemtric range of 38 to 400 meters. Our specimens were all collected in the middle of this geographic range, and generally also in its bathymetric range. *Propagurus haigae* has been found in a band extending from the Banda and Arafura Seas of Indonesia southeastward as far as New Caledonia, and southward along the eastern coast of Australia to Tasmania. All known specimens have been collected from depths ranging from 265 to 580 meters. The South American *P. gaudichaudii* is reported off the west coast of Chile, from as far north as Valparaiso southward through the Strait of Magellan and northward along the eastern coast of Argentina to Uruguay. Like *P. yokoyai* this species is found at relatively shallow depths. In particularly striking contrast is the geographic distribution of *P. deprofundis*, although its bathymetric range is also the greatest. Described originally from a single specimen collected off the southeastern coast of South Africa (Stebbing 1924), its range extends eastward and southward to southeastern Australia where it is quite abundant. It is equally abundant in the waters of both western and eastern New Zealand, and while not yet known from tropical western Pacific waters, it is clearly represented in Philippine waters and as far eastward as Hawaii. There are very few pagurid species known to have such a broad geographic range.

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Descriptions of two new Japanese hermit crabs (Decapoda: Paguridae: Diogenidae)

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Abstract.—Two hermit crab species, *Cancellus investigatoris* Alcock and *Paguristes setosus* (H. Milne Edwards), have been reported on a number of occasions from Japanese waters. Neither Japanese taxon has been correctly identified, and both are now recognized as new species. The true *Cancellus investigatoris* appears to be restricted in its distribution to Sri Lanka, whereas the true *Paguristes setosus* is endemic to New Zealand. The Japanese species are described herein as *Cancellus mayoae* new species, and *Paguristes miyakei* new species. Sources of the earlier mistakes are discussed.

As a corollary to a study of the hermit crab fauna of New Zealand (Forest & McLaughlin 1998), two species, *Cancellus investigatoris* Alcock, 1905, and *Paguristes setosus* (H. Milne Edwards 1848) that for many years have been considered part of the Japanese fauna have been reinvestigated. Neither of the Japanese taxa represent the species to which they have been attributed, and both are described herein as new species.

The holotype of *Cancellus mayoae* new species is the specimen from Miyake's (1978) material belonging to the Biological Laboratory of the Imperial Household (BLIH) that was borrowed and illustrated by Mayo (1973). The male paratype of *C. mayoae* has been returned to the National Museum of Natural History, Smithsonian Institution (USNM). All of Miyake's specimens identified as *Paguristes setosus* have been returned to the National Science Museum, Showa Memorial Institute, Tasukuba City (NSMT). Two additional specimens of *Paguristes miyakei* new species are in the collection of the Muséum national d'Histoire naturelle, Paris (MNHN). An indication of specimen size is given by the shield length (sl) measured from the tip of the rostrum to the midpoint of the posterior margin of the shield.

Cancellus mayoae, new species
Fig. 1A, B

Cancellus investigatoris.—Terao, 1914: 61, unnumbered fig.–Gordan, 1956:305 (lit.).—Miyake, 1960a:71; 1960b:93, ? pl. 46, fig. 8; 1962:93, ? pl. 46, fig. 8; 1978:21, text-fig. 7, ? pl. 4, fig. 2; 1982: 101, unnumbered text-fig., (? not pl. 34, fig. 1); 1991:101, unnumbered text-fig., (? not pl. 34, fig. 1).—Mayo, 1973:54, figs. 23–25.—Miyake & Imafuku, 1980: 2. Not *Cancellus investigatoris* Alcock, 1905.

Holotype.—Specimen described and figured by Mayo (1973: 54, figs. 23–25), ♀ (sl = 7.8 mm), Kannon-zuka-dashi, Sagami Bay, Japan, BLIH 9.

Paratype.—♂ (sl = 4.9 mm), *Albatross* sta 4876, 34°20′N, 130°10′E, 108 m, 2 Aug 1906, USNM 285521.

Diagnosis (after Mayo 1973).—Rostrum reaching approximately to level of lateral projections. Frontal rim (anterior margin of

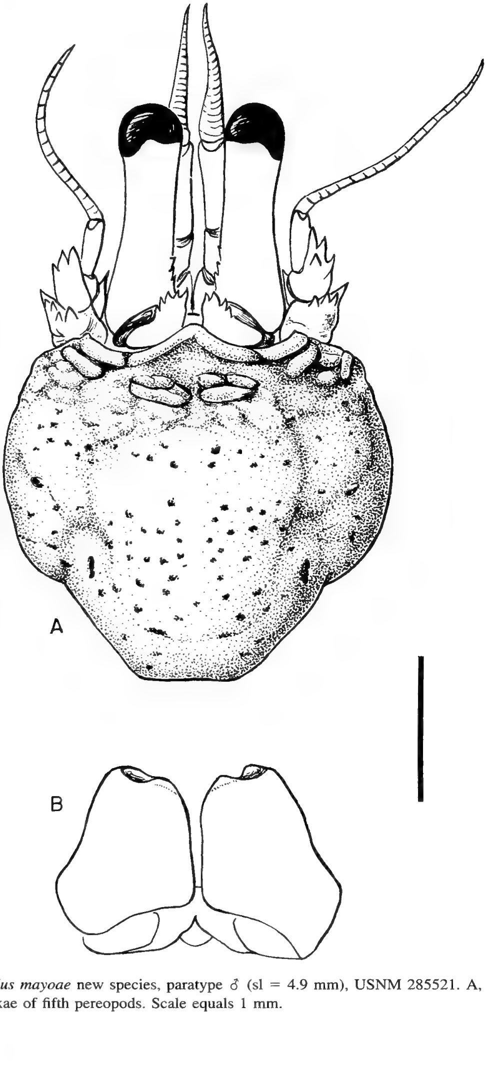

Fig. 1. *Cancellus mayoae* new species, paratype ♂ (sl = 4.9 mm), USNM 285521. A, shield and cephalic appendages; B, coxae of fifth pereopods. Scale equals 1 mm.

Mayo 1973) partially interrupted at level of orbital indentations (Fig. 1A). Ocular peduncles swollen basally, length equaling 0.55–0.65 of shield, mesial margins each with denticles in proximal third. Corneas slightly attenuated. Ocular acicles short, closely-spaced, with 3 or 4 distal teeth. Antennal peduncles with 3 or 4 teeth on distal margin of second segment. Antennal acicles reach or nearly reach distal extremity of fifth peduncular segment; lateral margins each with 2 teeth posterior to terminal point.

Opercular faces of chelipeds and second pereopods depressed, covered with spinose tubercles. Ventrolateral faces of propodi of chelipeds each with 9 smooth, parallel, transverse striae.

Tergite of sixth abdominal segment with transverse depression posterior to midlength, surface smooth, except for low tubercles on anterolateral margin. Telson unarmed; lateral margins concave in posterior half; terminal margin slightly concave.

Etymology.—This species is named for Barbara Schuler Mayo in recognition of her contribution to our understanding of the genus *Cancellus*.

Color.—Questionable (see Remarks).

Habitat.—Calcareous rock; polyzoan fragments, serpulid worm tubes.

Distribution.—Sagami Bay and Kii Peninsula, Japan; 60–110 m.

Comparison with C. investigatoris.—The ocular peduncles of *C. investigatoris* are much longer with a ratio of peduncular length to shield of 0.77, in contrast to 0.55 in the specimen of *C. mayoae* figured by Mayo (1973) and 0.65 in Miyake's (1978, 1982, 1991) text figure. The corneas are figured as weakly dilated in *C. investigatoris* but narrower in the Japanese species, except for the small male from the *Albatross* (see remarks). The antennal acicles do not reach beyond middle of last peduncular segment in Alcock's (1905) drawing, but reach the distal region in the Japanese specimens. The opercular surfaces of the chelipeds and ambulatory legs are described as finely granular in *C. investigatoris*, but covered with tubercles, some corneous-tipped in *C. mayoae*. Perhaps most important is Alcock's (1905) stated absence of striae on the ventrolateral surface of the propodi of the chelipeds of *C. investigatoris*; nine distinct striae are present in the Japanese species.

Remarks.—*Cancellus investigatoris* was described by Alcock (1905) from a single specimen collected off the southeast coast of Sri Lanka (Ceylon) in a depth of 58 m. Another specimen, lodged in a fragment of *Porites arenosus*, was recorded by Southwell (1906, 1910) from the west coast of Sri Lanka. Subsequently, the occurrence of this species in Sagami Bay, Japan was reported several times (e.g., Terao 1914, Miyake 1960a, b, 1962, 1978, 1982, 1991; Mayo 1973, Miyake & Imafuku 1980).

During the course of the study of the Coenobitoidea of New Zealand (Forest & McLaughlin 1998), we have examined several undescribed *Cancellus* species and compared these with known representatives of the genus. To this end, we have referred extensively to the excellent monograph of Mayo (1973), in which she very completely described and illustrated, from personal examination, all the species known at the time, except the aberrant *C. makrothrix* Stebbing, 1924. Mayo's (1973) detailed description and illustrations of *C. investigatoris* were based upon a specimen collected from Sagami Bay and subsequently reported upon by Miyake (1978). Mayo's (1973) documentation of the Japanese taxon has been supplemented by a specimen collected from Sagami Bay during a cruise of the U.S. Fish Commission steamer *Albatross* and deposited in the National Museum of Natural History. During our comparative study, it became apparent that the characters of the Japanese species identified as *C. investigatoris* differed notably from those of the type as described and figured by Alcock (1905). As indicated by Mayo (1973) from personal communication with B.K. Tikader of the Indian Museum, the type of *C. investigatoris* is in extremely poor condition.

Thus comparisons between Sri Lanka species and the Japanese taxon are very limited. Alcock's (1905: 77) description lacks many of the details provided by Mayo (1973: 55) for the Japanese taxon. Similarly Mayo's (1973: figs. 23–25) illustrations are much more detailed than Alcock's (1905: pl 5, figs. 8, 8a). Nonetheless, a certain number of characters cited by Alcock, or apparent from his figures, justify the conclusion that the Japanese species described and figured by Mayo (1973), and more recently by Miyake (1978, 1982, 1991) is not *C. investigatoris*, and cannot be attributed to any other known taxon. In the interest of the taxonomic lucidity of the genus *Cancellus* it is necessary to separate the Japanese taxon by providing it with its own distinct identity.

The male specimen from the *Albatross* exhibits the basic characters of this new species, notably the denticles on the proximal third of the mesial faces of the ocular peduncles; the 3 or 4 teeth on the distal margin of each second peduncular segment of the antennae; and the long antennal acicles which reach to or nearly to the extremity of the last peduncular segment. This male differs from the type of *C. mayoae* in the development of the corneas which are weakly dilated rather than attenuated; however, this may be related to its smaller size. Despite the small size of this male, the substantial development of the coxae of the fifth pereopods (Fig. 1B) with broadly open orifices shows that this is an adult specimen and that the definitive form of the coxae has been acquired. The coxae are depressed with their contours forming the shape of a bell.

The figures of *C. mayoae*, particularly the colored figures of Japanese authors, are somewhat contradictory, and for that reason we have included the latter in the synonymy questionably. Terao's (1914) report of *C. mayoae* (as *C. investigatoris*) appears to be the first record of the species in Sagami Bay. Terao's unnumbered figure consists only of the cephalothorax and abdomen without appendages except for ocular peduncles and the right antennal peduncle, with flagellum, but no antennal acicle distinguishable. Although the ocular peduncles are figured as being slightly broader basally, they are considerably longer than the antennal peduncle; the cornea of the left peduncle is attenuated, that of the right is slightly dilated.

Miyake's figure (1960b: pl. 46, fig. 8), repeated in subsequent editions of the Encyclopedia, is an artist's rendition that shows the ocular peduncles very slightly swollen basally, the corneas very faintly dilated, with the right slightly larger than the left. The antennal peduncles reach only to about mid-length of the ocular peduncles. The antennal flagella are appreciably longer than the one illustrated by Terao (1914). The dactyls of the third pereopods are relatively slender. Miyake's (1978: pl. 4, fig. 2) figure, although bearing a very distinct resemblance to his earlier one, has much stouter ocular peduncles with larger corneas, longer antennal peduncles, and stouter pereopodal dactyls. The length of the antennal peduncles is considerably greater than shown in Miyake's (1978: text-fig. 7) text figure. In Miyake's 1982 publication (reprinted in 1991), his earlier figure (Miyake 1978: text-fig. 7) is reproduced, but his color figure (Miyake 1982, 1991: pl. 34, fig. 1) is of an entirely different animal. Although the color patterns are similar to the earlier colored figures, the ocular peduncles are longer (ratio of peduncular length to shield = approximately 0.70) and the corneas are not as attenuated. Additionally, if the ambulatory legs of the photographed specimen are measured, the dactyls of the second pereopods are as long as the propodi, whereas they are clearly shorter in *C. mayoae* new species.

Paguristes miyakei, new species

Figs. 2A–E, 3A–C

Paguristes setosus.—Miyake, 1978:27, text-fig. 8; not *Paguristes setosus* (H. Milne Edwards 1848).

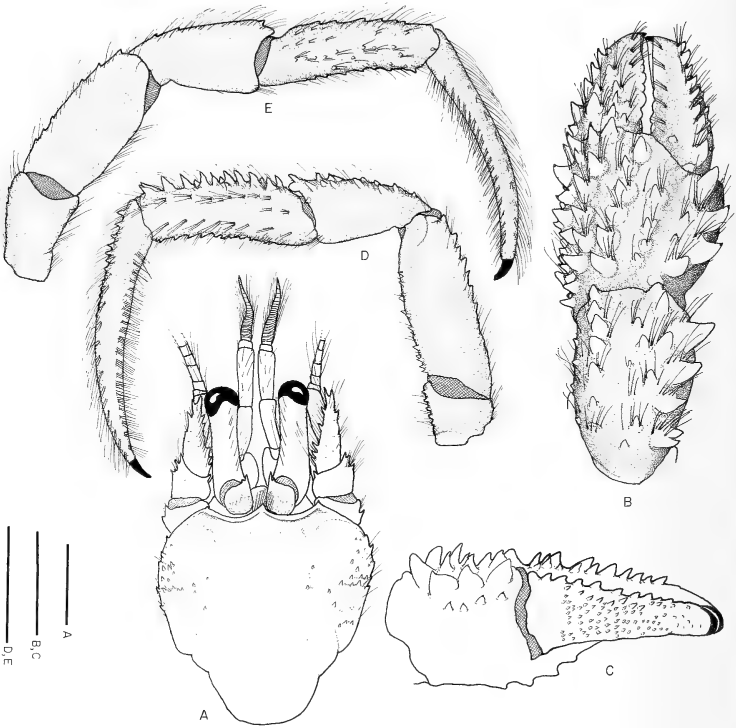

Fig. 2. *Paguristes miyakei* new species, holotype ♀ (sl = 5.5 mm), NSMT CrR 2296. A, shield and cephalic appendages; B, chela and carpus of left cheliped (dorsal view); C, chela of left cheliped (mesial view); D, right second pereopod (mesial view); E, left third pereopod (mesial view). Scales equal 1 mm (A), 2 mm (B, C), and 3 mm (D, E).

Holotype.—♀ (sl = 5.5 mm); east of Ohba-dashi (Bank), Sagami Bay, 180–280 m, 23 Jan 1965, NSMT CrR 2296.

Paratypes.—1 ♀ (sl = 7.2 mm); southeast of Maruyama-dashi (Bank), Sagami Bay; 180–240 m, 19 Jan 1955, NSMT CrR 896.—1 ♀ (sl = 4.5 mm); east of Ohba-dashi (Bank), Sagami Bay, 180–280 m, 23 Jan 1965, NSMT CrR 2295.—1 ♀ (sl = 7.1 mm), Tosa Bay, Feb-Apr 1963, coll. K. Sakai, MNHN Pg 2161.—1 ♀ (7.2 mm), Tosa Bay, 3–14 Nov 1963, coll. K. Sakai, MNHN Pg 2159.

Description.—Shield (Fig. 2A) longer than broad; dorsal surface rugose, with few spines marginally and/or laterally, and sparse tufts of moderately short setae. Lateral projections broadly triangular, acute, with terminal spine or spinule. Rostrum short, triangular, not reaching level of lateral projections; usually with terminal spinule partially obscured by moderately long

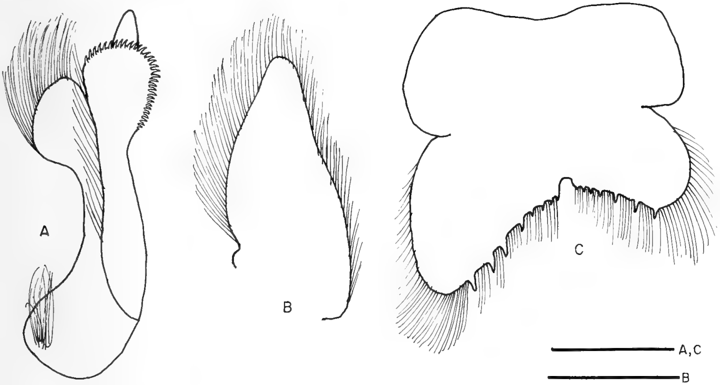

Fig. 3. *Paguristes miyakei* new species: A, paratype ♂ (sl = 7.2 mm), NSMT CrR 896; B, C, holotype ♀ (sl = 5.5 mm), NSMT CrR 2296. A, left first pleopod (external view); B, brood pouch (external view); C, telson. Scales equal 1 mm (A, C) and 3 mm (B).

plumose setae. Branchiostegites each with row of spines or spinules on dorsal margin, sometimes 2 or 3 stronger spines anteriorly, and 1 on anterior margin dorsally.

Ocular peduncles moderately slender; only slightly longer than half length of shield; longitudinal row of moderately long setae on dorsal surface mesially; corneas not dilated. Ocular acicles large, but only partially calcified; with simple or weakly bifid terminal spine.

Antennular peduncles when fully extended overreaching distal margins of corneas by approximately 0.65 to nearly entire length of ultimate segment. Ultimate and penultimate segments with some short setae. Basal segment with slender spine on dorsolateral margin of statocyst lobe, 1 or 2 spinules on laterodistal margin and spine or spinule on ventromesial distal angle.

Antennal peduncles reaching at least to mid-length of corneas, sometimes overreaching distal corneal margin by approximately 0.15 length of ultimate segment. Fifth segment with few scattered short setae. Fourth segment with small dorsodistal spine. Third segment with strong ventrodistal spine. Second segment produced distolaterally, terminating in moderate to strong bifid spine, 1 or 2 spinules or spines on lateral margin distally; dorsomesial distal angle with small spine. First segment unarmed or with small spine at laterodistal margin. Antennal acicle reaching nearly to distal margin of fully extended ultimate peduncular segment, with bifid terminal spine; mesial margin with 0–2 spines distally and 2–4 spines in proximal half, lateral margin with 0–3 spines in distal half. Antennal flagellum moderately long, somewhat longer than carapace; each article with several long randomly-set setae.

Third maxilliped with 1 or 2 spines on ventrodistal margin of ischium; 1 small spine on dorsodistal margin of merus, ventral margin with 4 or 5 spines; carpus with 1 dorsodistal spinule.

Chelipeds subequal; left (Fig. 2B) slightly larger; armature generally similar. Dactyl slightly longer than palm; dorsomesial margin with row of strong spines accompanied by tufts of stiff, moderately long setae, dorsal surface with 1 proximal spine or spinulose tubercle and row of low protuberances with tufts of stiff setae; mesial face (Fig. 2C) covered with small corneous-tipped spines or spinulose tubercles arranged in longitudinal or oblique rows; cutting edge with row of small calcareous teeth in proximal half, corneous teeth distally; terminating in small corneous claw and slightly overlapped by fixed finger. Palm shorter than carpus, dorsoventrally somewhat swollen; dorsomesial margin with row of 4 or 5 strong spines and tufts of stiff setae, dorsolateral margin not delimited, convex dorsolateral face and dorsal surface with 4–6 rows of somewhat smaller spines, each usually accompanied by tuft of stiff setae, 2 or 3 rows extending nearly entire length of fixed finger; mesial surface unarmed or with 2 or 3 transverse rows of low tubercles and tufts of setae; ventral surface with 1 or 2 rows of sometimes prominent spinose corneous-tipped tubercles and stiff setae; cutting edge of fixed finger with row of small calcareous teeth in proximal 0.75, corneous teeth distally; terminating in small corneous claw. Carpus slightly more than half length of merus; dorsomesial margin with row of strong spines, dorsal surface with 2 irregular rows of adjacent smaller spines separated by unarmed longitudinal strip from dorsolateral row of somewhat tuberculate spines; lateral face with row of small spines or tubercles and tufts of setae dorsally, laterodistal margin minutely tuberculate; mesial face with row of spines or tubercles adjacent of dorsal margin. Merus sometimes with 1 or 2 spines at dorsodistal margin; dorsal margin with row of spines decreasing in size proximally and accompanied by tufts of moderately long setae; ventromesial and ventrolateral margins each with row of spines and long setae. Ischium with row of spines or tubercles on ventromesial margin.

Ambulatory legs (Fig. 2D, E) with dactyls 1.25–1.40 as long as propodi; dorsal margins each with row of small corneous-tipped spines in proximal half, accompanied by numerous long bristle-like setae extending to claw (second), or only with bristle-like setae (third); lateral faces each with longitudinal row of sparse tufts of short setae dorsally and ventrally; mesial faces each with longitudinal row of tufts of stiff setae in dorsal half, row of longer and more dense stiff setae adjacent to ventral margin; ventral margins each with row of 20–28 small corneous spines. Propodi somewhat longer than carpi; dorsal margins each with double row of spines, strongest mesially and accompanied by tufts of long stiff setae (second), or only tufts of stiff setae sometimes arising from low protuberances (third); ventral margins each with irregular double row of small spines or tubercles, often corneous-tipped, or low protuberances frequently armed with corneous spinules, strongest on second; mesial faces each with single or irregular double row of small spines or spinulose tubercles accompanied by tufts of setae ventrally, and row of setae dorsally, distal margins with 1 to several corneous-tipped spinules; lateral surfaces each with longitudinal row of setae. Carpi slightly shorter to approximately equaling length of meri; dorsal margins each with irregular double row of strong spines (second) or small dorsodistal spine and 1 or 2 proximal spinules (third); lateral faces each with 1–3 longitudinal rows of sparse tufts of setae. Meri each with dorsal row of small spines (second) or few spinules (third); ventral margins each with double row of spines (second) or unarmed (third) and with tufts of moderately long setae. Ischia with spinules on dorsal and ventral margins, fewer in number on third.

Males with paired gonopores; paired first and second pleopods modified as gonopods. First pleopods (Fig. 3A) with tuft of setae basally on basal lobe; inferior lamella with row of setae on lateral margin, distal margin with row of curved spines extending considerable distance along mesial margin; internal lobe moderately small, with row of long setae on mesial margin; external lobe extending well beyond distal margin of inferior lamella. Female gonopores paired; paired first pleopods well developed. Brood pouch (Fig. 3B) elongate, moderately to quite slender.

Telson (Fig. 3C) with asymmetrical posterior lobes separated by shallow, moderately broad median cleft; left lobe usually appreciably elongate, subtriangular with rounded apex, terminal margin with row of small spines, increasing in size toward outer angle, not concealed by accompanying long setae; right lobe with terminal margin slightly oblique, with row of small spines, also increasing in size toward outer angle and accompanied by long setae.

Etymology.—This species is named for the eminent Japanese carcinologist, Sadayoshi Miyake, who provided the first detailed description of the species.

Color.—"Anterior half of carapace and basal segments of chelipeds and walking legs reddish brown; distal two segments of chelipeds and walking legs light reddish brown. Antennules and antennae light reddish brown, dorsal face of eyestalk light reddish brown; ventral face reddish brown" (Miyake 1978: 28).

Habitat.—Sandy mud bottoms.

Distribution.—Sagami Bay, Japan; 150–250 m.

Remarks.—*Paguristes pilosus* (H. Milne Edwards 1836) and *P. setosus* (H. Milne Edwards 1848), two rather aberrant and superficially very similar species endemic to New Zealand waters, have been a source of taxonomic perplexity for more than 150 years. Both were originally described by H. Milne Edwards in the genus *Pagurus* Fabricius, 1775, but subsequently transferred to *Paguristes* Dana, 1851. Although the description of *P. pilosus* was rather brief, the illustration clearly defined the taxon; the type locality was cited as New Zealand. *Paguristes setosus* was described only as very similar to *P. pilosus*; the type locality was cited as New Guinea. The ensuing confusion over the true identities of the two taxa was initiated in part by H. Milne Edwards himself through his incorrect publication of New Guinea as the type locality of *P. setosus*, and additional misinterpretations and errors by virtually all subsequent carcinologists have compounded the problem. Forest & McLaughlin (1998) have documented these transgressions as they relate to New Zealand carcinologists and that local fauna. However, as indicated in the synonymy, several authors, perhaps influenced by the incorrect locality assigned to *Paguristes setosus* in the original description, have identified specimens from the Japanese region as this species.

Initially, Ortmann (1892) recorded *P. setosus* from Sagami Bay, indicating that he had chosen to identify his species as *P. setosus* rather than *P. pilosus* because the chelipeds were less setose and the third pereopods more slender, as indicated by H. Milne Edwards (1848) in his original description of the former taxon. Although Ortmann's (1892:28, pl. 12, fig. 9) very diagrammatic figure illustrated only the shield and cephalic appendages, his description clearly showed that he was not dealing with H. Milne Edwards' (1848) species as he stated that the chelipeds were similar. It would appear that Ortmann did not consult H. Milne Edwards' (1836) original description or figure of *P. pilosus*, in which the left cheliped is described and illustrated as very much larger than the right. Yokoya (1933) reported *P. setosus* from several Japanese localities but provided only a reference to Ortmann's description and figure. Similarly Makarov (1938, 1962) paraphrased Ortmann's description and reproduced his illustration (Makarov 1938:167, fig. 67; 1962:158, fig. 67), but indicated that he had no personal knowledge of the species.

Miyake (1978:27, text-fig. 8a, b) presented a detailed description of a species he referred to as *Paguristes setosus* (H. Milne Edwards 1848) from New Guinea, and included the localities reported by Ortmann (1892) and Yokoya (1933) as well as his own. We have examined four of Miyake's (1978) five specimens, now in the collection of the National Science Museum, Showa Memorial Institute, as well as two additional specimens from Tosa Bay, presented as a gift to the Muséum national d'Histoire naturelle, Paris and identified by M. de Saint Laurent as "*Paguristes setosus* sensu Miyake (1978). Three of Miyake's four specimens for the most part agree with his description of what he interpreted as Milne Edwards (1848) taxon. These, listed by Miyake (1978:28) as Nos 95, 565, and 566, carry NSMT catalog numbers CrR 869, CrR 2295, and CrR 2296, respectively. It is for these five specimens of Miyake's (1978:27) "*Paguristes setosus*," that we establish the taxon, *Paguristes miyakei* new species.

Miyake's specimen No 84 (NSMT CrR 860) represents another species of *Paguristes* that conceivably might be *P. setosus* sensu Ortmann (1892). *Paguristes miyakei* new species has antennular peduncles that overreach the distal margins of the corneas by nearly the entire length of the ultimate segment, whereas Ortmann (1892: pl. 12, fig. 9) illustrated the antennular peduncles as exceeding the corneas by only half the length of that peduncular segment as is seen in CrR 860. However, as previously noted, Ortmann's figure is quite unsatisfactory; his description could apply to any number of species of *Paguristes*. The identities of any of Ortmann's species cannot be definitely established until his type materials are reexamined, a project currently in progress by Dr. Tomoyuki Komai of the Natural History Museum and Institute, Chiba, Japan. However, the equal chelipeds described by both Ortmann and Miyake clearly distinguish their taxon or taxa from H. Milne Edwards's (1848) *P. setosus*.

Miyake (1978) did not specify the specimen (or specimens) illustrated in his text-figures 8a, b. Text-figure 8a does not agree well with any of the specimens examined, including CrR 860; text-fig. 8b does not appear to be of the holotype of *P. miyakei* new species, as the ocular acicles each terminate in a simple spine, as is seen in both paratypes. Miyake described the ocular peduncles of his "*P. setosus*" as distinctly shorter than the antennal peduncles, but his figure (text-fig. 8b) shows the latter only very slight exceeding the distal margins of the corneas. Only in the male paratype of *P. miyakei* do the peduncles actually extend noticeably beyond the corneal margins.

In Miyake's (1978: text-fig. 8b) figure of the shield and cephalic appendages, the fourth segments of the antennal peduncles each has a strong subdistal ventral spine. Actually the fourth segment of *P. miyakei* new species has a small dorsodistal spine; the strong spine is on the ventrodistal margin of each third segment. Similarly, Miyake refers to the first peduncular segment as having three spinules on the lateral margin. Two or three spinules occur on each lateral margin of the second peduncular segment; each first segment has a single spine on the laterodistal margin only in the holotype.

Miyake described and illustrated (1978: text-fig. 8a) the dactyls of the chelipeds as having three sharp spines on the dorsomesial margin proximally. The dactyls of neither the holotype nor the paratypes of *P. miyakei* new species fit that description. Rather, each has a row of strong, frequently corneous-tipped spines accompanied by stiff setae on the dorsomesial margin. The mesial faces of the dactyls are covered with small corneous-tipped spines or spinulose tubercles, but these are much more numerous and more regularly arranged than suggested by Miyake's figure. In his figure, the dactyl is illustrated as twice the length of the palm; the latter has only 3 spines on the dorsomesial margin, although four are described. The dactyl is actually shorter (1.25–1.35 the length of the palm) in the holotype and both paratypes of *P. miyakei*; the carpus seems to have been omitted in Miyake's figure. Miyake described and illustrated the merus with an unarmed dorsal surface; however, it is actually armed with a row of spines.

Although Miyake described the third pereopods as being unarmed, the ischia of *P. miyakei* new species each has a few dorsal and at least 1 ventral spinule; the dorsal surfaces of the meri have one or two spinules in addition to a slightly larger dorsodistal spinule. The carpi each has a dorsodistal spine and a couple of proximal spinules. Additionally the propodi each has an irregular double ventral row of spinules or spinulose protuberances, a row of spinulose tubercles is present on the mesial face ventrally, and the mesiodistal margin has at least one corneous-tipped spinule.

Despite being smaller than the male specimen, the female specimen CrR 2296 has been selected as the holotype of *P. miyakei* new species as it best fits Miyake's description in terms of the number of spines on the dactyls of the second pereopods. The number of spines on these dactyls in the two paratypes (CrR 896 and CrR 2295) are fewer. Although Miyake (1978: 28) stated that both posterior telsonal margins had long setae, small spines are present on these margins in all three specimens.

The male specimen from Tosa Bay differs from Miyake's (1978) Sagami Bay specimens only in have the posterior lobes of the telson less asymmetrical. The female specimen is abnormal, in that the tips of the ocular peduncles and corneas, left antennular peduncle and both antennal peduncles have obviously regenerated after an injury. However there is no doubt that it is the same species. The telson of this female is very similar to the illustrated holotype; however, the brood pouch is somewhat more developed.

As it is not possible to ascertain the identities of the specimens reported by Yokoya (1933) from several Japanese localities, for the present we are reporting the distribution of this species as only Sagami Bay at depths ranging from 150–250 m.

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Redescription of *Microdiaptomus cokeri* (Crustacea: Copepoda: Diaptomidae) from caves in central Mexico, with the description of a new diaptomid subfamily

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Abstract.—*Microdiaptomus cokeri*, the only true troglobitic copepod from Mexico, is redescribed on the basis of new material collected from the type locality, Cueva Chica cave, state of San Luis Potosi, Mexico. This species bears a unique combination of features not present in any other subfamily of Diaptomidae: legs 1–4 with two-segmented exopods, one-segmented endopods, one seta on the inner margin of the first exopodal segment of legs 1–4, a right male fifth leg with a 1-segmented endopod, and absence of sensillae on pediger 5 and on genital somite. Therefore, the erection of the new subfamily Microdiaptominae is appropriate. The genus *Troglodiaptomus*, previously accomodated in the subfamily Speodiaptominae, was found to be closely related to *Microdiaptomus* and is reallocated to the Microdiaptominae. Because of its apparent limited distribution in a system related to a highly polluted basin, it is necessary to follow this species closely to assess its true distributional range and to establish its conservation status.

The aquatic fauna of Mexican caves has been surveyed for decades, and some checklists are available (Reddell & Mitchell 1971, Reddell 1977); however, several taxonomic groups remain practically unknown. Particularly, the troglobitic copepod fauna of Mexico needs revision, because several of the earlier identifications of these crustaceans seem to be unaccurate (Reid 1990, Suárez-Morales et al. 1996).

The troglobitic copepod genus *Microdiaptomus* was originally described as a subgenus of *Diaptomus* by Osorio-Tafall (1942), from specimens collected at caves located in the area of Sierra de El Abra, state of San Luis Potosí, central Mexico. The genus can be separated from all other diaptomid genera by several features, but mainly by legs 1–4 with 2-segmented exopods and 1-segmented endopods, a male right antennula with segments 13 to 18 undilated, female fifth leg without a third exopodal segment, and by the presence of one pad on the second exopodal segment of the male left fifth leg (Osorio-Tafall 1942, Dussart & Defaye 1995). The type species (by monotypy) of this genus is *Microdiaptomus cokeri*. With a size of ca. 0.7 mm, it is one of the smallest diaptomids known.

According to Osorio-Tafall (1942) data, and our own records, this species has been collected exclusively in caves along the Sierra de El Abra mountain system (Cueva Chica, Cueva de los Sabinos, Sótano de Montecillos), San Luis Potosí, Mexico. The type locality (Cueva Chica) has not been sampled for its planktonic fauna since 1940 (Reddell & Mitchell 1971). The type material was deposited in the collection of the Escuela Nacional de Ciencias Biológicas of the Mexican Instituto Politécnico Nacional, but was lost decades ago. Since this loss, preserved specimens of *M. cokeri* were not available until late 1995, when Janet W. Reid identified this species from material collected by Thomas M. Iliffe in May, 1991 at Sotano de Montecillos, a non-type locality (USNM 264171). A recent survey of the type locality yielded several adult male and female specimens of *Microdiaptomus cokeri*. In this work the species is redescribed based on this new material. Additional morphological data, including a description of mouthparts and thoracic legs, are also provided.

Methods

Specimens of *Microdiaptomus cokeri* were collected during a zooplankton survey carried out on 28 February 1996 at Cueva Chica cave, state of San Luis Potosí, Mexico. Samples were collected using a plankton net with a 0.05 mm mesh. The material was fixed in a 4% sugar-formalin solution. All copepods were sorted and preserved in 70% ethanol with a drop of glycerin. Male and female specimens of *M. cokeri* were sorted from the samples under a stereomicroscope and then processed for examination. Descriptions were made based on observations of whole and dissected specimens mounted in glycerin. Drawings were made with the aid of a camera lucida. A Student's "*t*" test was performed to detect length differences in both males and females from the two localities surveyed. Abbreviations used for descriptions are: Exp = Exopod, Enp = Endopod, P1–P4 = legs 1–4.

Material Examined

Cueva Chica: two adult males, one adult female deposited in the National Museum of Natural History at Washington, D.C., under catalog number USNM-285516; eight adult males, three adult females deposited in the Zooplankton Reference Collection of UNAM, Campus Iztacala, Tlalnepantla, Mexico, catalog numbers COP-197 and 198. One male and one female deposited in the Zooplankton Collection of El Colegio de la Frontera Sur, Chetumal, Mexico, under number ECO-CH-Z00223.

Sótano de Montecillos: three adult males, three adult females deposited at the Museum National d' Histoire Naturelle (Paris), catalog numbers MNHN-Cp1131 and MNHN-Cp1132, respectively. Additional material at El Colegio de la Frontera Sur (ECOSUR), Chetumal, Mexico, and Zooplankton Reference Collection at UNAM, Campus Iztacala, Mexico (COP-199 and 200).

Croatia: Two male and three female specimens of *Troglodiaptomus sketi* Petkovski, 1978 from the type locality, near Rovigno (=Rovinj).

Slovenia: A female specimen of *T. sketi* from Kompoljska cave, collected in August 18, 1996.

Family Diaptomidae Baird, 1850

Microdiaptominae, new subfamily

Diagnosis.—Legs 1–4 with 2-segmented exopods, 1-segmented endopods, with or without a seta on inner margin of the first segment of exopod. One or two setae on inner margin of second exopodal segment of legs 1–4. One outer distal spine on first exopodal segment of leg 1 and on second exopodal segments of legs 2–4. Endopod of male right leg 5 absent or 1-segmented, of left leg, 1 or 2-segmented. Endopods of female leg 5 reduced to a small bulb or 1-segmented. In both sexes, sensillae absent on pediger 5 and on female genital somite.

Remarks.—Previous assignment of *M. cokeri* to Diaptominae (e.g., Dussart & Defaye 1995) was based on the original description of Osorio-Tafall. However, in that work, no information was given on segmentation or setation patterns of the swimming legs or of most cephalic appendages.

Borutzky (1962) erected the subfamily Speodiaptominae to allocate the troglobitic *Speodiaptomus birsteini* Borutzky, 1962. This taxon is featured mainly by a 2/1, 2/2, 2/2, 3/2 segmentation pattern in legs 1–4.

The original diagnosis of this subfamily was later changed by Petkovski (1978) to accomodate the new genus *Troglodiaptomus*. The new definition of the Speodiaptominae included characters such as a variable segmentation pattern of legs 1–4 with exopods and endopods as: 2/1; 2/1–2; 2/1–2; 2–3/1–2, first exopod of first legs without inner seta, no dilated segments 13–18 on male right antennule, and endopod of the male right fifth leg absent (*Troglodiaptomus*) or 2-segmented (*Speodiaptomus*). This expanded scheme allowed both genera to be included within the Speodiaptominae; according to this diagnosis, *M. cokeri* should be included in this subfamily.

The main criterion used by Petkovski (1978) to include *Troglodiaptomus* in the Speodiaptominae was the reduction of the swimming legs as an adaptation to troglobious life. From the comparison of this taxon with other troglobitic genera such as *Spelaeodiaptomus* Dussart, 1970 and *Speodiaptomus*, he concluded that *Troglodiaptomus* represented the cave-adapted extreme while *Spelaeodiaptomus* with fewer reductions and a member of the Diaptominae, showed the least adapted pattern. He considered that these reductions related *Speodiaptomus* and *Troglodiaptomus*, and included both genera in the Speodiaptominae. However, he recognized the possibility that *Troglodiaptomus* could be a representative of a new subfamily.

Borutzky (1962) and Borutzky et al. (1991) emphasized the taxonomic relevance of the segmentation pattern of swimming legs within the Calanoida at the subfamily level. This is the main criterion we used herein to justify the creation of the new subfamily Microdiaptominae. Following this criterion, both, *Troglodiaptomus* and *Microdiaptomus* should be included in the new subfamily. The new subfamily includes the only two diaptomids bearing this unique segmentation pattern of 2/1 in exopods/endopods of legs 1–4. Moreover, *Troglodiaptomus sketi* Petkovski, 1978, which is an hypogean form (Brancelj 1987, 1991; Dussart & Defaye 1995), and is the type species of *Troglodiaptomus*, shares some relevant additional characters with *M. cokeri*. Such characters include the structure of the male right antennule with undilated segments (in both only segment 14 is slightly wider than the others), the absence of sensilla on fifth pedigerous or genital somites, and the structure of other appendages such as the antennae and the maxillipeds. The male and female fifth legs of both *Troglodiaptomus* and *Microdiaptomus* have strong similarities between them (see Table 1). These legs differ from *Speodiaptomus* in the general structure but particularly in the endopods, which are 2-segmented in the right male and female P5 of the latter (see Petkovski 1978, Brancelj 1987, Dussart & Defaye 1995). The original Borutzky's diagnosis of the Speodiaptominae should then be retained.

The information available does not allow us to conclude if a common ancestor existed for both, the European *Troglodiaptomus* and the American *Microdiaptomus* or if they evolved independently in a similar environment from epigean forms. Considering the peculiar characters they share, it is evident that both forms are related. *Microdiaptomus cokeri* is distributed in caves located in one of the geologically oldest zones of Mexico (Padilla y-Sánchez & Aceves-Quesada 1990).

Microdiaptomus cokeri
(Osorio-Tafall 1942)

Microdiaptomus cokeri Osorio-Tafall, 1942:206–210, figs. 1–17 (*Diaptomus* (*Microdiaptomus*) *cokeri*); Osorio-Tafall, 1943:49–53, 56 (*Diaptomus* (*Microdiaptomus*) *cokeri*); Wilson, 1959:780, fig. 29.67 (*Diaptomus cokeri*); Reddell & Mitchell, 1971:141 (*Diaptomus* (*Microdiaptomus*) *cokeri*); Reid, 1990:179; Dussart & Defaye, 1995:180–181, fig. L73.

Figs. 1–23

Description.—Male: Mean body length of Cueva Chica specimens: 0.723 mm;

Table 1.—Comparison of characters among *Microdiaptomus cokeri, Stygodiaptomus birsteini* and *Troglodiaptomus sketi.*

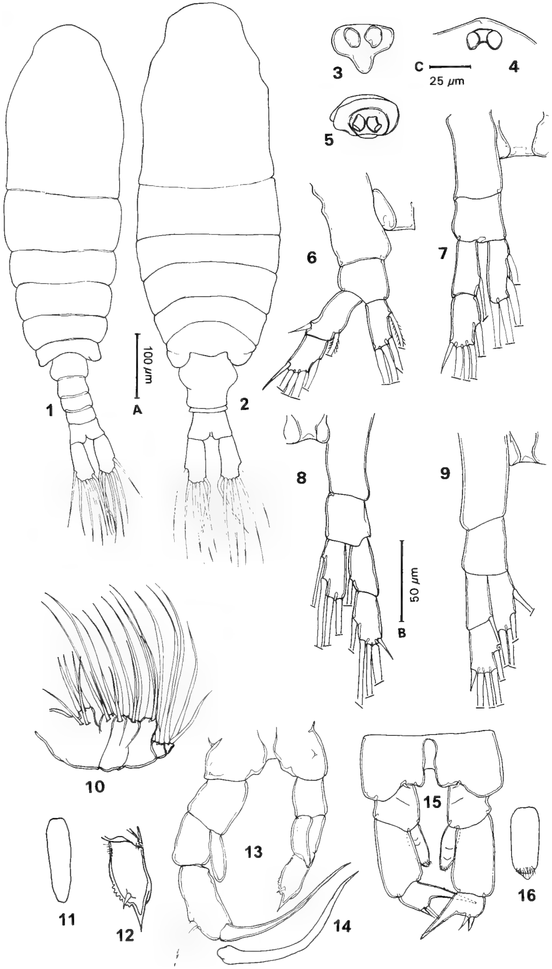
Character	*M. cokeri*	*S. birsteini*	*T. sketi*
Segments on P1-P4 (exp/end)	2/1;2/1;2/1;2/1	2/1;2/2;2/2;3/2	2/1;2/1;2/1;2/1
Inner setae on exp 1 P1-P4	1;1;1;1	0;0;0;0	0;0;0;0
Outer spines on exp 1 P1-P4	1;0;0;0	1;1;1;1	1;0;0;0
Setae on exp 2 P1-P4 inner/apical	1/3;2/2;2/2;2/2	2/3;2/3;2/3;1/0	2/3;2/3;2/3;2/3
Outer spine on exp 2 P1-P4	1;1;1;1	1;1;1;1	1;1;1;1
Setae on terminal segment of endopods P1-P4 inner/apical	1/3;2/2;2/2;2/2	1/3;2/3;2/3;2/3	0/3;0/3;0/3;0/3
2-segmented endopod(s) in male P5	No	Yes	Yes
2-segmented endopod(s) in female P5	No	Yes	No
Reduced endopod in female P5	No	No	Yes

range = 0.69–0.74 mm. Sótano de Montecillos, mean: 0.752 mm; range 0.70–0.79 mm. Body slender, with a typical diaptomid shape (Fig. 1). Eyes or eye-related structures absent or quite reduced, body unpigmented. Rostral filaments absent, rostrum represented by two rounded, heavily chitinized projections (Fig. 4).

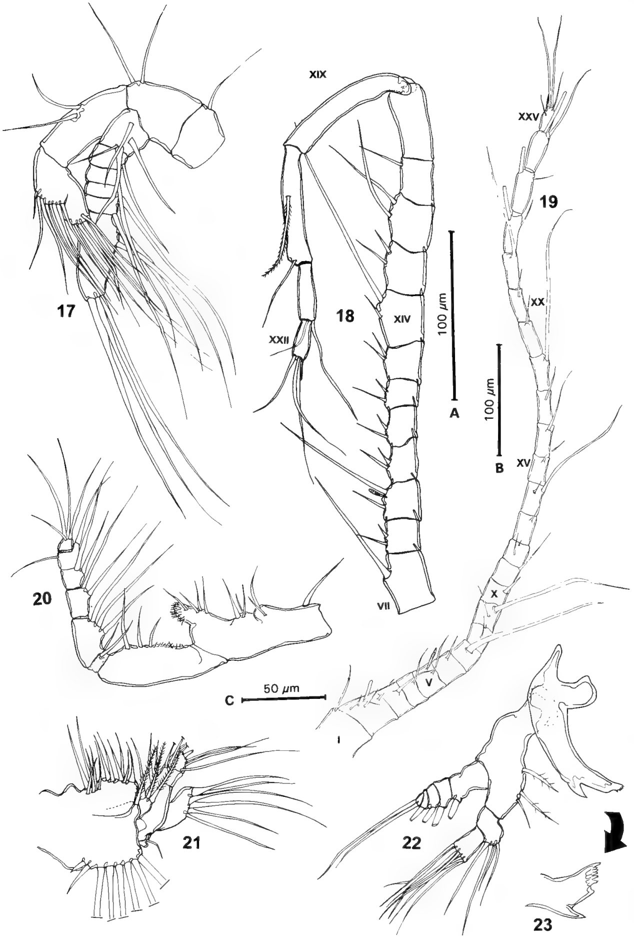
Pediger 4 slightly wider than pediger 5, which tapers posteriorly. Pediger 5 (sixth thoracic somite) slightly asymmetrical, right side with a more evident rounded process (Fig. 1), without dorsal ornamentation. Sensillae absent on both sides. Urosome (Fig. 1) symmetrical, five-segmented, relative lengths of urosomites being: 26.6:21.6: 16.8:15:20 = 100. Urosomite 1 (genital somite) asymmetrical, posterior half of left lateral margin slightly protuberant. Dorsal surface of urosomites unornamented, posterior margins smooth. Caudal rami nearly two times longer than wide, inner and outer margins smooth, with 5 terminal caudal setae subequal in length and width, plus the dorsal one, subterminally inserted. Caudal setae finely plumose, non-articulated, relatively short, about 2.0 times length of caudal rami. Inner and outer margins of caudal rami naked.

Antennules relatively shorter than in female, reaching anterior margin of caudal rami. Right antennule 22-segmented (Fig. 18), with one large seta on segment 7; segment 8 with one spine and one seta; 9 with one long and a short setae plus one aesthetasc; 10–13 each with spine and a longer seta; 14 with one long and a short setae; segment 15 with one setae and a spine; 16 with two setae; 17 with one spiniform seta; 20 with two setae, penultimate segment with two long seta; last segment with three terminal setae plus one aesthetasc. Setation of left antennule as in female. Antennae, mouthparts and swimming legs 1–4 as in female.

Fifth legs biramous: Right one (Fig. 13): Coxa with small rounded process on anterolateral margin tipped with short sensilla. Basis 1.2 times as long as first exopodal segment and larger than that of left leg. Outer margin of exopod 1 almost straight, inner margin smooth. Exopod 2 ca. 1.7 times length of exopod 1. Lateral spine curved and borne at distal ⅔ of segment,



Figs. 1–16. *Microdiaptomus cokeri* Osorio-Tafall, 1942. 1. Habitus, male. 2. Habitus, female. 3. Rostral area, female. 4. Rostral area, male. 5. Genital opening, female. 6. First leg, female. 7. Second leg, female. 8. Third leg, female. 9. Fourth leg, female. 10. Second maxilla, female. 11. Right fifth endopod, male. 12. Close view of second segment, fifth left exopod, male. 13. Fifth leg, frontal view, male. 14. Variation in the shape of terminal claw, right exopod, male. 15. Fifth leg, anterior, female. 16. Fifth left endopod, female. Scale bar A: Figs. 1,2; B: Figs. 6–16; C: Figs. 3–5.



Figs. 17–23. *Microdiaptomus cokeri* Osorio-Tafall, 1942. 17. Antenna, female. 18. Right antennule, male, segments VII–XXII. 19. Left antennule, female. 20. Maxilliped, female. 21. First maxilla, female. 22. Mandible, female. 23. Mandibular blade, female. Scale bar A: Fig. 18; B: Fig. 19; C: Figs. 17,20–23.

about half as thick as endopod, almost 0.7 length of exopod 2, and about same length as exopod 1. Terminal claw relatively slender, curved, with a slight sigmoid shape in some animals, inner margin smooth (Figs. 13, 14), tapering gradually from enlarged base, about 1.4 times longer than exopods 1 and 2 combined. Endopod 1-segmented reaching about ⅓ beyond distal margin of first exopodal segment (Figs. 11, 13).

Left leg 5 (Fig. 13) reaching proximal ⅖ of inner margin of right second exopodal segment. Coxa with small rounded process tipped with short sensillum near outer margin. Basis with short lateral seta on outer margin. First exopodal segment almost as long as segment 2, in some specimens with short hairs on distal portion of inner margin. Second exopodal segment ending in acute distal process with a stout, smooth subterminal spiniform structure. Along inner margin of distal pad in exopod 2, there are several rows of 8–10 small vesicle-like structures (Fig. 12). Endopod one-segmented, asymmetrical, narrowing abruptly at distal ⅓ and reaching proximal ⅓ of exopod 2. Tip of endopod with short hairs.

Female: Cueva Chica, mean length 0.723 mm; range = 0.64–0.78 mm. Sótano de Montecillos, mean 0.814 mm; range = 0.74–0.89 mm. Prosome relatively wide in dorsal view, symmetrical, first pedigerous somite separated from cephalic area (Fig. 2). Pedigers 4 and 5 separated, pediger 5 with rounded posterolateral margins, smooth, with no sensilla on them. Urosome with three segments, relative lengths of each being: 61.5:13.4:25.1 = 100. Genital double somite about 1.6 times as long as remaining urosomites together, slightly asymmetrical in dorsal view, with lateral rounded protuberances, and no lateral sensillas present. Genital double somite ventrally expanded, with genital openings as shown in Fig. 5; posterior margin slender. Second somite very short, partially telescoped into the genital double somite. Anal somite large. Furca and caudal setae similar to male. Rostral points represented by two strong, rounded projections (Fig. 3).

Antennules longer than in male (Fig. 19), 25-segmented, reaching beyond posterior margin of caudal rami. Seta on segment 1 short, reaching distal margin of segment 2. Largest setae on segments 7, 9, 14, 18, and 21. Armature per segment as follows (Roman numerals = segment, Arabic numerals = number of setae, a = aesthetasc, sp = spine): I(1), II(4 + a), III(1), IV(1), V(1 + a), VI(1), VII(1), VIII(1), IX(2), X(sp), XI (1), XII (2), XIII(1), XIV(2), XV(1), XVI(1), XVII(1), XVIII(1), XIX(1), XX(1), XXI(1), XXII(2), XXIII(2), XXIV (2), XXV (4 + a).

Antenna (Fig. 17) with exopod slightly longer than endopod. Coxa with one seta, basis with two long setae. Endopod with two segments, distal portion of terminal endopodal segment with two lobes, inner lobe with six anterior setae; outer lobe with one short, two medium-sized, and five long setae. Exopod 6-segmented, with 4 setae on first segment (fused original segments 1 + 2), one seta, each on segments 2–5, and terminal segment with two setae on proximal third plus three terminal setae.

Mandible (Fig. 22) with 6–7 teeth on gnathobase; outermost ventral tooth relatively high (Fig. 23). Basis with three subequal setae, two of them plumose; endopod with 2 segments, proximal segment with protuberance on inner margin, with four setae, two medium-sized, and two long; distal segment short, as long as wide, with 7 anterior and one posterior setae. Exopod 5-segmented, with 1, 1, 1, 1 and 2 setae.

First maxilla (Fig. 21) with praecoxal arthrite with 12 spiniform setae, 8 of which are apical, plus 4 posterior setae. Coxal epipodite with 8 spiniform setae, proximal two shorter than the others. Two and three setae on coxal and first basal endites, respectively. Endopod 2-segmented, articulating with basis, with two seate on first segment and four setae on second. Exopod with 6 long setae.

Second maxilla (Fig. 10) with two praecoxal and two coxal lobes, and well developed basal lobe carrying 5, 3, 3, 3 and 3 setae. Endopod 2-segmented, with two setae on first and three on distal segments.

Maxilliped (Fig. 20) well developed. Coxa with three coxal endites, proximal and medial with three subequal setae each, third endite represented by anterior protuberance projecting beyond next segment, with short hairs on tip and 4 simple setae inserted along process. Basis with group of three setae increasing in length distally, inserted on distal half of inner margin; proximal half hairy. Endopod 6-segmented, with first segment partially fused to basis, bearing 2 subequal setae. Second endopodal segment with three subequal setae, third and fourth with 2, fifth with two setae; terminal segment with one short and four long setae.

Legs 1–4 with 1-segmented endopods and 2-segmented exopods, coxa and basis without setae (Figs. 6–9). Armament formula for swimming legs as:

	coxa	basis	exopod	endopod
leg 1	0-0	0-0	I-1; I, 3, 1	0-0, 2, 2
leg 2	0-0	0-0	0-1; I, 3, 1	0-0, 2, 2
leg 3	0-0	0-0	0-1; I, 3, 1	0-0, 2, 2
leg 4	0-0	0-0	0-1; I, 3, 1	0-0, 2, 2

Leg 5 (Fig. 15): Coxa with small protuberance tipped with short spiniform structure on the middle of inner distal margin. Basis with inner margin slightly rounded. Endopod one-segmented, relatively wide, reaching two thirds of first exopodal segment; tip protruding in a relatively acute process, partly covered with short hairs (Fig. 16). First exopodal segment about 2 times longer than exopod 2, with smooth margins. Inner margin of claw armed with short row of hairs along distal half of both margins. Exopod 3 absent, represented by two short, strong, subequal spiniform processes.

Habitat.–Cueva Chica cave (21°51′35″N, 98°56′07″W) is located within a private farm near the town of El Pujal, south of Ciudad Valles, state of San Luis Potosi, central Mexico. Access to the cave is limited, but the system is well preserved, considering that it was first surveyed more than 60 years ago by Hubbs & Innes (1936), who described the blind fish currently known as *Astyanax mexicanus jordani*. Breder (1942) published a detailed synthesis of the ecology, geology, hydrology, and physiography of this cave, with an explicit account of the blind fish.

A brief description of the cave is as follows: the main entrance is a low opening which leads into a large chamber originating a partially flooded passage that opens into a small chamber with a pool; access into this secondary chamber is wide and about 1 m high. There is another larger pool at the bottom, which was not surveyed by us because the access was covered by excreta of several bat species (*Atribeus jamaicensis yucatanicus* Allen, *Desmodus rotundus murinus* Wagner, *Mormoops megalophylla megalophylla* Peters, *Pteronotus davyi fulvus* (Thomas), *P. parnellii* (Gray), *Natalus stramineus* Gray) dwelling in the cave (Reddell & Mitchell 1971). Therefore, all our sampling was made only in the first pool and flooded passage. *Microdiaptomus cokeri* was present only in the pool. The pool water is clear, with abundant blind fishes. It is a vase-shaped water body; its main physical and chemical characteristics are summarized in Table 2. Several cyclopoid copepods were collected. Sótano de Montecillos is also part of the Sierra de El Abra system, and is located north of Ciudad Valles.

Remarks.—Microdiaptomus cokeri has been recorded in at least three different caves of the Sierra de El Abra system, which contains 39 caves (Reddell & Mitchell 1971). Its occurrence in several other caves in this mountain system should be expected, since it could follow a similar distributional pattern to that of other local troglobionts, such as the blind fish *Astyanax*

Table 2.—Main physical and chemical variables from the surveyed pool in Cueva Chica. For comparison data of Breder (1942) are shown (measurements from March 11, 1940). ** Data from the adjacent pool, possibly connected to one surveyed in this work. NA = not available.

	Data from November 28, 1996	Data from Breder (1942)
Altitude above sea level (m)	185	NA
Depth (m)	4.5	NA
Temperature (°C)	26	26.1–27
Dissolved oxygen (mg/l)	1.2	NA
pH	6.88	8.0
Conductivity (μS)	700	NA
Alkalinity (mg $CaCO_3$/l)	343	282**
Hardness (mg $CaCO_3$/l)	205.8	310**

mexicanus jordani, widely distributed in this zone (Wiley & Mitchell 1971).

Specimens from Sótano de Montecillos were larger ($p > 0.95$) than those collected from Cueva Chica. This observation is similar to the differences reported by Osorio-Tafall (1942, 1943), who compared material from Los Sabinos Cave and Cueva Chica. This author stated that space limitation and temperature were factors associated with this size difference. It is possible that predation, mainly from the blind fish, could be added to these factors, but further analysis is needed to support this statement.

The feeding habits of *M. cokeri* are still unknown, but the type of mandibular blade, the development of its other mouthparts, and the slender aspect of its thoracic appendages suggest that it is an epibenthic, omnivorous species feeding upon particles deposited on the walls of the pool. Most of the specimens were collected by littoral surface hauls.

The restricted distributional range of this copepod is probably shared by the fish *Astyanax mexicanus jordani*. Both species dwell in an ecologically fragile environment since the surveyed caves are hydrologically connected to the highly polluted Pánuco Basin (Vázquez-Gutiérrez 1994). We consider that these conditions would favor the idea of *M. cokeri* as a species to be followed closely in the next years. A more intense sampling in the area would be required to assess the true distributional range and conservation status of this troglobitic copepod. In 1996 the IUCN Red List included 37 diaptomid copepod species, of which several are cavernicole (Baillie & Groombridge 1996).

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Setation and setal groups on antenna 1 of *Ridgewayia klausruetzleri*, *Pleuromamma xiphias*, and *Pseudocalanus elongatus* (Crustacea: Copepoda: Calanoida) during the copepodid phase of their development

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Abstract.—Setae added to the antenna 1 of three species of calanoid copepods during copepodid development are allocated to setal groups present on the adult antenna 1. Development of these setal groups is not homogeneous; for a given setal group the copepodid stage at which the first seta appears and at which setal addition is completed varies; whether the setal group is trithek or quadrithek in adult males also varies. These variations suggest several sets of setal groups as candidates for the presumed extra groups added during the adaption of an ancestral calanoid copepod to the pelagic environment. Among these, a set of late developing setal groups is preferred. A model for adding setal groups during copepodid development assumes three source groups are responsible for adding 16 progeny groups.

Antenna 1 of calanoid copepods usually consists of 25 articulating segments in adult females (Giesbrecht 1892) although 27 articulating segments have been found in some adult female epacteriscids (Fosshagen 1985). A calanoid antenna 1 with 27 articulating segments has been explained in one of two ways. The 27 segmented antenna 1 may be a state for calanoids which has been derived by fusion of the ultimate and penultimate segments from an ancestral copepod state with 28 segments (Huys & Boxshall 1991). Alternatively, it may be a state derived through the acquisition of extra segments, as the result of adaption by an ancestral calanoid to pelagic habitats, from an ancestral copepod state of about 20 segments (Stock 1991).

Here we examine these two hypotheses using data derived from the copepodid development of the calanoids *Ridgewayia klausruetzleri* Ferrari 1995, *Pleuromamma xiphias* (Giesbrecht 1889) [=*Pl. xiphias*] and *Pseudocalanus elongatus* (Boeck 1865) [*Ps. elongatus*]. We analyze setation patterns of antenna 1 during development of these three calanoids. We allocate each seta at each copepodid stage to a setal group to which the seta will be associated in the adult female antenna 1, and derive developmental patterns for each setal group. We also discuss whether a homogeneous pattern of setation is present from which all of the setal groups in an ancestral 28-segmented appendage can be inferred, or whether several patterns are present among which is a pattern unique to a set of setal groups which can be identified as the extra, derived setal groups of calanoids. Finally we present a model for the addition of setal groups to antenna 1 during copepodid development of the three calanoids.

Methods

Ferrari (1995) described antenna 1 during the copepodid phase of development of *R. klausruetzleri*; Ferrari (1985) described the development of copepodid (C) II–VI of *Pl. xiphias*; and Oberg (1906) described antenna 1 for CI-IV of *Ps. elongatus*. Here we add descriptions of antenna 1 of CI of *Pl. xiphias* and of CV-VI of *Ps. elongatus*, and redescribe the morphology of all of the stages while comparing the three calanoids.

The setose edge of antenna 1 has been called anterior (the direction of antenna 1 is held in calanoids) (Hulsemann 1991) but we note that among the remaining copepod appendages, most setae are found on the ventral edge (in descriptive work usually noted as medial) of an endopod; a few setae are found dorsally (usually noted as lateral). If the distal segments of antenna 1 are endopodal then the anterior edge of antenna 1 is ventral in copepods. The trithek/quadrithek groupings of setae on antenna 1 (Giesbrecht 1892) refers to the following set of setae: in the adult female a pair of setae originate close together often immediately proximal to an arthrodial membrane; one is a simple seta and the second, usually a modified, poorly sclerotized seta often is called an aesthetasc. A third simple seta is located proximal to the pair. In the CVI male a fourth, poorly sclerotized seta or aesthetasc may be present near the location of the above-mentioned pair.

Phylogenetic relationships among the 269 calanoid genera have not been proposed. The 43 calanoid families are grouped into 11 superfamilies and phylogenetic relationships among eight or 10 of those superfamilies have been hypothesized respectively by Andronov (1974) and Park (1986). *Ridgewayia klausruetzleri* [Ridgewayiidae, three genera] belongs to the Pseudocyclopoidea [three families], one of the two presumed oldest superfamilies, along with Epacteriscoidea; *Pl. xiphias* [Metridinidae, three genera] belongs to the Arietelloidea [eight families], the next most derived superfamily and presumedly the oldest superfamily of pelagic calanoids; *Ps. elongatus* [Clausocalanidae, seven genera] belongs to the Clausocalanoidea [11 families] the youngest superfamily. The analyses of Andronov (1974) and Park (1985), which revealed these relationships, used some of the same characters but neither analysis included as a character the number of segments of antenna 1.

Results

At CI, antenna 1 of all three calanoids has ten articulated segments. The setation of *R. klausruetzleri* from the proximal segment is 3, 2, 1, 2, 0, 1, 1, 3, 2, 7 (Figs. 1A, 2E), and for *Pl. xiphias* and *Ps. elongatus* it is 3, 2, 1, 2, 0, 1, 1, 2, 2, 7 (Figs. 3A, 4D, 5A, G).

At CII, antenna 1 of *R. klausruetzleri* has 17 articulated segments with 1, 4, 0, 1, 0, 2, 0, 1, 0, 1, 2, 1, 1, 1, 3, 2, 7 setae (Figs. 1B, 2D). Antenna 1 of *Pl. xiphias* has 15 articulated segments with two poorly expressed arthrodial membranes within the third segment; there are 3, 4, 1, 2, 0, 1, 0, 1, 2, 1, 1, 2, 2, 2, 7 setae (Figs. 3B, 4E). Antenna 1 of *Ps. elongatus* has 16 articulated segments with one poorly expressed arthrodial membrane within the first segment; there are 5, 0, 1, 0, 2, 0, 1, 0, 1, 2, 1, 1, 2, 2, 2, 7 setae (Fig. 5B, H).

At CIII, antenna 1 of *R. klausruetzleri* has 24 articulated segments with 1, 2, 1, 2, 0, 1, 0, 2, 0, 1, 1, 1, 2, 1, 1, 1, 1, 3, 1, 1, 2, 3, 2, 7 setae (Figs. 1C, 2C). Antenna 1 of *Pl. xiphias* has 20 articulated segments with two poorly expressed arthrodial membranes within the sixth segment; there are 5, 1, 2, 0, 1, 2, 1, 2, 2, 1, 1, 1, 1, 3, 1, 1, 2, 3, 2, 7 setae (Figs. 3C, 4F). *Pseudocalanus elongatus* has 19 articulated segments with poorly expressed arthrodial membranes within the first, fifth, sixth and seventh segments; there are 6, 2, 0, 1, 2, 1, 2, 2, 1, 1, 1, 1, 2, 1, 1, 2, 2, 2, 7 setae (Fig. 5C, I).

At CIV, antenna 1 of *R. klausruetzleri* has 25 articulated segments with 2, 3, 1, 2, 1, 2, 1, 1, 3, 1, 1, 3, 2, 2, 2, 3, 2, 2, 3, 1, 1, 2, 3, 2, 7 setae (Figs. 1D, 2C). Antenna 1 of *Pl. xiphias* has 23 articulated segments with two poorly expressed arthrodial mem-

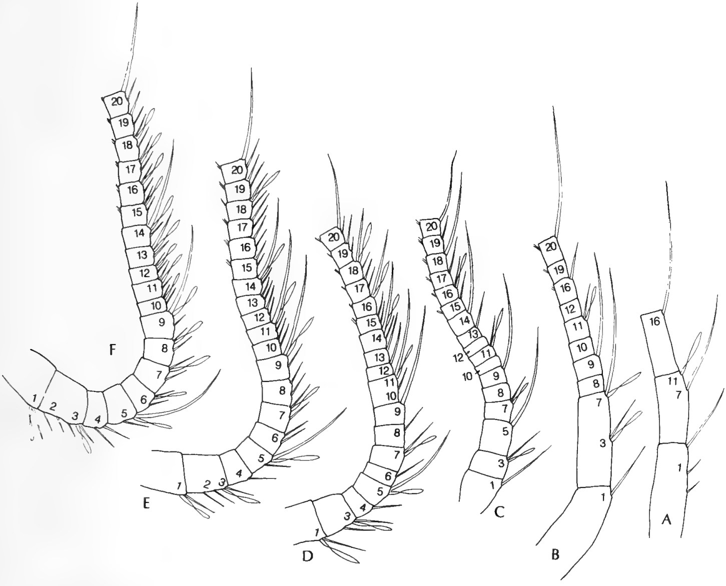

Fig. 1. Proximal section of antenna 1 of *Ridgewayia klausruetzleri*. A, CI; B, CII; C, CIII; D, CIV; E, CV; F, CVI female. Illustrations not to scale; proximal is down; proximal section includes setal groups 1–20, if present; setal groups are numbered.

branes within the eighth segment; there are 7, 1, 2, 1, 2, 1, 1, 4, 1, 3, 2, 3, 2, 3, 2, 2, 3, 1, 1, 2, 3, 2, 7 setae (Figs. 3D, 4F). Antenna 1 of *Ps. elongatus* has 22 articulated segments with two poorly expressed arthrodial membranes within the first segment and one poorly expressed arthrodial membrane within the fourth segment; there are 7, 2, 1, 3, 1, 3, 1, 1, 3, 1, 3, 1, 1, 1, 2, 2, 1, 1, 2, 2, 2, 7 setae (Fig. 5D, I).

At CV, antenna 1 of *R. klausruetzleri* has 26 articulated segments with 2, 4, 1, 3, 2, 3, 2, 3, 2, 3, 2, 2, 3, 2, 2, 2, 3, 2, 2, 3, 1, 1, 2, 3, 2, 7 setae (Figs. 1E, 2C). Antenna 1 of *Pl. xiphias* has 23 articulated segments with two poorly expressed arthrodial membranes within the eighth segment; there are 9, 2, 3, 2, 3, 2, 3, 7, 3, 3, 3, 3, 3, 3, 3, 3, 3, 1, 1, 2, 3, 2, 7 setae (Figs. 3E, 4F). Antenna 1 of *Ps. elongatus* has 23 articulated segments with two poorly expressed arthrodial membranes within the first segment; there are 10, 3, 2, 3, 2, 2, 4, 1, 1, 3, 2, 3, 1, 1, 1, 2, 2, 1, 1, 2, 2, 2, 7 setae (not illustrated but see Fig. 5E, I).

At CVI, the female antenna 1 of *R. klausruetzleri* has 26 articulated segments with 2, 5, 2, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 2, 2, 3, 1, 1, 2, 3, 2, 7 setae (Figs. 1F, 2C). Antenna 1 of *Pl. xiphias* has 22 articulated segments with three poorly expressed arthrodial membranes within the seventh segment; there are 10, 3, 3, 3, 3, 3, 12, 3, 3, 3, 3, 3, 3, 3, 3, 3, 1, 1, 2, 3, 2, 7 setae (Figs. 3F, 4F). Antenna 1 of *Ps. elongatus* has 24 articulated segments with one

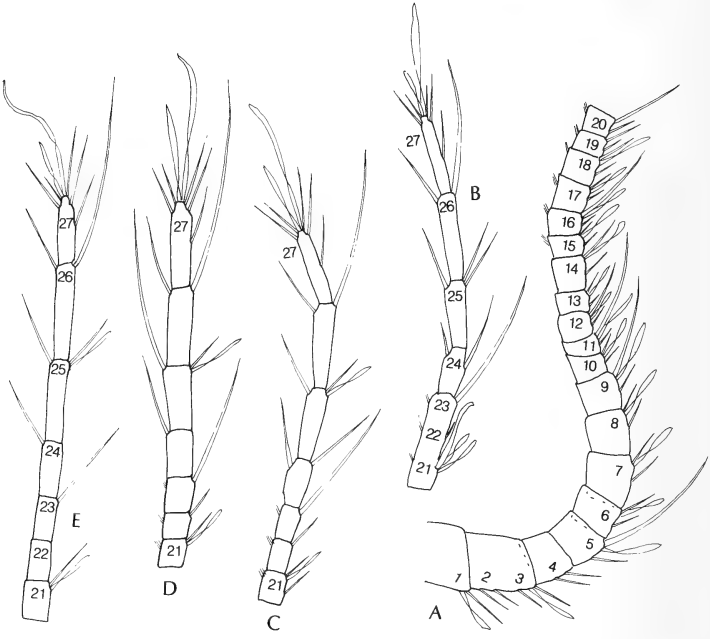

Fig. 2. Antenna 1 of *Ridgewayia klausruetzleri*. A, proximal section of CVI male; B, distal section of CVI male; C, distal section of CIII (distal section of CIV, CV, and CVI female is identical); D, distal section of CII; E, distal section of CI. Distal section includes setal groups 21–27; remaining explanation as for Fig 1.

poorly expressed arthrodial membrane within the second segment; there are 3, 7, 3, 2, 3, 2, 2, 4, 1, 1, 3, 2, 3, 1, 1, 1, 2, 2, 1, 1, 2, 2, 2, 7 setae (Fig. 5E, I).

At CVI, the right male antenna 1 of *R. klausruetzleri* has 24 segments with 2, 5, 2, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 2, 2, 5, 2, 3, 2, 7 setae (Fig. 2A, B); there is a geniculation between the 19th and the 20th segments. The right male antenna 1 of *Pl. xiphias* has 15 segments with three poorly expressed arthrodial membranes in the sixth segment and one in the seventh segment; there are 12, 4, 3, 4, 3, 14, 10, 6, 3, 2, 3, 5, 5, 2, 7 setae (Fig. 4A, B); there is a geniculation between the 11th and the 12th segments. Segment 12 bears distally a segmental attenuation which appears similar to two stiff, poorly-articulated setae found proximally on the segment; there also is a stiff, poorly-articulated seta on segments 10 and 11 (Fig. 4C). The right male antenna 1 of *Ps. elongatus* has 19 segments with 12, 4, 3, 4, 3, 4, 11, 2, 3, 2, 2, 2, 3, 2, 2, 2, 2, 2, 7 setae (Fig. 5F); there is no articulation. Morphology of the left antenna 1 of the CVI male is identical to that of the CVI female for all three calanoids.

There is a posterior seta on each of the last four segments of all three species at all six copepodid stages.

Fig. 3. Proximal section of antenna 1 of *Pleuromamma xiphias*. A, CI; B, CII; C, CIII; D, CIV; E, CV; F, CVI female. Dotted lines indicate incompletely formed arthrodial membranes; remaining explanation as for Fig 1.

Discussion

The presence of a proximal and a distal arthrodial membrane delimiting a group of setae traditionally has been used to identify the segments of antenna 1. Variation in expression of the arthrodial membranes, as described below, has led us to assign all setae present at each stage of development to one of 27 setal groups present in the adult female antenna 1 (Tables 1–3) without regard to the presence of arthrodial membranes. Assignment of setae during copepodid development to a setal group is based on the following four assumptions: during development, setae usually are conserved (an exception is the loss of a seta by setal group 1 of *R. klausruetzleri* during the molt to CII); new setal groups usually bear one seta (exceptions: *R. klausruetzleri* setal groups 1, 3, 21, 25, 26, 27; *Pl. xiphias* setal groups 1, 3, 21, 25, 26, 27; and *Ps. elongatus* setal groups 1, 21, 25, 26, 27); arthrodial membranes may establish the location of a setal group before the first seta of that group is formed (setal groups 8, 10, 12, 19, 22 of all three species); and setae are added to a group so that the trithek/quadrithek groupings are conserved (a tri-

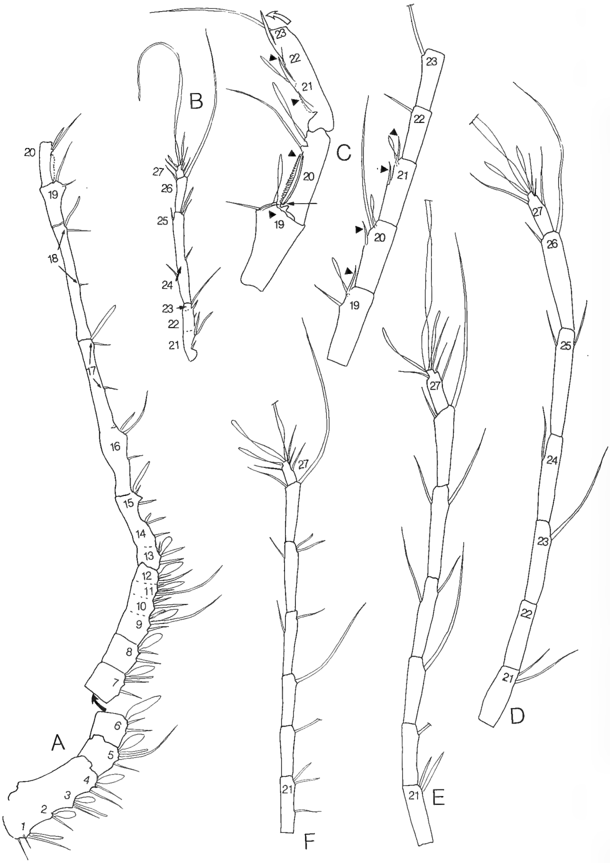

Fig. 4. *Pleuromamma xiphias*. A, proximal section of right antenna 1 of CVI male (curved arrow unites setal group 6 with setal group 7); B, distal section of right antenna 1 of CVI male; C, detail of setal groups 19–23 on CV (to right) and CVI (to left) male right antenna 1 (long arrow near articulation of the proximal seta of setal group 20; arrowheads near poorly articulated setae of setal groups 19–21; open arrow near attenuation of segment bearing setal group 22); D, distal section of CI; E, distal section of CII; F, distal section of CIII (distal section of CIV, CV, and CVI female is identical). Explanations as for Fig 2.

thek/quadrithek grouping is not the outcome for setal group 1).

Aside from truncations of setal addition (Tables 1–3), developmental patterns of setae generally agree among the three species. The resulting adult female series aligns with the 28-segmented adult antenna 1 presumed for the ancestral copepod by Huys &

Fig. 5. Antenna 1 of *Pseudocalanus elongatus*. A, proximal section of CI; B, proximal section of CII; C, proximal section of CIII; D, proximal section of CIV; E, proximal section of CVI female (arrow indicates arthrodial membrane absent in CV; otherwise CV identical to CVI female); F, CVI male; G, distal section of CI; H, distal section of CII (distal section of CIII, CIV, CV, and CVI female is identical). Explanations as for Fig 2.

Boxshall (1991) with the exception of our distal setal group, which is represented by segments XXVII and XXVIII in the 28-segmented adult ancestor. As a result of this alignment, the geniculation on antenna 1 for the male of *R. klausruetzleri* and *Pl. xiphias* occurs between homologous setal groups 20 and 21, as suggested for calanoids by Huys & Boxshall (1991) for their equivalent segments XX and XXI. However, our alignment does not match that suggested by Oberg (1906) for CI–CIV of *Ps. minutus*

Table 1.—For copepodids I–V, VI female (=f) and VI male (=m) [rows] of *Ridgewayia klausruetzleri,* setae are allocated to setal groups [columns]. Minus on the same side of contiguous numbers indicates that there is no or an incomplete arthrodial membrane between contiguous groups (e.g., between setal groups 7 and 11 in copepodid I).

Stage	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
I	3						−1				−1					1					2	0	1	1	3	2	7
II	1		−2				−2	0	1	0	2	0				1			0	1	2	1	1	1	3	2	7
III	1		2		1		2	0	1	0	2	0	1	1	1	2	1	1	1	1	3	1	1	2	3	2	7
IV	2		3	1	2	1	2	1	1	1	2	1	1	3	2	2	2	3	2	2	3	1	1	2	3	2	7
V	2	−1	−3	1	3	2	3	2	3	2	3	2	2	3	2	2	2	3	2	2	3	1	1	2	3	2	7
VIf	2	−2	−3	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	2	2	3	1	1	2	3	2	7
VIm	2	−2	−3	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	2	2	−3	−1	−1	2	3	2	7

for which the four setae on the proximal section of CI are setal groups 9, 11, 16 and 20, and not setal groups 1, 7, 11 and 16 as proposed here (Table 3).

Incomplete arthrodial membranes vary among the stages of *Pl. xiphias* and *Ps. elongatus* studied here. However, in all cases the section of the arthrodial membrane that was present was much thinner than a complete arthrodial membrane, and the sector of the segment in which the arthrodial membrane was absent always included the anterior face. The above hypothesized setal allotments result in a complicated association of setal groups with arthrodial membranes. Early in development, arthrodial membranes are not expressed between setal groups that later in development become separated by arthrodial membranes; e.g., setal groups 7 and 11 at CI, and setal groups 3 and 7 at CII of all three species are not separated by an arthrodial membrane. Development of *Pl. xiphias* is more complicated. There is no arthrodial membrane between setal groups 3 and 7 at CII, but there is an arthrodial membrane between setal groups 1 and 3. At CIII the latter arthrodial membrane is not expressed, but a new arthrodial membrane is expressed between setal groups 3 and 7; thus setal group 3 becomes associated with setal group 1. Failure of arthrodial membrane expression is more common in adult males; e.g., compare adult male and female setal groups 3–4, 14–15, 16–17, 21–22, 22–23 and 24–25 of *Pl. xiphias*; setal groups 21–22 and 22–23 of *R. klausruetzleri*; or setal groups 3–4, 10–11, 11–12, 12–13, 13–14 and 22–23 of *Ps. elongatus*. Among the three calanoids, failure of arthrodial membrane expression proximal to one setal group coupled with a new membrane expression distal to the same setal group during immature copepodid development is found only in *Pl. xiphias*. However, this pattern may explain the phenomenon of setae that appear to jump across article boundaries at molts in other crustaceans (Grygier 1994).

Table 2.—For copepopodids I–V, VI female (=f), and VI male (=m) [rows] of *Pleuromamma xiphias,* setae are allocated to setal groups [columns]. Minus on the same side of contiguous numbers indicates that there is no or an incomplete arthrodial membrane between contiguous groups (e.g., between setal groups 7 and 11 in copepodid I).

Stage	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
I	3						−1				−1					1					2	0	1	1	2	2	7
II	3		−2				2	−0	−1	−0	2	0				1			0	1	2	1	1	2	2	2	7
III	−3		−2		1		2	0	1	0	−2	−0	1	1	1	2	1	1	1	1	3	1	1	2	3	2	7
IV	−4	−1	2	1	2	1	2	1	1	−1	2	1	1	3	2	3	2	3	2	2	3	1	1	2	3	2	7
V	−4	−2	−3	2	3	2	3	2	3	−2	−3	−2	3	3	3	3	3	3	3	3	3	1	1	2	3	2	7
VIf	−4	−3	−3	3	3	3	3	3	3	−3	−3	−3	3	3	3	3	3	3	3	3	3	1	1	2	3	2	7
VIm	−4	−2	−3	−3	4	3	4	3	4	−3	−4	−3	4−	3−	3−	−3	−3	3	2	3	−3	−1	−1	2−	3−	2	7

There is no evidence from the setal development patterns of these three calanoids for a homogenous pattern of setal development for all of the setal groups. The addition of the first seta to a setal group exhibits little variation; an exception is setal group 2 of *R. klausruetzleri* whose first seta appears at CV, rather than CIV as for the other two species (Table 4). However, not all setal groups begin with a single seta and not all setal groups add their second and third seta during contiguous molts. This lack of homogeneity may result from the addition of 16 setal groups during only five copepodid molts, unlike the thoracopods in which up to three setal groups are added during five copepodid molts. Alternatively these groups may not be homogeneous in their development because they are not evolutionarily equivalent; if the ancestral copepod possessed fewer than 27 setal groups, then different sets of setal groups may have been added to antenna 1 at different times during evolution to the calanoids.

Setal groups can be divided into several sets that differ in the number of setae present in each group of the adult male, or the initial condition of the setal group in its earliest copepodid stage, or the developmental pattern of the setal group. We will examine these sets for evidence of a set of setal groups that were added secondarily to the ancestral copepod state as an adaption to the pelagic environment.

There are no quadrithek setal groups on the male antenna 1 of *R. klausruetzleri*, perhaps because these animals spend part of each day in monospecific swarms (Fosshagen 1991, Ferrari 1995), where finding a female receptive to mating may not require searching a significant volume of water. If quadrithek setal groups are an adaption of calanoid males to search for receptive females in significant volumes of pelagic water, quadrithek setal groups may be the extra setal groups of calanoids. We do not consider the first setal group, which bears four setae in both adult males and females of *Pl. xiphias*, to be a true quadrithek. There are

Table 3.—For copepodids I–V, VI female (=f), and VI male (=m) [rows] of *Pseudocalanus elongatus*, setae are allocated to setal groups [columns]. Minus on the same side of contiguous numbers indicates that there is no or an incomplete arthrodial membrane between contiguous groups (e.g., between setal groups 7 and 11 in copepodid I).

Stage	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
I	3						−1				−1					1					2	0	1	1	2	2	7
II	−3		−1				−1	0	1	0	2	0				1			0	1	2	1	1	2	2	2	7
III	−3		−2		−1		2	0	1	−0	−2	0−	1−	−1	−1	2	1	1	1	1	2	1	1	2	2	2	7
IV	−3	−1	−2	−1	2	1	−2	−1	1	−1	−2	1	1	3	1	3	1	1	1	2	2	1	1	2	2	2	7
V	−3	−2	−3	−2	3	2	3	2	2	−1	−3	1	1	3	2	3	1	1	1	2	2	1	1	2	2	2	7
VIf	3	−2	−3	−2	3	2	3	2	2	−1	−3	1	1	3	2	3	1	1	1	2	2	1	1	2	2	2	7
VIm	−3	−3	−3	−3	4	3	4	3	4	−1	−4	−1	−1	−4	2	3	2	2	2	3	2	−1	−1	2	2	2	7

five other setal groups (5, 7, 9, 11, 13) of the male of *Pl. xiphias* that bear four setae including a distinctive flask-shaped aesthetasc peculiar to the males. However, seven other setal groups (2–4, 6, 8, 10, 12) with only three setae also bear a distinctive, male-specific, flask-shaped aesthetasc. Males of *Ps. elongatus* also have five setal groups (5, 7, 9, 11, 14) of four setae, but seven other setal groups (4, 6, 8, 17–20) bearing one more aesthetasc than the female. Differing numbers of quadrithek setal groups and an apparent lack of serial homology of some setal groups bearing quadritheks, or distinctive or extra aesthetascs, suggests that setal groups with these identities are unlikely candidates for the set of extra setal groups of calanoids.

The initial condition of setal groups is variable but we can identify two sets: a set of five groups (8, 10, 12, 19, 22) whose location initially is established by the presence of a proximal and a distal arthrodial membrane before the first seta of that setal group appears; and a set of six setal groups (1, 3, 21, 25, 26, 27) that initially appear with more than one seta. Either of these setal groups are likely to be the extra set of the calanoids.

Setal development patterns also may be used to identify extra setal groups. In the case of adult females, there are setal groups that complete development late (those for which setation becomes complete at CVI or those for which the third seta of the trithek is added at CVI), and setal groups that begin development late (those for which the first seta appears at CIV) (Table 4). While the numbers of setal groups in each of these categories usually differ (Table 5, columns C–E), the setal groups, when present, are always homologous among the three species and are always found among the following set of setal groups: 2, 4, 6, 8, 10, and 12. We believe this set is the best candidate for the set of extra setal groups of calanoids, because development of these six setal groups is initiated and terminated late.

We hypothesize that some of the late de-

Table 4.—Copepodid stages (Arabic numerals) of *Ridgewayia klausruetzleri*, *Pleuromamma xiphias*, and *Pseudocalanus elongatus* at which the 1st, 2nd, and 3rd seta [rows] are added to a setal group [columns].

Seta	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Ridgewayia klausruetzleri																											
1st	1	5	2	4	3	4	1	4	2	4	1	4	3	3	3	1	3	3	3	2	1	2	1	1	1	1	1
2nd	4	6	2	6	4	5	2	5	5	5	2	5	5	4	5	5	5	4	4	4	1			3	1	1	1
3rd			4		5	6	5	6	5	6	5	6	6	4	6	6	6	4			3				1		1
Pleuromamma xiphias																											
1st	1	4	2	4	3	4	1	4	2	4	1	4	3	3	3	1	3	3	3	2	1	2	1	1	1	1	1
2nd	1	5	4	5	4	5	4	5	5	5	2	5	5	4	4	3	4	4	4	4	1			2	1	1	1
3rd	1	6	5	6	5	6	5	6	5	6	5	6	5	4	5	4	5	4	5	5	2				4		1
Pseudocalanus elongatus																											
1st	1	4	2	4	3	4	1	4	2	4	1	4	3	3	3	1	3	3	3	2	1	2	1	1	1	1	1
2nd	1	5	3	5	4	5	2	5	5		2			4	5	3				4	1			2	1	1	1
3rd	1				5		5				5			4		4											1

Table 5.—Numbers of quadrithek setal groups of adult males (A); setal groups of the adult male with more setae than for the adult female (B); setal groups of the adult female in which the setation is completed at CVI (C); setal groups of the adult female with the third seta added at CVI (D); setal groups of the adult female in which the first seta appears at CIV (E).

	A	B	C	D	E
Ridgewayia klausruetzleri	0	0	10	8	5
Pleuromamma xiphias	5	7	6	6	6
Pseudocalanus elongatus	5	7	0	0	6

veloping setal groups are derived from the ectodermal cells of setal groups present during the early development of antenna 1. For the three calanoids studied here, we propose a model of development using five assumptions about which setal groups were likely source groups for later developing progeny groups: the number of source groups should be minimized; source groups usually should be present at CI; a source group may form more than one progeny group during the same molt; the location of a progeny group may be either proximal or distal to the source group; and a progeny group may be located between two arthrodial membranes before a seta appears. The first, third and fourth assumptions follow the segmentation model for harpacticoid copepods of Dahms (1989).

The model for these three calanoids (Fig. 6) includes three source groups (setal groups 3, 7, and 16). Two of them are present at CI (setal groups 7 and 16) and are not juxtaposed. At CI, 11 setal groups are present; group 22 lacks a seta. During the molt to CII, setal group 16 is the source of group 12 proximally and groups 19 and 20 distally; groups 12 and 19 each lack a seta. Setal group 7 is the source of group 3 proximally and groups 8–10 distally; group 3 possesses two setae at its formation and the distal groups 8 and 10 lack a seta. Group 22 has added its first seta. During the molt to CIII, setal group 16 is the source of groups 13–15 proximally and groups 17 and 18 distally; all have a seta and the first

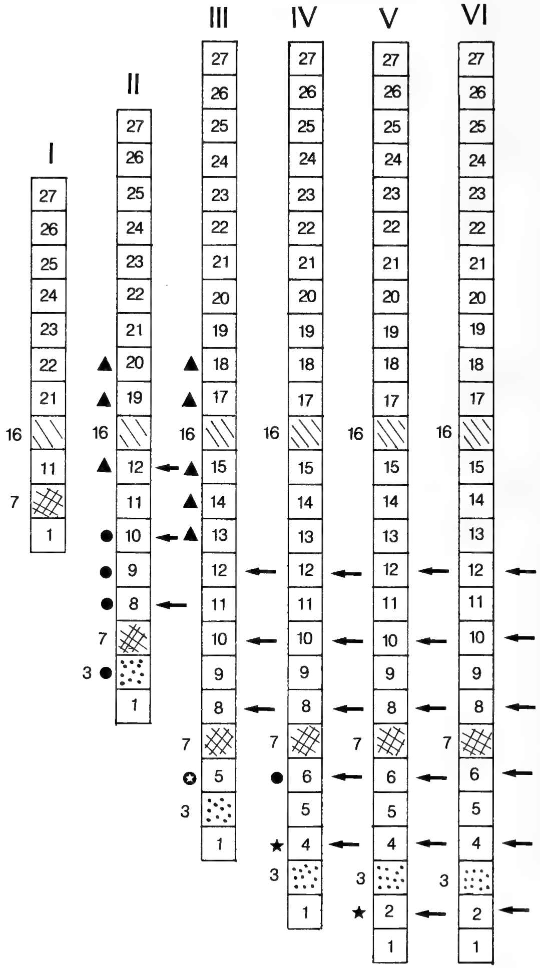

Fig. 6. Illustrated model of addition of setal groups to antenna 1 for CI–CVI (I–VI) of *Ridgewayia klausruetzleri*, *Pleuromamma xiphias*, and *Pseudocalanus elongatus*. Horizontal lines arbitrarily delimit setal groups (which are numbered) but do not necessarily indicate the location of arthrodial membranes; source group 16 is hatched; source group 7 is cross-hatched; source group 3 is stippled; triangles are to left of progeny of source group 16; circles are left of progeny of source group 7; stars are left of progeny of source group 3; setal group 5 (star in circle) may be a progeny of source group 7 or source group 3; arrows are to right of the preferred candidate set of extra, derived setal groups of calanoids, relative to an approximately 20-segmented state for the ancestral copepod.

seta of group 19 is added. Setal group 7 or setal group 3 may be the source of group 5, which has a seta. During the molt to CIV, setal group 16 is not active, but of its progeny, group 12 has added its first seta. Setal group 7 is the source of group 6, proximally, with its seta; of its earlier distal progeny, groups 8 and 10 each have added a first seta. During the molt to CV, setal group 3 is the source of setal group 2 proximally with its seta; setal group 3 is the only secondary source group formed from another source group (setal group 7).

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Haemopis caeca (Annelida: Hirudinea: Arhynchobdellida: Haemopidae), a new species of troglobitic leech from a chemoautotrophically based groundwater ecosystem in Romania

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Abstract.—A new species of leech, *Haemopis caeca*, is described from a unique chemoautotrophically based groundwater ecosystem, in southern Dobruja, Romania, containing thermomineral H_2S rich water. Fifty invertebrate species have been identified from the cave, 33 of which are endemic species. *Haemopis caeca* is the second species in the genus recorded from Europe, and the other Palearctic Region is *H. sanguisuga*. *Haemopis caeca*, a cave adapted species, was observed exhibiting macrophagous feeding on the earthworm, *Allolobophora* sp., an undescribed species.

The new species, *Haemopis caeca*, belongs to the Order Arhynchobdellida Blanchard 1894; Family Haemopidae Richardson 1969, Sawyer 1986b. The genus *Haemopis* Savigny 1822 contains nine recognized species of which eight are endemic to the Nearctic Region (Richardson 1969, Soos 1969, Klemm 1985, Sawyer 1986b, Davies 1991). The species are *H. caballeroi* (Richardson 1971), *H. grandis* (Verrill 1874), *H. kingi* Mathers 1954, *H. lateromaculata* Mathers 1963, *H. marmorata* (Say 1824), *H. plumbea* Moore 1912, *H. septagon* Sawyer & Shelley 1976, and *H. terrestris* (Forbes 1890). Until now, the type species, *H. sanguisuga* (Linnaeus 1758), has been the only species of *Haemopis* reported to occur in the Palearctic Region (Mann 1961, Soos 1970). However, *H. sanguisuga* has been reported from the Sino-Japanese Region of the Amur River Basin, in eastern Siberia, (Lukin 1955).

The three genera of Arhynchobdellida reported from Europe, *Hirudo* Linnaeus 1758; *Haemopis* Savigny 1822; and *Limnatis* Moquin-Tandon 1826, are also present in Romania (Cristea & Manoleli 1977, Manoleli 1972, 1974, Ruckert 1985, Soos 1969). However, none of these genera has been reported specifically in caves. The Natural History Museum of Oradea, Romania contains three specimens of *H. sanguisuga*, which were collected in 1892 in the Western Carpathians (Apuseni Mountains). The label mentions "cave habitat" with no further details. Scriban & Autrum (1934) examined the three specimens and found five pairs of eyes, and they all resembled morphologically the classic description of the (type) species, *H. sanguisuga*.

Materials and Methods

Fifteen leeches were collected by hand from the shoreline or near shoreline (0–20 cm) of the sulfidic lake in Movile Cave, southern Romania (location in Sarbu 1996, Sarbu & Kane 1995). Nine specimens were observed while alive in the field and laboratory. Leeches to be preserved were first anesthetized by adding 70% ethanol slowly to a small amount of water containing the specimens until they no longer responded to stimulation. They were then preserved in either 70% ethyl alcohol or fixed overnight in 10% formalin and later stored in 70% alcohol. All drawings were made using either a IOR-MC1 dissecting microscope or a Zeiss Stemi SV6 dissecting microscope.

Systematics

Family Haemopidae Richardson, 1969; (Sawyer 1986b, revised)

Genus *Haemopis* Savigny, 1822

Haemopis caeca, new species

Type material.—Holotype, deposited in the Muzeul de Istorie Naturala Bucuresti (MINB-49.999), Bucharest, Romania, and 2 representative paratypes (MINB-50.000), (collected 15 Jun 1992, sulfidic lake in Movile Cave, collector Serban M. Sarbu). Three additional paratypes, United States National Museum (USNM 178821), deposited in the National Museum of Natural History, Division of Worms, Smithsonian Institution, Washington, D.C.), collected 18 Jun 1996, sulfidic lake in Movile Cave, collector Serban M. Sarbu; 1 specimen, collected 20 Dec 1991, same locality, collector and collection Serban M. Sarbu; and 9 Oct 1994; 18 Jun 1996, same locality, collector Serban M. Sarbu, five specimens in the collection of Donald J. Klemm.

Type locality.—Movile Cave, southern Dobrogea, Romania.

Diagnosis.—without body pigment and eyes; body firm and muscular; annuli VIIa3 and VIIIa1 not subdivided ventrally; 25 annuli from oral cavity to annulus XIa2 bearing the male gonopore. Gonopores separated by 4 ½ annuli; jaws absent or vestigial (agnathous), denticles (teeth) absent; entrance to mouth and lumen of pharynx not strongly reduced; pharynx with 12 internal ridges; testisac 8–10 pairs (8 in holotype); anterior edge of prostate at XII; penis sheath long, extends back to annuli XIIa2; penis has knot in its proximal end; vagina shaped like a bagpipe, proximal portion is thin; vaginal duct connects to the vagina subapically; vaginal duct exhibits a bifid shape in profile view; anus small, not prominent; macrophagous feeding (predaceous carnivore and scavenger); aquatic to semiaquatic (amphibious).

Description of Holotype (Fig. 1B–E)

External anatomy (Fig. 1A, B).—Body firm, muscular (living and preserved), size medium, never large, body elongate, slender; length 50–63 mm, body-width 5–6 mm, depth 2–3 mm, body smooth, very contractile; the central portion with parallel or nearly parallel margins, usually terete anteriorly, pigment absent. Epidermis, transparent, and lacking chromatophores. Live animals red-brownish due to visible vascularization of muscle tissue. Annuli VIIa3 and VIIIa1 slightly enlarged, and faintly subdivided or not divided at all; 25 distinct annuli from oral cavity to annulus XIa2, bearing male gonopore; male and female gonopores separated by 4 ½ annuli. Anterior rim of mouth lip-like; one paratype exhibited a slight "emarginate" of the prostomium (Fig. 1A) and slight pigmentation strictly limited to this "emarginate," other paratypes mouth more lip-like. Eyes absent in living and preserved specimens. Segment annuli I = 1, II = 1, II = 1, IV = 2, V = 2, VI = 3, VII = 3, VIII = 4, IX–XXIII-5, XXIV = 3, XXV = 2, XXVI = 1, XXVII = 2. Anus small, not prominent on segment XXVII with no post-anal annuli; caudal sucker circular (width 3–4 mm), broadly and centrally attached to posterior end of body; nephridiopores 17, located paramedially on posterior portion of b2 annulus from segment VIII to XXIV; body with 15 complete (five annulate) segments from IX to XXIV; male genital pore located on segment XIa2; female genital pore lo-

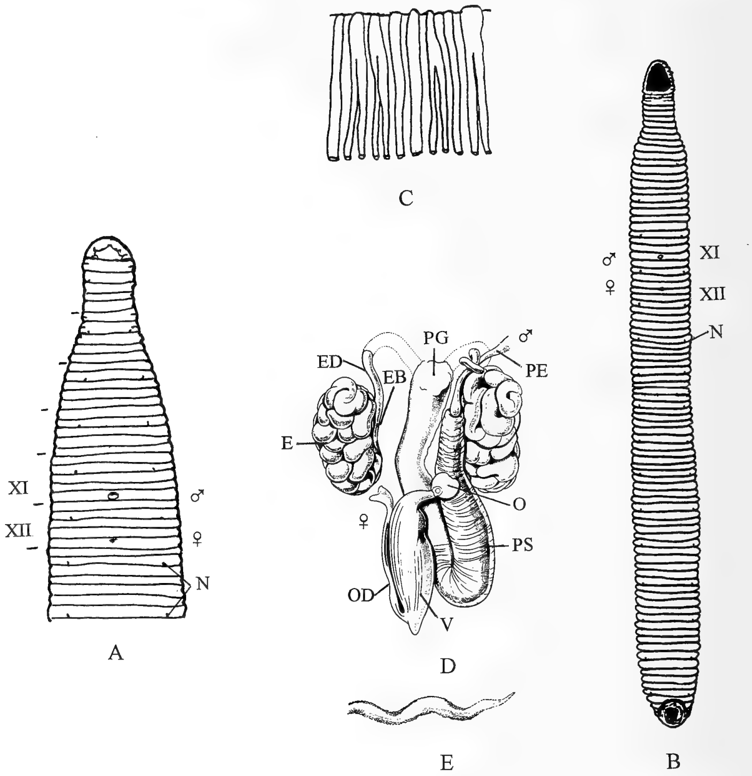

Fig. 1. *Haemopis caeca.* A, Ventral view: Annuli VIIa3 and VIIIa1 not subdivided, 25 distinct annuli from oral cavity to segment XIa2, bearing the male gonopore; and male and female gonopores separated by 4 ½ annuli; B, Ventral view of *Haemopis caeca*; C, Pharynx, opened the mid-ventral line; D, Dorsal view of male and female reproduction systems; E, Distal end of the penis. Abbreviations: N, nephridiopore; Segments XI and XII; E, epididymis; EB, ejaculatory bulb; ED, ejaculatory duct; O, ovary; OD, oviduct; PG, prostate gland; PE, Penis; PS, penis sheath; V, vagina.

cated on segment XIIb2/a2; penis when fully extended, moderately long, small diameter (filamentous) proximal end, and distal end with a corkscrew-like tip (Fig. 1E).

Internal anatomy, male genitalia (Fig. 1D).—Epididymis occupying the space between the two genital pores; ejaculatory ducts short; sheath of penis extends back reaching segment XIVb1; penis has a knot in its proximal end; testisacs 8–10 pairs. Female genitalia (Fig. 1D).—vagina has shape of a bagpipe; proximal portion of vagina is thin; vaginal oviduct connects to vagina subapically; proximal end of oviduct exhibits a bifid-shape in profile view. Digestive system.—pharynx euthylaematous, without jaws (agnathous) and denticles, no salivary papillae; wall of pharynx intimately associated with muscles of body-wall; entrance to, and lumen of pharynx unrestricted with some 12 internal ridges, with four single ridges and four paired ridges, all terminating on the margin of the entrance to the pharynx (Fig. 1C); pharynx ending at X; crop tubular acaecate, thin wall, elongate posterior crop caeca extending from XIX to XXIV; medium intertine, extending from XIX to XXIX; rectum, extending from XXIII to anus; anus small, not prominent.

Additional observations of paratypes.—The paratypes agree with the holotype externally and internally except for the "emarginate" of the prostomium (Fig. 1A) in a few specimens (this may be due to preservation); none of the specimens examined have eyes and all specimens have the same number of annuli between gonopores, 4 ½ annuli.

Remarks.—The structure of the reproductive system shows that this species belongs to the genus *Haemopis.*

Habitat and ecology.—A unique chemoautotrophically based groundwater ecosystem was discovered in Movile Cave, at Mangalia, Dobrogea, Romania, near the Black Sea (Sarbu and Kane 1995). The cave was opened by an artificial shaft in 1986, and it represents a window to a vast network of fissures and cave passages of phreatic origin, associated with the thermomineral sulfidic waters present in the Mangalia region (Constantinescu 1989, Lascu 1989, Sarbu & Kane 1995). The lower level of the cave is flooded by mesothermal waters (21°C) with a high content of H_2S (0.3 mMol/L).

The cave contains rich aquatic and terrestrial troglobitic invertebrate communities (Lascu et al. 1993, Sarbu & Kane 1995). Thirty-three new invertebrate species, including *H. caeca*, have been discovered so far, and other discoveries are expected (Decu et al. 1994, Gruia et al. 1994, Weiss & Sarbu 1994). The food base of both the aquatic and terrestrial communities is produced *in situ* by a rich chemoautotrophic microbiota. These microbiota fix the carbon using the energy that results from the oxidation of H_2S at the surface of the water in the cave in aerobic conditions (Sarbu & Kane 1995). The Movile Cave ecosystem appears to be the first known subterranean ecosystem existing independently of the photoautotrophic carbon fixation in green plants at the surface. The cave ecosystem relies entirely on the *in situ* chemoautotrophically produced food base (Sarbu & Kane 1995, Sarbu et al. 1996).

Haemopis caeca and another recently described endemic species, *Nepa anophthalma* (Decu et al. 1994), (Heteroptera: Nepidae), are the only known predators in the aquatic and semi-aquatic community and are thus far the largest animals found inhabiting the cave (Decu et al. 1994). Fifteen *H. cacea* have been observed above the shoreline displaying macrophagous feeding on earthworms (*Allolobophora* sp., an undescribed species). This aquatic and semiaquatic leech was also observed in the cave creeping along the shores of the sufidic lake. Specimens of the leech have often been seen swimming in the sufidic lake, always in shallow water (0–15 cm deep).

Discussion

The genus *Haemopis* was subdivided in North America by Richardson (1969, 1971) into three genera, *Percymoorensis*, *Mollibdella*, and *Bdellarogatis*. The revision was followed by Soos (1969) Davies (1971, 1991), and Klemm (1972). Sawyer (1972, 1986b, 1986c) and Sawyer & Shelley (1976) rejected this revision based on additional anatomical information and the description of a new species, *Haemopis. septagon* (Sawyer & Shelley 1976). Klemm (1977, 1982, 1985, 1990) later also followed their recommendations for the genus *Haemopis*, which are followed by the authors of this paper.

The absence of eyes, body pigment, jaws, and denticles are four characteristics that distinguish *H. caeca* from *H. sanguisuga*, the only other Palearctic Region species of the genus (Sawyer 1986b, Soos 1969). The anatomical examination of the two closely related Palearctic Region species reveals specific differences between *H. caeca*, the subterranean form, and the surface form of *H. sanguisuga*: the absence of eyes, epidermal chromatophores, jaws, and teeth; separation of the gonopores by 4 ½ annuli (*H. caeca*) rather than by 5–5 ½ annuli (*H. sanguisuga*). The male pore is located on XIa2 rather than XIb6, while the female pore is located on XIIb2/a2 rather than XIIb6. The body color of *H. caeca* is red-brownish dorsally and ventrally, but in *H. sanguisuga* the dorsal color varies from dark grey-green, to pale yellow-green, to almost black, and paler ventrally, with variable amounts of black flecking. The anus is small, less prominent in *H. caeca*, but is very conspicuous in *H. sanguisuga*. The examination of the paleogeographic data regarding the Mangalia region indicates that *H. caeca* may have been isolated underground for a considerable period of time, suggesting that the characteristics found in this stygobiotic species are genetically determined. All specimens of *H. caeca*, living and preserved, that have been examined thus far were found with eyes absent. All the other nine species of *Haemopis*, including *H. sanguisuga*, have five pairs of eyes, and they have never been reported in the literature without eyes or variable number of eyes when collected and studied. All specimens of *H. caeca* examined internally were found with jaws and denticles absent. Seven species of *Haemopis* possess low and rounded jaws with two distinct rows of large, course, blunt distichodont denticles, and the distichous denticles vary in numbers from 9–25. The other two Nearctic Region *Haemopis* species, *H. grandis* (Verrill 1874) and *H. plumbea* Moore 1912, have vestigial or absent jaws and denticles. The total length of all *H. caeca* collected so far are also shorter (80–83 mm) and thinner (5–9 mm) than *H. sanguisuga*. The pharynx and related structures are haemopisoid but are less prominent than in *H. sanguisuga*. Also, Segment VI and Segment VII have three annuli each in *H. caeca*, but in *H. sanguisuga* Segment VI has three annuli and Segment VII has four.

Turquin (1984) stated that several species belonging to the Order Arhynchobdellida and the Family Haemopidae may exhibit a certain degree of troglophylly and can be found in dark places such as sewage systems where they seem to be attracted by the abundance of food such as aquatic worms and insect larvae. However, none of these troglophilic invertebrate populations exhibit any morphological modifications compared to the populations living in surface waters. Agtelek Cave in Hungary is inhabited by *Typhlobdella kavatsi* Deising 1850 (a junior synonym of *H. sanguisuga*), which exhibits all of the external characteristics found in *H. sanguisuga* (Lukin 1976, Soos 1969). Peck (1988) reported *H. terrestris* (Nearctic Region) from mines in Ontario, Canada. *Haemopis terrestris* occurs in North America in two forms, either found living in freshwater or living in semi-aquatic to moist terrestrial habitats (Miller 1929, Klemm 1985, Sawyer 1986b).

In Erpobdellidae, a different family of leeches, Sawyer (1986a) reported that most troglophilic leech species (e.g., *Trocheta bykowskii* Gedroyc (1915), of southeastern Europe), reported in caves and other subterranean habitats, are only migrants from outside the cave area and are indistinguishable from the surface-dwelling forms. However, Sawyer (1986a) stated that some truly cave-adapted aquatic erpobdellid species and closely related forms of uncertain taxonomic standing of *Dina lineata* (Muller 1774) live in caves in southern Europe and southwest Asia. For example, *D. absoloni* Johansson (1913), an unpigmented species, lives in caves of Yugoslavia and Bulgaria, and the subspecies, *D. absoloni ratschaensis* Kobakhidze (1958), lives in caves of western Georgian. Soos (1966) reported that a few truly unpigmented cave dwelling forms of *D. absoloni* have been reported from Yugoslavia and Bulgaria with and without pigmented eyes and the integument unpigmented.

Haemopis caeca, discovered in the Movile Cave and collected later from a sulfidic spring in the same aquifer, about 4 km north of the cave, appears to be the only truly known cave-adapted species of *Haemopis* (Family Haemopidae). The spring also contains other blind and unpigmented troglobitic animals, such as *Asellus aquaticus* (Isopoda: Asellidae); *Niphargus* sp., an undescribed species, and *Pontoniphargus racovitzai* (Amphipoda: Gammaridae). All of these species also are present in Movile Cave.

Etymology.—From the Latin adjective *Caecus*, *—a*, *—um* meaning blind.

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Description of *Eunice weintraubi* and *E. wui*, two new species of eunicid polychaetes from northern Gulf of Mexico

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Abstract.—*Eunice weintraubi* and *Eunice wui* are described from shallow waters of the Gulf of Mexico and variability of morphological characters is discussed. Because large numbers of specimens are available, some features of the ontogeny of *Eunice wui* are also noted. The morphological characters of two related species, *Eunice fauchaldi* and *Eunice multicylindri* are compared to each other and to *Eunice wui.*

Eunicid polychaetes from the Gulf of Mexico were studied by Gathof (1984) based on benthic surveys off Florida, Louisiana and Texas. The specimens from these surveys and other, similar surveys were deposited in the Smithsonian Institution. A study intended to verify the accuracy of identifications showed that many of the previous identifications were inaccurate at the species level. The specimens here studied were in part those reported by Gathof (1984), but much of the material has never before been reported in a systematic study.

The morphological terminology was defined in Fauchald (1992) except for interpretation of the prostomial appendages. Traditionally these have been considered as one to five occipital antennae; terms such as outer lateral, inner lateral and median antennae have been used (Fauchald 1992 used the abbreviations AI-AIII) for the antennae, and other terms may be found in the literature (Fauvel 1923, Hartman 1944). Orrhage (1995), based on innervation, demonstrated that the outer lateral antennae (=AI) are homologous with palps in other polychaetes. Consequently, the eunicids have three antennae: a median antenna and paired lateral antennae. Orrhage also suggested that the so-called frontal antennae (Fauchald 1982a) or frontal palps (Paxton 1986) of onuphids are paired dorsal lips. This finding has consequences for our understanding of the eunicid prostomium. The anterior end of the head in eunicids is usually notched or bifid. Positionally, this notch corresponds to the cleft between the dorsal lips of the onuphids. If the cleft portion of the eunicid head corresponds to the onuphid dorsal lips, the position of the antennae can no longer be considered occipital. Instead the eunicid antennae become located in much the same position as in other polychaetes (e.g., hesionids, syllids and scale-worms). The eunicid prostomial appendages are here renamed to include a median and paired lateral antennae and a pair of palps usually found lateral to and in front of the lateral antennae.

All the specimens were observed under stereo and compound light microscopes; sketches for the illustrations were made using camera lucida.

Eunice weintraubi, new species
Figs. 1a–h, 2

Materials examined.—Holotype: USNM 090037, off Panama City, Florida, MAFLA, 37 m, STA V-2528, 29°54′59″N, 86°04′59″W, Feb. 1978. Paratype: USNM 090037 (*n* = 1, STA v-2528); USNM 090039 (*n* = 3, STA 2528).

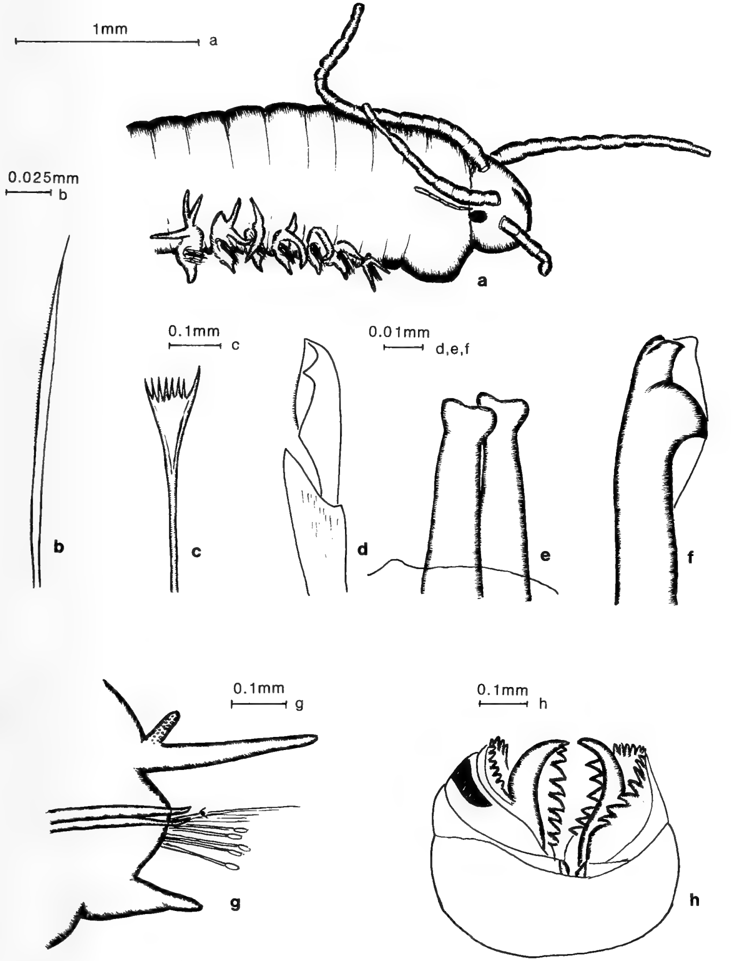

Fig. 1. *Eunice weintraubi*, new species: a, anterior end (Paratype USNM 090039), lateral view; b, limbate chaeta; c, pectinate chaeta; d, compound falciger; e, hammer-headed aciculae, 30th chaetiger; f. subacicular hook, 25th parapodia; g, 25th parapodium, anterior view; h, maxillae (Paratype USNM 090039).

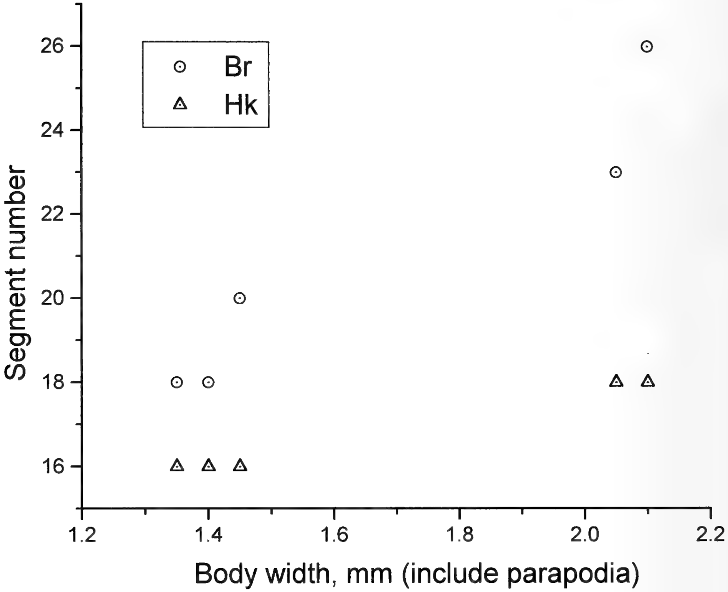

Fig. 2. The size-dependent variation of the ending position of chaetiger with branchiae (Br) and the start position of subacicular hook (Hk) in type specimens of *Eunice weintraubi*, new species.

Description.—The holotype (Fig. 1a) is a complete specimen with 74 chaetigers, the total length is 13.5 mm; the first 10 chaetigers measure 1.8 mm in length, the widest part measures 1.6 mm without parapodia (2.1 mm with parapodia). As preserved, the specimen is pale without distinct color patterns.

Distal end of prostomium clearly notched (i.e., a sulcus present, but very short). Prostomium shorter and narrower than peristomium, a little less than half the length of peristomium. One pair large black eyes situated outside lateral antennae behind the palps. Palps and antennae evenly spaced. Palps a little thinner than antennae. Styles of antennae and palps with moniliform articulations that become drop-shaped distally. Palpostyles have four articulations and palps reach first chaetiger. Lateral antennae with ten articulations and reaching third chaetiger. Median antenna with 14 articulations, it reaching chaetiger 6. Anterior ring of peristomium about $4/5$ total length of peristomium; separation between first and second ring is clear dorsally and ventrally. Peristomial cirri with several articulations, reaching posterior end of prostomium.

Anterior notopodial cirri finger-shaped, always longer than ventral cirri, with indistinct articulations. First two pairs of ventral cirri slender; ventral cirri with ovate base from third parapodium to middle region of the body, becoming digiti-form toward the posterior.

Branchiae first appear from fourth chaetiger; end on chaetiger 26. Where best developed, around chaetiger 10, pectinate branchiae with four filaments, first and last several (Fig. 1g) branchiae with single filament. Both branchiae and individual filament shorter than notopodial cirri.

Limbate chaetae (Fig. 1b) marginally serrated. Pectinate setae (Fig. 1c) with 6–9 teeth, one outer tooth slightly longer than other teeth. Compound falcigers (Fig. 1d) with two teeth; distal tooth strongly curved and pointing in same direction as proximal tooth. Proximal tooth slightly larger than distal one. Guards lack mucros, but distally asymmetrically bluntly pointed and basally serrated. Shafts of compound falcigers marginally serrated, with a distinct core. Pseudocompound falcigers and compound spinigers absent. Neuropodia usually with two yellow aciculae; they blunt-tipped anteriorly, becoming hammer-headed (Fig. 1e) from about chaetiger 20, becoming blunt-tipped or pointed in last few chaetigers. Subacicular hooks (Fig. 1f) present from chaetiger 18; always single, yellow and tridentate with distinct hoods. The teeth form a crest and increase in size from distal tooth to proximal tooth.

Two pairs of anal cirri present; dorsal pair long and finger-shaped and as long as last seven chaetigers; ventral pair only ⅛ length of dorsal pair.

Maxillae not examined in holotype; in paratype (USNM 090039, fig. 1h), maxillae formula: 1 + 1, 8 + 6, 7 + 0, 11 + 8, 1 + 1.

Variation of morphological characters (Fig. 2).—In all five specimens examined, the starting position of the branchiae is always chaetiger 4; but the ending position appears size-dependent, varying from chaetiger 18 to 26. The maximum number of branchial filaments is three or four. The first occurrence of subacicular hooks also appears size-dependent, starting from chaetiger 16 in a 1.4 mm-wide (at the widest part, including parapodia,) specimen to chaetiger 18 in a 2.1 mm-wide specimen.

Discussion.—The specimens of *E. weintraubi* studied by Gathof (1984) were identified as *Eunice antennata*. According to the revision of the genus *Eunice* by Fauchald (1992), these specimens differ from *E. antennata* in the following characters: Branchiae are present from chaetiger 4 in *E. weintraubi* and not until chaetiger 7 in *E. antennata*; they are present on less than half of the total chaetigers in *E. weintraubi* and are present to near the posterior end in *E. antennata*. Furthermore, the limbate setae are marginally serrated in *E. weintraubi*, rather than smooth as in *E. antennata*.

Eunice weintraubi resembles *Eunice papeetensis* Chamberlin from Tahiti and *Eunice pellucida* Kinberg from the West Indies. It differs from *E. papeetensis* in that it has pectinate branchiae; in *E. papeetensis* the branchiae are palmate. *E. weintraubi* has branchiae from chaetiger 4; *E. papeetensis* has branchiae from chaetiger 6. *Eunice weintraubi* differs from *E. pellucida* in that eyes are present rather than absent. Branchiae always appear from chaetiger 4 in *E. weintraubi* rather than from chaetigers 5–6 as in *E. pellucida*. The maximum number of branchial filaments is only four in *E. weintraubi*, rather than eight as in *E. pellucida*, in similarly sized specimens. Finally, the median antennal style has up to 30 rings in *E. pellucida* and only 14 in *E. weintraubi*.

Etymology.—The species is named for the late Dr. Robert Weintraub, former Professor of Zoology, George Washington University, for his contribution to systematic zoology.

Eunice wui, new species
Figs. 3a–h, 4–6

Materials examined.—Holotype: USNM 129729, off Florida, Gulf of Mexico, SOFLA, 14 m, STA 52, 25°17′48″N, 81°39′48″W, 10 Dec. 1982. Paratypes: Gulf of Mexico, off Florida, SOFLA : USNM 090032 (*n* = 8, 24 m, STA 2), USNM 112103 (*n* = 2, 16 m, STA 43), USNM 129729 (*n* = 32, 14 m, STA 52), USNM 129777 (*n* = 40, 14 m, STA 52), USNM 130071 (*n* = 17, 14 m, STA 52), USNM 130126 (*n* = 5, 14 m,

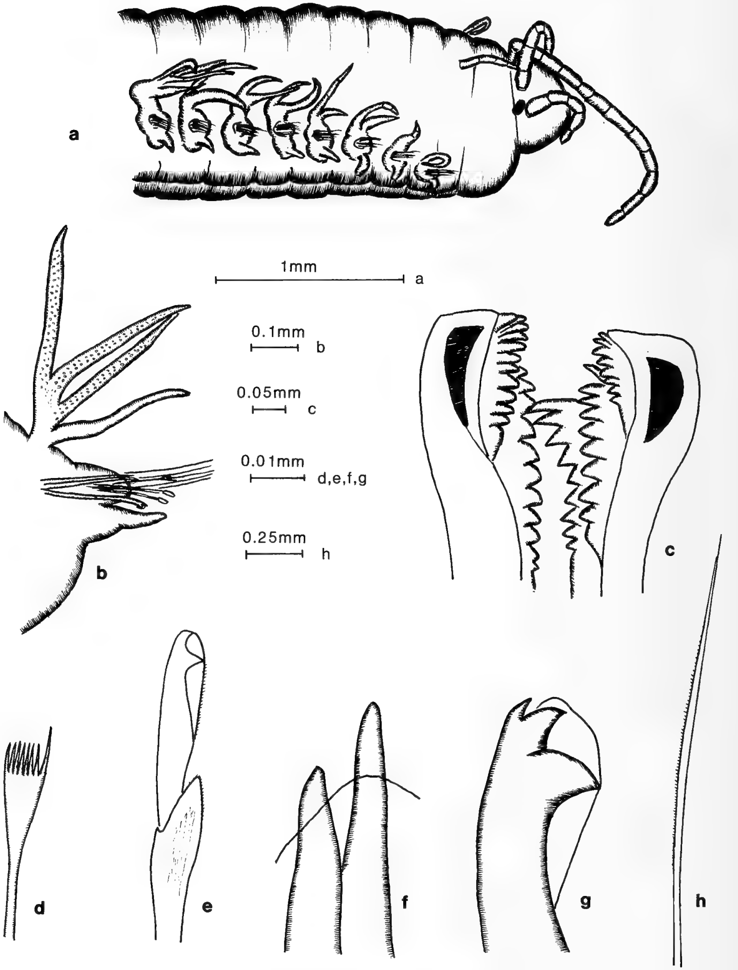

Fig. 3. *Eunice wui*, new species: a, anterior end (Paratype USNM 129729), lateral view. b, 32rd parapodium, anterior view; c. limbate chaeta; d, pectinate chaeta; e, compound falciger; f, aciculae; g, subacicular hook, 32rd parapodium; h, maxillae, (paratype USNM 129729).

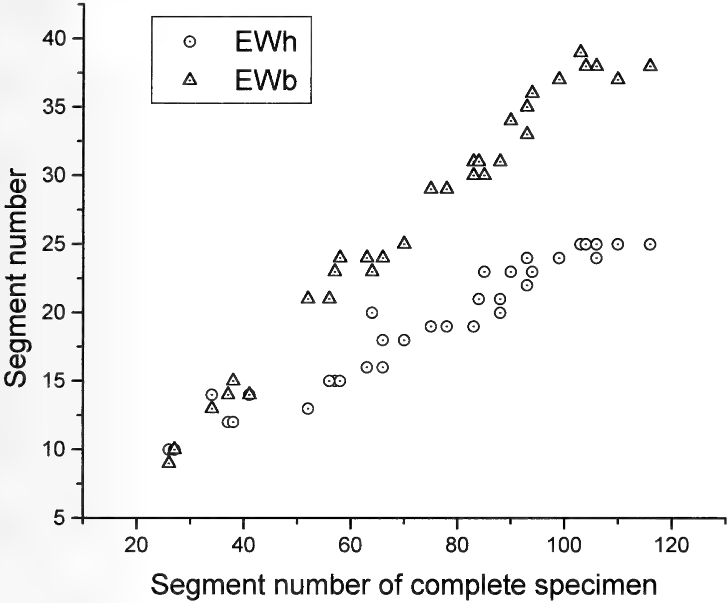

Fig. 4. Relationships between the first occurrence of the subacicular hook (EWh), the ending position of the branchiaed chaetiger (EWb) and the number of chaetigers in *Eunice wui*.

STA 52), USNM 130185 (*n* = 1, 14 m, STA 52), USNM 130254 (*n* = 5 14 m, STA 52), USNM 130330 (*n* = 21, 14 m, STA 52), USNM 130424 (*n* = 3, 14 m, STA 52), USNM 130515 (*n* = 5, 14 m, STA 52), USNM 130551 (*n* = 11, 10 m, STA 50; Gulf of Mexico, Texas, Southern Bank, STOCS: USNM 090033 (*n* = 1, 82 m, STA SB3, 27°26′06″N, 096°31′47″W, Dec. 1976), USNM 090034 (*n* = 1, 75 m, STA HR1), USNM 090035 (*n* = 1, 75 m, STA HR1), USNM 090036 (*n* = 6, 75 m, STA HR1).

Description.—Holotype specimen (Fig. 3a) complete, with 110 chaetigers, tapering abruptly from the posterior part. Length is about 25 mm; first ten chaetigers 2.3 mm; widest part 1.1 mm without parapodia (1.8 mm with parapodia).

Prostomium anteriorly rounded; median sulcus very shallow dorsally but forming a deep groove on ventral side. Prostomium slightly narrower than peristomium, about same length and about ½ depth of peristomium; small specimens with relatively thicker prostomia. One pair eyes present behind palps. Palps and antennae similar in thickness; palps and lateral antennae slightly closer to each other than lateral antennae are to median antenna. All styles with cylindrical rings. Palps with six rings and reaching middle of second peristomial ring. Lateral antennae with nine rings and reaching posterior end of chaetiger 4. Median an-

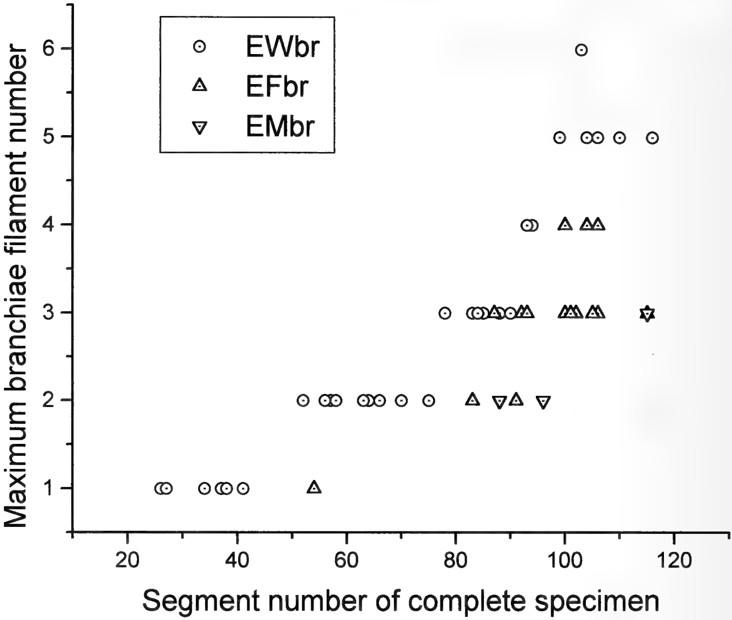

Fig. 5. Relationships between the maximum number of branchiae filament number and the number of chaetigers for *Eunice wui*, new species (EWbr), *E. fauchaldi* (EFbr) and *E. multicylindri* (EMbr).

tenna with 11 rings and reaching chaetiger 7. First peristomial ring is approximately ⅔ total length of peristomium. Peristomial cirri small, with about six articulations and reaching middle of prostomium.

Dorsal cirri long digiti-form, always longer than ventral cirri; become slender in posterior end of body. Anterior dorsal cirri with irregular articulations. Ventral cirri with ovate inflated bases in anterior-median parapodia; inflated bases decreasing in size from about chaetiger 30 (Fig. 3b). Ventral cirri digiti-form posteriorly.

Branchiae begin on chaetiger 3, end at chaetiger 38. First four and last branchiated chaetigers with only one filament, all other branchiae with at least two filaments and a maximum of five filaments in a pectinate arrangement from chaetigers 14 to 23. Branchiae present on approximately ⅓ of total number of chaetigers. Most branchiae (stem + filament) slightly longer than dorsal cirri except on first several and last few branchiated chaetigers.

Limbate chaetae (Fig. 3c) marginally serrated. Pectinate chaetae (Fig. 3d) with one lateral tooth much longer and thicker than other teeth; number of teeth varies from 5–8. Compound chaetae (Fig. 3e) yellow and bidentate; guards with short bluntly pointed heads and basally serrated, lacking mucros; edge of shaft also serrated. Pseudocompound falciger and compound spiniger absent. Aciculum (Fig. 3f) always paired; distally bluntly pointed, some with a pointed sheath. Subacicular hooks (Fig. 3g) start in

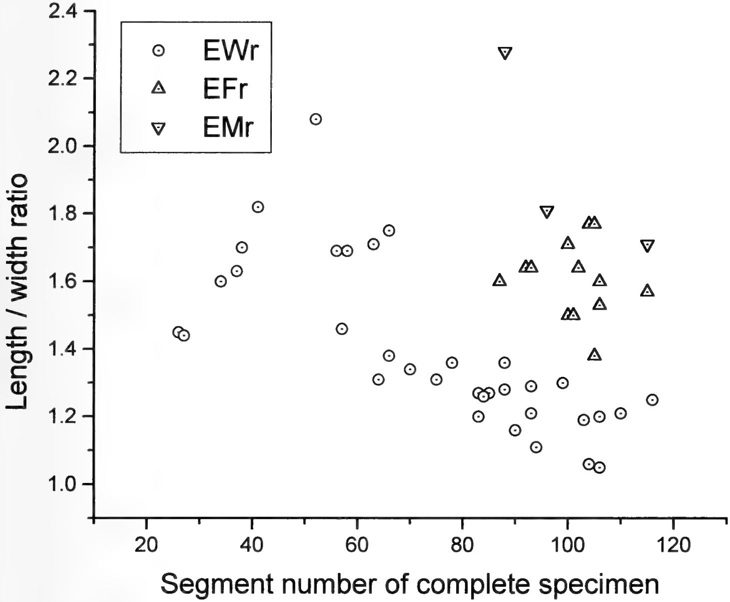

Fig. 6. Relationships between the Length/Width ratio and the number of chaetigers in *Eunice wui* new species (EWr), *E. fauchaldi* (EFr) and *E. multicylindri* (EMr).

chaetiger 25; yellow and tridentate; teeth in a crest increasing in size from distal to proximal tooth. Subacicular hooks always single except where replacement hooks have formed; stouter than aciculae.

Two pairs anal cirri present; larger dorsal pair is as long as last five chaetigers, ventral pair only ⅓ length of dorsal one.

Maxillae not examined in holotype; maxillae of paratype (USNM 129729, Fig. 3h) poorly sclerotinized, nearly transparent; with formula: 1 + 1, 11 + 9, 0 + 8, 11 + 9, 1 + 1.

Variation in morphological characters.—168 specimens examined, with 36 of these complete, including both juveniles and adults. It is thus possible to delimit certain ontogenetic patterns. These patterns include the following:

Palps: In USNM 129777, there are two complete juveniles with 26 and 27 chaetigers respectively; both of these have three antennae but lack palps. In the same lot, there are two complete specimens, with 37 and 38 chaetigers respectively, in which the palps are present. Similarly, in USNM 129972 a 34-chaetiger specimen has the three antennae and the palps. Consequently, it appears that palps of *E. wui* do not emerge until they have reached more than 27, but fewer than 34 chaetigers.

Peristomial cirri: Specimens with 26 and 27 chaetigers (USNM 129777) lack peristomial cirri; a pair of very short cirri is present in specimens with 34, 37 and 38 chaetigers. The development of the peristomial cirri appears to be simultaneous with that of the palps. The length of the cirri varies from a small protuberance in specimens with less than 34 chaetigers, to reaching the first peristomial ring in specimens with 65 chaetigers, while reaching the middle of the prostomium in specimens with more than 100 chaetigers.

Eyes: Eyes are present in all specimens, but change in color from light red in juveniles to black in large specimens.

Branchial pattern: Branchiae are always present from the third chaetiger independent of the size of the specimen. The numbers of pairs of branchiae and the maximum number of filaments are size-dependent (Figs. 4, 5). For example, in a 26-chaetiger juvenile, branchiae are present in chaetigers 3 through 9, all having only a single filament; on the other hand, in a 116-chaetiger specimen, branchiae are present from chaetigers 3 through 39, with a maximum of five filaments. Usually, *E. wui* has a maximum of two branchial filaments by the time they reach 50 chaetigers, a maximum of three filaments at about 75–80 chaetigers, a maximum of four filaments at 90 chaetigers, and a maximum of five or even six filaments when they reach 100 chaetigers.

Subacicular hooks: Subacicular hooks are always single, yellow and tridentate. The starting position (Fig. 4) is size-dependent. They appear from chaetiger 10 in a 26-chaetiger juvenile, but from chaetiger 25 in a 116-chaetiger adult.

From Figs. 4 & 5, the approximate total chaetiger number of an incomplete specimen can be estimated either by the numbers of pairs of branchiae or the starting position of subacicular hooks, or by a combined estimate using the above factors.

Length/width ratio: From Fig. 6, it is obvious that the length/width ratio of *E. wui* changes during its development. The ratio increases with the increasing number of chaetigers, it reaches a peak for a 50-chaetiger specimen. From there the ratio decreases steadily as more chaetigers are added. For example, the length ratio is about 1.45 for a 26-chaetiger specimen, 2.08 for a 51-chaetiger specimen, and 1.25 for a 116 chaetiger one. Thus, before a specimen of *E. wui* reaches 50 chaetigers, its length increases relatively faster than the width; thereafter, its width increases relatively faster than the length.

Based on the information about variation in morphological patterns, we believe it may be useful to recognize three stages:

Early juvenile stage, from metatrochophore stage until the juveniles reach about 30 chaetigers. Characteristic of this stage are absence of palps and peristomial cirri, branchiae with only single filament and the body length growing relatively faster than the width.

Late juvenile stage, from about 30 chaetigers to about 50 chaetigers. The juvenile retains the branchial pattern and growth pattern of the early juvenile, but has at this stage developed both palps and peristomium cirri.

Adult stage, in which the specimen has at least 50 chaetigers. Characteristic of this stage is branchiae with two or more branchial filaments and body width increases relatively more rapidly than body length.

Discussion.—This species was listed as *Eunice vittata* (Fauvel 1923, Fauchald 1992) by Gathof (1984). It differs from *E. vittata* most notably in that subacicular hooks are always single, not multiple as in *E. vittata*. Furthermore, in specimens with similar chaetiger counts, the maximum number of branchial filaments is strikingly different: In a 75-chaetiger *E. vittata* a maximum of 12 filaments is present, but in a specimen of *E. wui*, with a similar chaetiger count, only three filaments are present.

Eunice wui resembles *Eunice fauchaldi* Miura from Japan and *Eunice multicylindri* Shisko from the Californian coast. Paratype material of both species (20 specimens of *E. fauchaldi*, of which 13 are complete; 7 specimens of *E. multicylindri*, of which three are complete) were available for ex-

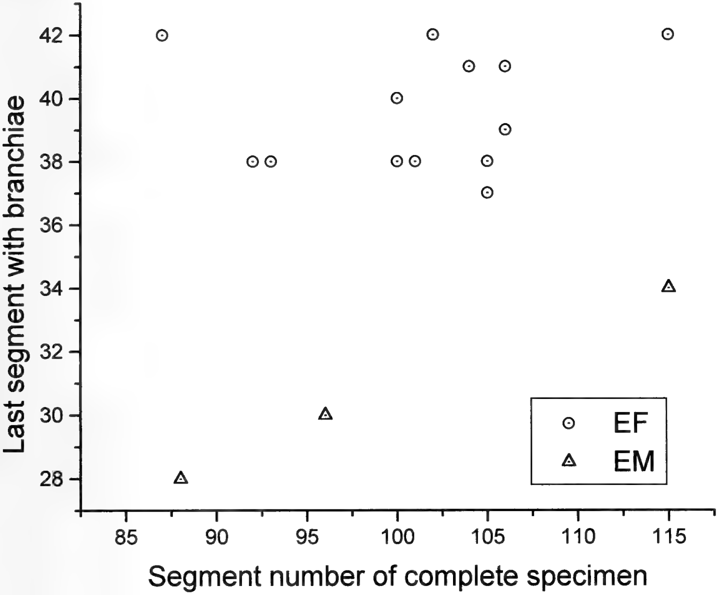

Fig. 7. Relationship between the numbers of pairs of branchiae and the number of chaetigers for *Eunice fauchaldi* (EF) and *E. multicylindri* (EM).

amination. Variations in morphological characters were compared with those of *E. wui*. Figs. 5 and 6 show that *E. wui* differs from these two species in the following features: in similarly sized (same width) specimens, *E. wui* has a higher number of branchial filaments than the other two species (Fig. 5). For example, at 100–116 chaetigers, the average maximum number of filaments of *E. wui* (*n* = 7) is 5.1; in *E. fauchaldi* (*n* = 10) it is 3.3, and in *E. multicylindri* (only one specimen with 116 chaetigers) only 3 filaments. The length/width ratio is different (Fig. 6). For a similarly sized specimen, the new species appears stouter than the others. For example, at 100–116 chaetigers, the average maximum length/width ratio of *E. wui* (*n* = 7) is 1.17, that of *E. fauchaldi* (*n* = 10) is 1.60, and *E. multicylindri* (*n* = 1, 116 chaetigers) has a ratio of 1.71.

In both *E. fauchaldi* and *E. multicylindri* branchiae start on chaetiger 3, but the numbers of pairs of branchiae are different (Fig. 7). For example, a 115-chaetiger *E. fauchaldi* specimen has branchiae from chaetigers 3 through 42, but in a specimen of *E. multicylindri* with a similar chaetiger-count (116 chaetigers), branchiae are present from chaetigers 3 through 34 only.

Morphometric studies on polychaete worms have already been conducted by many workers, including Fauchald (1982b, 1991), Mackie (1984), and Sigvaldadóttir & Mackie (1986). Those previous papers and the current study indicated that certain morphological characters of the polychaetes vary in a size-dependent fashion. Whenever material is available, a statistical study is highly recommended, it will not only help clarify relations among similar species later, but will also help to identify phylogenetically important characters, and may yield ecologically interesting results.

Etymology.—This species is named in honor of Professor Baoling Wu, Honorary Director of the First Institute of Oceanography, SOA, China, for his many contributions to the study of polychaetes, and in appreciation of his several years of guidance to the first author.

Acknowledgments

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Description of a new species of *Sphaerosyllis* from Australia and New Zealand (Polychaeta: Syllidae: Exogoninae)

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Abstract.—Examination of several specimens of the genus *Sphaerosyllis* from Australia, loaned by the Australian Museum, as well as specimens of this genus from New Zealand given by Dr. Nathan W. Riser, revealed the presence of a new species described in this paper as *Sphaerosyllis nathani.* This new species is characterized by having very long dorsal cirri and very long papillae on the dorsal and ventral surfaces.

Sphaerosyllis is one of the larger and more difficult genera of the Subfamily Exogoninae. In Australia, contributions to the knowledge of this genus have been made by Augener (1913, 1927), Haswell (1920), and, more recently, by Hutchings & Rainer (1979, 1980), Hutchings & Murray (1984) and Hartmann-Schröder, who described and reported several species in her papers of 1979, 1980, 1981, 1982, 1983, 1984, 1985, 1986, 1987, 1989, 1990, and 1991. In New Zealand, contributions to the knowledge of *Sphaerosyllis* were made by Augener (1924a, 1924b) and Riser (1985, 1991). The genus was revised by San Martín (1984a, 1984b), who reported about 44 species, but many other species have been described since then. An evaluation of the systematics of this genus was made by Riser (1991).

A study of several unidentified specimens of the genus *Sphaerosyllis*, deposited in the Australian Museum, revealed two specimens belonging to an undescribed species. Another specimen of the same new species was found amidst a collection of *Sphaerosyllis kerguelensis* from New Zealand, donated to us by Dr. Nathan W. Riser. We describe and discuss here, the new species.

The specimens are preserved in 70% ethanol. Observations and measurements were made using interference contrast optics (Nomarsky). Drawings were made with a "camera lucida". The specimens are deposited in the polychaete collection of the Australian Museum, Sidney (AM).

Family Syllidae Grube, 1850
Subfamily Exogoninae Rioja, 1925
Genus *Sphaerosyllis* Claparède, 1863
Subgenus *Prosphaerosyllis* San Martín, 1984

Sphaerosyllis (Prosphaerosyllis) nathani, new species

Fig. 1

Material examined.—Holotype (W22146) from 300 m NE of Green Point, Hawkesbury River (33°34′S–151°13.5′E), NSW, Australia, 5 m depth, sandy mud, A. R. Jones and A. Murray coll., Hawkesbury Estuary Study 1977–84. Paratype 1 (W23142) from reef S of Lucas Island (15°16′S–124°29′E), Western Australia, P. Hutchings coll. Paratype 2 (W23483) from Kaikoura, New Zealand, holdfast of *Lessonia*, N. W. Riser coll.

Description.—Holotype complete specimen, in good condition, 2.1 mm long, 0.22 mm wide, with 23 setigers. Paratype 1 anterior fragment. Paratype 2 complete specimen, 2.5 mm long, 0.24 mm wide, with 28 setigers. Body small, slender, without color markings. Prostomium rectangular, partially

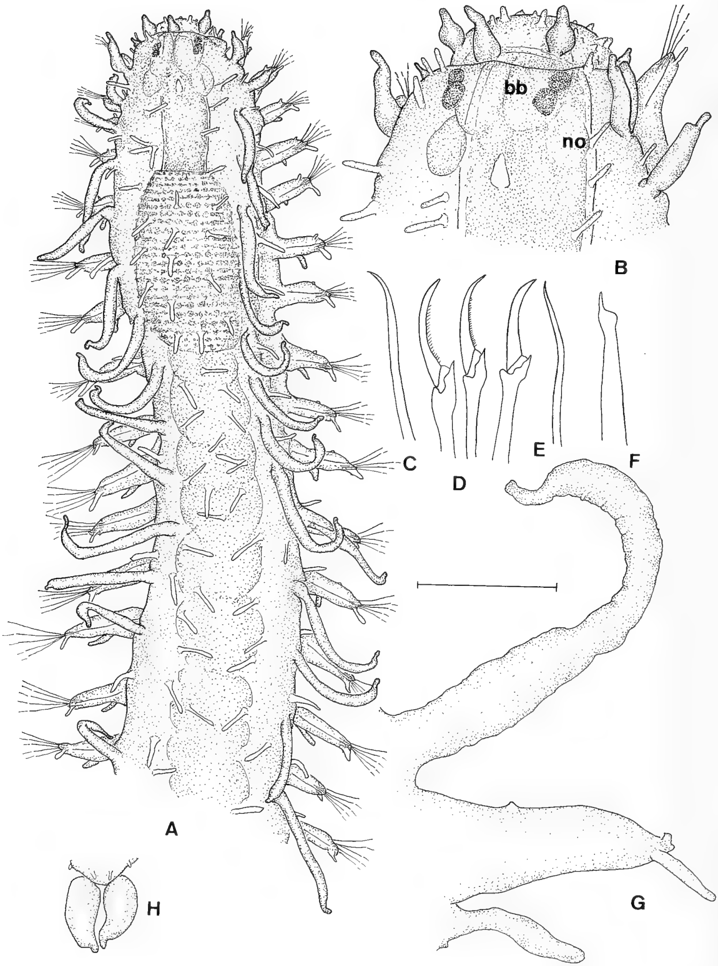

Fig. 1. *Sphaerosyllis nathani* new species. Holotype. A, anterior and midbody, dorsal view. B, detail of anterior end (bb: bilobed brain; no: nuchal organ). C, dorsal simple seta. D, compound setae. E, ventral simple seta. F, aciculum. G, parapodium of midbody, posterior view. H, pygidium (Paratype 2). Scale.—A, H: 0.18 mm. B: 98 μm. C–F: 20 μm. G: 48 μm.

covered by peristomium; four large eyes in rectangular arrangement, close to each other on each side and two small anterior eyespots (only seen on paratypes); three short antennae, each with bulbous base and short tip. Palps fused to prostomium, broad and short, ventrally folded, bearing several papillae. Peristomium short; tentacular cirri similar in shape to antennae, but much smaller (Fig. 1A, B). Dorsum with little debris; dorsal papillae long, thin, arranged in three dorsal irregular rows; each segment bearing solitary papillae dorsolaterally between dorsal cirri; as result there are five papillae visible dorsally on each segment (Fig. 1A). Ventral side with long papillae, similar to those of dorsum, also arranged on five irregular longitudinal rows. Dorsal cirri on all setigers, those of anterior segments long, similar in length to parapodial lobes (Fig. 1A, B), those of remaining segments longer than parapodial lobes (Fig. 1A, G), but somewhat shorter toward far posterior end of body. Ventral cirri relatively long, digitiform, shorter than parapodial lobes. Parapodial lobes elongated, conical, each with small anterior papilla, inconspicuous presetal papilla and very long postsetal papilla (Fig. 1A, G). Parapodium with solitary dorsal simple seta thin, smooth, curved, present from setiger 1 (Fig. 1C); solitary ventral simple seta similar, but thinner, present only on far posterior parapodia (Fig. 1E). Parapodia each with four compound setae; setae similar throughout, heterogomph, with blades unidentate and somewhat falciform; dorsal blades with short spines on cutting margin, ventral blades smooth (Fig. 1D); all blades about 16 μm long. Solitary aciculum tapered and, with thin, filiform tip (Fig. 1F). Pygidium semicircular, with two long, wide anal cirri and two dorsal and two lateral papillae (Fig. 1H). Bilobed brain and nuchal organs (cf. Riser 1991) easily visible (Fig. 1A, B). Pharynx partially everted, extending through four segments, shorter than proventriculus; pharyngeal tooth well back from margin, anterior to middle of pharynx (Fig. 1A, B). Proventriculus long and wide, through three and a half segments, with about 25 muscle-cell rows (Fig. 1A).

Remarks.—The dorsal cirri of the new species are very long and slender, distinctly different from the typical cirri of the genus, which have a bulbous base and a short thin tip. The holotype of *Sphaerosyllis nathani* was labeled *Pionosyllis* sp. in the collections of the Australian Museum. However, several species of the group of species defined by San Martín (1984b) as subgenus *Prosphaerosyllis* have the cirri formed into a more or less elongate bulbous proximal part and a retractile, short cylindrical distal part, for example *S. xarifae* Hartmann-Schröder 1960, *S. riseri* Perkins 1981, etc. The dorsal cirri of *S. nathani* are an extreme case of this tendency; the major part of the dorsal cirrus is formed by the proximal part, whereas the distal part is a non-retractile and distal narrowing. In contrast, *S. giandoi* Somaschini & San Martín 1994, has very small, papilliform dorsal cirri, being the opposite extreme form of the dorsal cirri.

The most similar species to *Sphaerosyllis nathani* is *S. bilineata* Kudenov & Harris 1995, described from California; this species also has elongate dorsal cirri, long dorsal papillae and body and setae of similar shape. However, *S. bilineata* has differently shaped dorsal cirri, which are somewhat thickened basally, proportionally shorter than those of *S. nathani*. The dorsal papillae of *S. bilineata* are arranged in two longitudinal dorsal rows and are alternating long and short, whereas the papillae of *S. nathani* are all long and arranged in three irregular dorsal longitudinal rows and two dorsolateral ones.

Sphaerosyllis longipapillata Hartmann-Schröder 1979, from Australia, also has long dorsal papillae, but the dorsal cirri of that species are much shorter and have the shape typical for those of most other members of the genus.

Etymology.—The species is named in honor of Dr. Nathan W. Riser, in acknowledgment of his important contributions to the knowledge of this genus, and in appreciation for the help given to us in this and other papers.

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We wish to express our acknowledgment to Dr. P. Berents, the Australian Museum, Sydney, for the loan of the specimens. Dr. P. Hutchings, from the same institution, gave us useful advice and additional data about the material studied. Dr. Nathan W. Riser, Northeastern University, Massachusetts, USA, provided specimens from New Zealand and revised the manuscript.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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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 1997 in Vol. 54, Part 3 of the *Bulletin of Zoological Nomenclature*. Comment or advice on any of these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary (I.C.Z.N.), c/o The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Case No.

3013 *Helix draparnaudi* Beck, 1837 (currently *Oxychilus draparnaudi*; Mollusca, Gastropoda): proposed conservation of the specific name.
2954 *Suchonella* Spizharsky, 1937 (Crustacea, Ostracoda): proposed designation of *S. typica* Spizharsky, 1939 as the type species.
3002 *Fapilio camillus* Fabricius, 1781 (currently *Cyrestis camillus*) and *Limenitis reducta* Staudinger, 1901 (Insecta, Lepidoptera): proposed conservation of the specific names.
3001 *Lactura* Walker, 1854 (Insecta, Lepidoptera): proposed conservation, and proposed conservation of the specific name of *Eustixis pupula* Hübner, [1831] (currently *Lactura pupula*).
2361 *Stroagylopus* Tschudi, 1838 (Amphibia, Anura): proposed designation of *Rana fasciata* Smith, 1849 as the type species.
3049 *Cnemidophorus neomexicanus* Lowe & Zweifel, 1952 (Reptilia, Squamata): proposed conservation of the specific name.
3044 Generic and specific names of birds (Aves) conventionally accepted as published in the *Proceedings of the Zoological Society of London* and monographic works by John Gould and other contemporary zoologists: proposed conservation by suppression of all prior usages.

The following Applications were published on 18 December 1997 in Vol. 54, Part 4 of the *Bulletin of Zoological Nomenclature*.

Case No.

3035	*Trachelocerca* Ehrenberg (Ciliophora): proposed conservation of authorship as Ehrenberg (1840), with fixation of *Vibrio sagitta* Müller, 1786 as the type species.
2948	*Turrilites gravesianus* d'Orbigny, 1842 (currently *Hypoturrilites gravesianus*; Mollusca, Ammonoidea): proposed conservation of the specific name and designation of a replacement lectotype; *Turrilites tuberculatus* Bosc, 1801 (currently *Hypoturrilites tuberculatus*): proposed designation of a neotype.
3009	*Polyrhachis* Smith, 1857 (Insecta, Hymenoptera): proposed precedence over *Myrma* Billberg, 1820.
2924	MELOIDAE Gyllenhal, 1810 and NEMOGNATHINAE Castelnau, 1840 (Insecta, Coleoptera): proposed precedence over HORIIDAE Latreille, 1802.
3046	*Papilio sylvanus* Esper, [1779] (currently known as *Ochlodes venata* or *Augiades sylvanus*; Insecta, Lepidoptera): proposed conservation of the specific name.
3034	*Waagenoconcha* Chao, 1927 and *Gruntoconcha* Angiolini, 1995 (Brachiopoda): proposed conservation.

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 30 September 1997 in Vol. 54, Part 3 of the *Bulletin of Zoological Nomenclature*. Copies of these Opinions can be obtained free of charge from the Executive Secretary, I.C.Z.N., c/o The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Opinion No.

1875. *Hapalotrema* Looss, 1899 (Digenea): *Hapalotrema loossi* Price, 1934 designated as the type species.
1876. *Nygolaimus* Cobb, 1913 (Nematoda): *Dorylaimus brachyuris* de Man, 1880 designated as the type species.
1877. D.L.G. Karsten (1789), *Museum Leskeanum*, vol. 1 (Regnum Animale): suppressed for nomenclatural purposes.
1878. *Paraphronima crassipes* Claus, 1879 (Crustacea, Amphipoda): specific name conserved.
1879. *Cacoxenus indagator* Loew, 1858 (Insecta, Diptera): generic and specific names conserved.
1880. PLUTONIINAE Bollman, 1893 (Arthropoda, Chilopoda): spelling emended to PLUTONIUMINAE, so removing the homonymy with PLUTONIINAE Cockerell, 1893 (Mollusca, Gastropoda).
1881. *Stilpon* Loew, 1859 (Insecta, Diptera): conserved.
1882. *Dialictus* Robertson, 1902 and *Chloralictus* Robertson, 1902 (Insecta, Hymenoptera): given precedence over *Paralictus* Robertson, 1901.
1883. *Monograptus riccartonensis* Lapworth, 1876 (Graptolithina): lecto-type replaced by a neotype.
1884. *Cyclodomorphus praealtus* (Reptilia, Squamata): specific name first available from the intended original description by Shea, 1995.
1885. *Tyrannula minima* Baird & Baird, 1843 (currently *Empidonax minimus*) and *Contopus pertinax* Cabanis & Heine, 1859 (Aves, Passeriformes): specific names conserved.

The 125th Annual Meeting of the Biological Society of Washington will be held on Thursday, 7 May, 1998, at 11:00 in the Waldo Schmitt Room, National Museum of Natural History, Washington, D.C.

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.

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Nomenclatural remarks on the family-group names of the Phylum Echiura

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Abstract.—The spellings, authorships, and dates of publication of all the family-group names of the Phylum Echiura were reexamined critically, following strictly the International Code of Zoological Nomenclature. The following corrections of current usages are noted: Bonelliidae Lacaze-Duthiers, 1858, instead of Baird, 1868; Echiuridae Quatrefages, 1847, instead of Blainville, 1827 (consisting of Echiurinae Quatrefages, 1847 and Thalassematinae Forbes & Goodsir, 1841, instead of Monro, 1927); and Ikedidae Bock, 1942, instead of Ikedaidae Dawydoff, 1959. Furthermore, the spelling of the here unadopted subfamilies Bonellinae, Acanthobonellinae, and Archibonellinae, all of which were originated by DattaGupta (1976), are corrected respectively to Bonelliinae, Acanthobonelliinae, and Archibonelliinae. The erroneous attribution of the family name Urechidae to Fisher & MacGinitie (1928) is also corrected to Monro (1927), although the former affiliation has already been entered into the Official List of Family-Group Names in Zoology.

The echiurans constitute an exclusively marine, coelomate phylum, which is generally regarded to consist of four families (Stephen & Edmonds 1972; see Table 1). Among many papers on echiurans, I happened to find some discrepancies in the spellings, authorships, and dates of publication of the family-group names. While inquiring after the correct ones, I found defects not only in my own chapter contributed to a recent book (Nishikawa 1992), but also in many other publications, including the excellent monograph by Stephen & Edmonds (1972).

"Systematics is not simply the activity of collecting data or organisms and interpreting their historical relationships. Systematists must also be historical . . . scholars, . . . at the level of tracing the history of names and in finding and interpreting those data and ideas presented by earlier workers." (Wiley 1981). In the spirit of historical scholarship, I present here my conclusions concerning the above-mentioned inquiries, strictly following the International Code of Zoological Nomenclature, 3rd edition (abbreviated as ICZN; International Commission on Zoological Nomenclature 1985). When citing earlier works, the original orthography is followed.

Family Bonelliidae

The family Bonelliidae has been sometimes spelled incorrectly as "Bonellidae" (e.g., DattaGupta 1976, 1981; Saiz Salinas 1987, Nishikawa 1992). Moreover, the authorship of this family has been wrongly attributed to Baird (1868). Lacaze-Duthiers (1858) seems to have been the true author of the family Bonelliidae.

When Lacaze-Duthiers (1858) erected "la famille des Bonellines" based on *Bonellia viridis,* he formally named it "*BONELLIEA*" as the third family of the "Gephyrea", following the families "*ECHIUREA*" and "*SIPUNCULEA*". The family name Bonelliea can be regarded as available (ICZN Art. 11f), but should be corrected to Bonelliidae with the original au-

Table 1.—Recent trends in and my present conclusions concerning the spellings and, when cited, the authorships and dates of the family-group names of the phylum Echiura, as used in several publications since the monograph of Stephen & Edmonds (1972). Ordering of the names follows that adopted in the monograph.

Authors	Family-group names
Stephen & Edmonds (1972)	Bonelliidae Baird, 1868
	Echiuridae de Blainville, 1827
	Echiurinae Monro, 1927
	Thalassematinae Monro, 1927
	Urechidae Fisher & MacGinitie, 1928
	Ikedaidae Dawydoff, 1959
DattaGupta (1976)	Bonellidae Baird
	Bonellinae[a] novo[b]
	Acanthobonellinae[a] novo
	Acanthohaminginae novo
	Archibonellinae[a] novo
	Echiuridae de Blainville, 1827
	Thalassematidae Bock
	Ochetostomatinae novo
	Thalassematinae Bock
	Urechidae Fisher & MacGinitie
	Ikedaidae Dawydoff
Saiz Salinas[c] (1987)	Bonellidae Baird, 1868
	Echiuridae de Blainville, 1827
	Thalassematidae Bock, 1942
Edmonds[c] (1987)	Bonelliidae
	Echiuridae
	Ikedaidae
Nishikawa (1992)	Bonellidae
	Echiuridae
	Urechiidae
	Ikedaidae
Nishikawa (present study)	Bonelliidae Lacaze-Duthiers, 1858
	Echiuridae Quatrefages, 1847
	Echiurinae Quatrefages, 1847
	Thalassematinae Forbes & Goodsir, 1841
	Urechidae Monro, 1927
	Ikedidae Bock, 1942

[a] Bonellinae should be corrected to Bonelliinae, Acanthobonellinae to Acanthobonelliinae, and Archibonellinae to Archibonelliinae (see the text).

[b] The author of this nominotypical subfamily should be the same as that of the family (ICZN Art. 36a).

[c] The author didn't refer to all the family-group names.

thorship and date (ICZN Art. 11f(ii)). "Bonelli-" is the stem of the generic name *Bonellia,* which was proposed by Rolando (1821) and derived from the surname of his "Collègue et Ami le professeur Bonelli", with the Latin suffix "-a" (ICZN Art. 29b(i)). Later, Quatrefages (1865) erected the family "Bonellea" and Baird (1868) proposed "Bonellidae", both names being based similarly on the genus *Bonellia.* However, following ICZN Art. 50a, it is obvious that the author and date of the family Bonelliidae should be Lacaze-Duthiers 1858, who first published a latinized version of this name.

DattaGupta (1976) proposed 4 subfamily names within the "Bonellidae", Bonellinae, Acanthobonellinae, Archibonellinae, and Acanthohaminginae, all of which he attributed to himself. Although they are available names, fulfilling the requirements of ICZN Arts. 11 and 13, several corrections seem necessary for the first three. As the stem of "-bonellia" is "-bonelli-" as stated above, Bonellinae should be corrected to Bonelliinae, Acanthobonellinae to Acanthobonelliinae, and Archibonellinae to Archibonelliinae; the latter two are attributed again to DattaGupta (1976), but the nominotypical subfamily should be ascribed to Lacaze-Duthiers (1858), the author of the family Bonelliidae (ICZN Art. 36a). On the other hand, the spelling of the subfamily name Acanthohaminginae need not be changed. The name of its type genus *Acanthohamingia* was derived from another genus, *Hamingia,* the origin of which was the Norwegian word "Hamingja, the Fortuna of Northern Mythology" (Danielssen & Koren 1881). As *Acanthohamingia* ends "in a word not Greek or Latin", the stem for the family-group name is "that used by the author who establishes a family-group name based on that generic name" (ICZN Art. 29b(ii)). Therefore, DattaGupta's spelling, using the stem "Acanthohaming-", should be treated as the correct original spelling.

Family Echiuridae

The family name Echiuridae has been attributed to Blainville 1828 (see Table 1). If this is correct, then the authorship and date of the nominotypical subfamily Echiurinae should be the same, according to the Principle of Coordination (ICZN Art. 36), instead of Monro (1927), as was given by Stephen & Edmonds (1972) (see Table 1). However, it seems quite strange that Blainville's (1828) "origination" of the family-group name should have preceded, rather than followed, the establishment of the genus *Echiurus,* which has been rightly attributed to Guérin-Méneville (1831) (e.g., Monro 1927, Stephen & Edmonds 1972, for details see below). According to ICZN Art. 11f(i)(1), a family-group name must be "based on the generic name then used as valid for a genus contained in that family-group taxon". When Blainville (1828) first used the name of "Fam. VI. Les Échiurides, *Echiuridea*", he referred only to two genera as its members, "THALASSÈME: *Thalassema,* Gaertner" and "STERNAPSE: *Sternapsis,* Otto". In his description of this family, the former genus contained "Esp. [=The species] La THALASSÈME ECHIURE: *T. echiurus; Lumbricus echiurus* . . .", but no further references were made to the word "echiurus" nor to its derivatives, even for a collective group. Therefore, Blainville's "Echiuridea" should be regarded as an unavailable family name, not because of its wrong ending, but because of the lack of typification. This is also true for Lamarck's (1816) "LES ÉCHIURÉES" as the name of "la deuxième famille de nos annelides apodes", containing the genus "THALASSÈME. (Thalassema.)". Its description mentioned only the single species "Thalassème échiure. *Thalassema echiura*", but no references were detectable to the type genus of the family name "Échiurées". And in any case, Lamarck's name for the family was not latinized, but was in vernacular French, and does not meet the criteria for availability of such names outlined in Art. 11f(iii).

Guérin-Méneville's (1831) origination of the generic name *Echiurus* (see below) was clearly affected by Cuvier's (1830) system. This is plain from Guérin-Méneville's text explanation of plate 6 in page 9 of the "Zoophytes" section included in volume 3 of his "Iconographie du Regne Animal de G. Cuvier"; the publication year of the "livraison" including the mentioned explanation may be 1842, 1843, or 1844, because the publication of the volume was permitted by the "Académie" on the 21st of November, 1842 (see its "avis") and because the execution of this publication was recorded in No. 36 of the "XXIII^{e} Année" volume of the "Bibliographie de la France", dated the 7th of September, 1844. Cuvier's system divided *Thalassema* into "LES THALASSÈMES proprement dits.", "LES ECHIURES", and "LES STERNAPSIS. Otto.". Although Cuvier's "LES ECHIURES" was accompanied by a diagnosis, mentioning only the single species *Lumbricus echiurus* Pallas, it should not be regarded as an available genus-group name because it was obviously used as a French vernacular name, rather than "a scientific name by the author when published" (ICZN Art. 11b).

The genus-group name *Echiurus* was originated by Guérin-Méneville (1831) in the explanation of figure 3 of his plate 6, printed below the plate as follows: "Echiurus *Pallasii Nob.* (*L.* [=*Lumbricus*] *Echiurus, Gm. Pallas*)" (brackets mine); "Nob." is an abbreviation of the latin "nobis" (=ours). The genus-group name *Echiurus* and the specific name *pallasii* are safely regarded as available by indication, because they were newly proposed "in association with an illustration of the taxon being named" (ICZN Art. 12b(7)). The mentioned explanation below the plate is nearly the same as that given in the work's main text published in 1842 or later (see above). The text's explanation was followed by a note stating that the author was obliged to give the earlier name [=*L. echiurus*] a new name [=*E. pallasii*], because "il était impossible de l'appeler *Echiurus echiurus* Pallas". Of course, the ICZN (Art. 18) does currently allow tautonymous names. This note clearly shows that *Echiurus pallasii* was first published as an unjustified replacement name for *Echiurus echiurus* (Pallas). The specific name *pallasii* is available (ICZN Arts. 12b(3) and 10g), though not valid.

The type species of the subgenus *Echiurus* is *Lumbricus echiurus* Pallas, 1766, fixed by monotypy (ICZN Art. 68d), as has been generally accepted by Spengel (1912), Monro (1927), Fisher (1946), Stephen & Edmonds (1972), etc. Lastly, by the Principle of Coordination (ICZN Art. 43), the authorship, date, and type species of the genus *Echiurus* are quite the same as those for the nominal subgenus.

So far as I am aware, Quatrefages (1847) was the first to use the family name "Echiurea" expressly based on the genus name *Echiurus*. When he proposed this family name to denote one of "les deux familles établies par M. de Blainville" (see above), the family contained the genera "Echiure" and "Sternapse". Undoubtedly, "Echiure" was used here as a vernacular name for the genus *Echiurus,* because he also wrote "ECHIURE DE GAERTNER (*ECHIURUS GAERTNERII* . . .)". From context, then, *Echiurus* can be recognized as the base of the family name and so the latter is available from this publication (ICZN Art. 11f(i, 1)). The stem of *Echiurus* is "Echiur-", so the original incorrect spelling of "Echiurea" should be corrected to Echiuridae, though still attributed to Quatrefages 1847 (ICZN Art. 33b(ii)), not to Baird (1868), who first spelled it that way. Lacaze-Duthiers' (1858) family name "*ECHIUREA*" and Skorikov's (1909) subfamily name "Echiurini" are incorrect subsequent spellings of this family-group name (ICZN Art. 33c). According to the Principle of Coordination (ICZN Art. 36), the nominotypical subfamily name Echiurinae also should be attributed to Quatrefages, 1847.

The other subfamily, Thalassematinae, or the family Thalassematidae in another system, has sometimes been attributed incorrectly to Monro (1927) or Bock (1942) (see Table 1). However, the authorship of this family-group name should be corrected to Forbes & Goodsir (1841), who first used the name as ". . . *Thalassema Neptuni* and *Echiurus vulgaris,* members of the family *Thalassemacea* in the order *Sipunculidae*". As the family name Thalassemacea is obviously based on the then valid genus name *Thalassema* Pallas, 1774 (see below), it is available, though regarded as an incorrect original spelling (ICZN Art. 32c(iii)). Although Forbes (1841) also used this family name in quite the same sense as Forbes & Goodsir (1841), I give precedence to the latter as follows.

Forbes & Goodsir's (1841) paper was published in April, as shown on the cover of the issue in which it appeared (Reference Service of the University of Tokyo Library, pers. comm.). And it seems that Forbes'

(1841) book appeared at the latest in April, because it was included in the "List of new publications, from January to April 1841" of "The Edinburgh Review" vol. 73, no. 147, which was published in April, 1841. Further information has not yet become available as to the publication date of either work. Therefore, Forbes & Goodsir (1841) and Forbes (1841) are both deemed to have been published on the last day of April, 1841 (ICZN Art. 21c(i)). Under these circumstances, I give precedence to Forbes & Goodsir (1841) over Forbes (1841), following the "Principle of the First Reviser" (ICZN Art. 24a).

The generic name *Thalassema* has been incorrectly attributed to Lamarck (1801) (e.g., see Stephen & Edmonds 1972), and even to Cuvier (date unspecified). However, the authorship of the name should be changed to Pallas (1774).

When Pallas (1774) originated the name of the species "LUMBRICUS *THALASSEMA*", he mentioned the manuscript name "*Thalassema Neptuni*" proposed for the same species by Gaertner, who had discovered it. The generic name *Thalassema,* published there as a junior synonym of *Lumbricus,* is available, because prior to 1961 it was used as an available name (see ICZN Art. 11e and its example), as seen in many older papers (e.g., Blainville 1828, see p. 251). The genus *Thalassema* is credited to Pallas, 1774, and its type species is *Lumbricus thalassema* by monotypy, because it is the only species with which *Thalassema* was firstly associated (see ICZN Art 67l).

Lamarck's (1801) *Thalassema* is undoubtedly available, because it was accompanied by a clear definition. However, the genus-group name *Thalassema* is clearly attributed to Pallas, 1774, not to Lamarck, 1801, by the Principle of Priority. This name was once often ascribed to Cuvier, e.g., by Lamarck (1801) who wrote, "THALASSÈME. *Thalassema.* Cuv.". Stephen & Edmonds (1972) tried "to find in any of the books at our disposal Cuvier's pre-1801 citation of *Thalassema*", but in vain. Fortunately, however, I could find that Cuvier (1800) listed "Thalassèmes ··· *Thalassema*" in the table titled "Classification des vers" without any associated nominal species, and that Cuvier (1805) used the former vernacular name as "les thalassèmes (*lumbricus thalassema* et *echiurus*)". These works of Cuvier were based on his pre-1801 "course on comparative anatomy, delivered at the Muséum national d'histoire naturelle" (Smith 1993). Therefore, Lamarck's (1801) above-stated credit of Cuvier for the generic name obviously derived from the course itself and/or its transcripts. At any rate, Cuvier's (1800) generic name *Thalassema* is unavailable, because it was unaccompanied "by a description or a definition of the taxon that it denotes, or by an indication" (ICZN Art. 12a).

The stem of *Thalassema* when forming a family name can be confirmed clearly as follows. Pallas (1774) wrote, "DESCRIPTIO *LUMBRICI THALASSEMATIS*" in the original description of *Lumbricus thalassema,* now called *Thalassema thalassema* (Pallas 1774). This means that *Thalassema* can be regarded as a neuter noun in the 3rd declension (S. Ootsuki, pers. comm.), and it confirms that the stem of *Thalassema* is "Thalassemat-". The family name should therefore be corrected to Thalassematidae Forbes & Goodsir, 1841, with the original authorship and date unchanged (ICZN Art. 33b(ii)). Furthermore, following the Principle of Coordination (ICZN Art. 36a), the subfamily Thalassematinae also should be attributed to Forbes & Goodsir 1841 (see Table 1). Later, Monro (1927) erected a subfamily Thalassematinae in the family Echiuridae, and Bock (1942) proposed a "Family Thalassematidae, nov." and "Subfamily Thalassematinae, nov.". However, neither Monro nor Bock can be regarded as the author of this family group (ICZN Art. 50). Dawydoff's (1959) "Thalassemidae" is an incorrect subsequent spelling of the valid family name Thalassematidae, and is thus regarded as unavailable (ICZN Art. 33c).

DattaGupta (1976) proposed a new available subfamily name, Ochetostomatinae. This is the original correct spelling, although this subfamily name is not used here. The type genus *Ochetostoma* is a neuter noun in the 3rd declension, with the stem of "Ochetostomat-".

Family Urechidae

The family-group name Urechidae Fisher & MacGinitie, 1928 has been entered into the Official List of Family-Group Names in Zoology as the result of Opinion Number 941, published in 1971 (see Bulletin of Zoological Nomenclature, 27: 216–217). However, I found that Monro (1927) erected the "Subfamily Urechinae" of the "Family Echiuridae", clearly prior to Fisher & MacGinitie (1928). Monro's (1927) Urechinae is available, because it was based on the valid name *Urechis* Seiz, 1907 and accompanied by a description, thus fulfilling the other requirements of ICZN Arts. 11 and 12. Then, the family name Urechidae is also credited to Monro 1927 by the Principle of Coordination (ICZN Art. 36a), not to Fisher & MacGinitie 1928. I intend to ask the International Commission on Zoological Nomenclature to change the authorship in the Official List. Nishikawa (1992) published the obviously incorrect subsequent spelling "Urechiidae".

Family Ikedidae

Ikedaidae Dawydoff, 1959, although generally accepted by most recent users including Nishikawa (1992), is actually wrong in spelling, authorship, and date.

The type genus *Ikeda* was proposed by Wharton (1913) on the basis of *Thalassema taenioides* Ikeda. The generic name *Ikeda* was derived wholly from the surname of a Japanese taxonomist, the late Prof. Iwaji Ikeda, who was the author of the type species. The stem of the family-group name based on the generic name *Ikeda,* which "is or ends in a word not Greek or Latin", is "that used by the author who established a family-group name based on that generic name" (ICZN Art. 29b(ii)). Bock (1942) first erected the "Sub-family Ikedinae" based on the genus *Ikeda,* with the stem "Iked-". Following the Principle of Coordination (ICZN Art. 36a), the family name Ikedidae should be considered the correct original spelling and attributed to Bock (1942). Dawydoff's (1959) "Ikedaidae" is an incorrect subsequent spelling of the valid family name Ikedidae, and therefore regarded as unavailable (ICZN Art. 33c).

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A new species of Hesionidae, *Glyphohesione nicoyensis* (Annelida: Polychaeta), from the Gulf of Nicoya, Costa Rica

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Abstract.—A new species, *Glyphohesione nicoyensis* (Family Hesionidae), is described from the Gulf of Nicoya on the Pacific coast of Costa Rica. Several morphological characters described for the species *G. klatti* Friedrich, 1950, and *G. longocirrata* Licher, 1994 are clarified.

The species *Glyphohesione klatti* Friedrich, 1950 was first collected from Helgoland and originally included in the family Hesionidae (Friedrich 1950). Eliason (1962) subsequently transferred this species to the genus *Ancystrosyllis* in the family Pilargidae due to the presence of emergent notopodial spines similar to those described for *Synelmis albini* (Langerhans, 1881) (=*Ancistrosyllis albini*). Pettibone (1966) later assigned this species to the genus *Synelmis* Chamberlin, 1919, and suggested that *S. klatti* was perhaps a juvenile form of *S. albini.*

In a review of the gross morphology of the pilargid brain, Fitzhugh & Wolf (1990) noted significant differences between the brain of *S. klatti* and that of other species within the genus (*S. ewingi* Wolf, 1986, and *S. acuminata* Wolf, 1986). Fitzhugh & Wolf (1990), therefore, recommended that *S. klatti* be removed from *Synelmis* and perhaps returned to its original genus, *Glyphohesione* Friedrich. Licher & Westheide (1994) formally removed *Glyphohesione* from synonomy with the genus *Synelmis* based on its lack of emergent neuropodial spines, which are considered apomorphic for *Synelmis.* Results of a cladistic analysis of the family Pilargidae by Licher & Westheide (1994), based on 28 morphological characters, also indicated that *G. klatti* shares many plesiomorphic characters with juveniles of the family Hesionidae Licher (1994) thus transferred the genus *Glyphohesione* Friedrich to the family Hesionidae based on its elongate palpostyles, anteriorly situated lateral antennae and well developed antennae, tentacular cirri, parapodial cirri, and anal cirri. Licher (1994) restricted the known distribution of *G. klatti* Friedrich, 1950, to northern Europe and the Mediterranean and described a new species, *G. longocirrata* Licher, 1994, from material collected in the Gulf of Mexico and originally identified as *S. klatti* by Wolf (1984).

Material collected during benthic sampling in the Gulf of Nicoya, Costa Rica (see Maurer & Vargas 1984 for station data), and previously identified as *Synelmis klatti* Friedrich by Dean (1996), was re-examined in light of Licher's (1994) redescription of *G. klatti* and a new species of *Glyphohesione* is here described.

Glyphohesione nicoyensis, new species
Figs. 1, 2

Synelmis albini (Langerhans).—Maurer & Vargas, 1984:101 (in part); Maurer et al., 1988:48 (in part).

Synelmis klatti (Friedrich).—Dean, 1996: 74.

Material examined.—Gulf of Nicoya, Sta. 23, 9°48′35″N, 84°43′50″W, 35 m, mud, Jul 1980, (1, USNM 079958). Sta. 24, 9°49′25″N, 84°41′20″W, 11 m, sand, Jun 1981, (4 Paratypes, UCR 113-01-A and 1); Aug 1981, (4). Sta. 28, 9°52′16″N, 84°45′30″W, 26 m, mud, Jul 1980, (2) (USNM 079964); Oct 1980, (1); Jan 1981, (2 Paratypes, MCZ 4018 & 4020): Jun 1981, (2 Paratypes, MCZ 4017); Aug 1981, (3, Paratypes UCR 113-01-B, 1 Paratype USNM 180394). Sta. 29,9°54′55″N, 84° 45′15″W, 18 m, muddy sand, Jul 1980, (2) (USNM 079968); Aug 1981, (3 Paratypes, MCZ 4019). Sta. 30, 9°54′40″N, 84° 45′50″W, 18 m, muddy sand, Oct 1980, (3); Jan 1981, (4); Apr 1981, (2); Jun 1981, (2). Punta Morales, 10°04′N, 85°58′W, intertidal, Lagartos sand flat, Aug 1996; muddy sand (1 Holotype, MCZ 4015), intertidal, boat ramp, sand (1), intertidal, rocky sand (1, Paratype UCR 113-01-C), intertidal, sand (1).

Additional material examined.—*Glyphohesione* Friedrich, English Channel: Survey Sta. M 16T, 51°24.6′N, 08°05′W, 112 m, J. P. Hartley coll., Aug 1975 (USNM 58901), 2 incomplete specimens.—*Glyphohesione longocirrata* Licher, Northwest North Atlantic Ocean: Gulf of Maine: Massachusetts, off Cape Cod: NEEB Sta. 41, 41°37.30′N, 69°15.42′W, 164 m, 27 Feb 1977 (USNM 91310, 5 specimens).

Type locality.—Gulf of Nicoya, Punta Morales mid intertidal, western side of the Lagatos sandflat, muddy sand.

Description.—Holotype complete, 37 segments, 4.0 mm long, 0.5 mm maximum width (setiger 6) without parapodia, 0.6 mm wide including parapodia (Fig. 1A). Anterior 6 segments cylindrical, remaining segments dorso-ventrally flattened and deeply incised (Fig. 1B). Fifth and sixth segments enlarged in holotype (these segments also enlarged in paratype MCZ 4020 with dense white (in ethanol) material identified as developing ova by squash preparation). Mid dorsum and dorsal parapodial lobes light tan to dark grey in mid and posterior region, anterior region colorless in ethanol.

Prostomium as long as or slightly longer than wide, divided anteriorly by a wide furrow, lateral margins slightly concave. Palpophores fused to prostomium, inserted anterio-ventrally, palpostyles filiform, shorter than lateral antennae (Fig. 1A). Three well-developed cirriform antennae, laterals inserted anteriorly, median at posterior margin of prostomium, median subequal in length, more slender than laterals. Paired, pigmented eyespots at anterior third of the prostomium. Dissection in CMCP-10 mounting medium revealed brain morphology similar to that of *Sigambra tentaculata* (Fitzhugh and Wolf, 1990, Fig. 1a) with indistinct separation between hindbrain and midbrain and tapering bilobed hindbrain (lobes somewhat more elongate and pointed than that of *S. tentaculata*). Pigmented nuchal organs present (Fig. 1A, nu), paired nuchal slits at posterio-lateral margin of the prostomium; no cilia noted using oil immersion.

First segment encircles prostomium posteriorly, clearly distinct from prostomium (Fig. 1A). Two pairs of subequal tentacular cirri, more robust and longer than lateral antennae. Large, brown, pigmented bulging areas (actually sub-dermal nuchal organs) posterior to prostomium dorso-laterally (Fig. 1A).

Parapodia biramous, distinctly set apart from trunk, except in anterior segments. Dorsal and ventral cirri of first setiger longer than those of other setigers (Fig. 1C); those of posterior setigers shorter than tentacular cirri, extending beyond tip of neuropodial lobe (Fig. 1D). Single notaciculum with stout emergent notopodial spine from setiger 8 (7–10) (Fig. 2A).

Neuropodia conical, truncate, with a cone-shaped presetal lobe. Holotype with up to 14 setae per neuropodium (a maximum of 14–18 neurosetae in other specimens) decreasing in number posteriorly. Single neuracicula; neurosetae simple, of varying length, finely serrate with smooth slightly crooked tip (Figs. 2B); longer neurosetae finely serrate, serrations becoming minute and difficult to see distally (Fig. 2C). Ventral cirri one-half length of dorsal

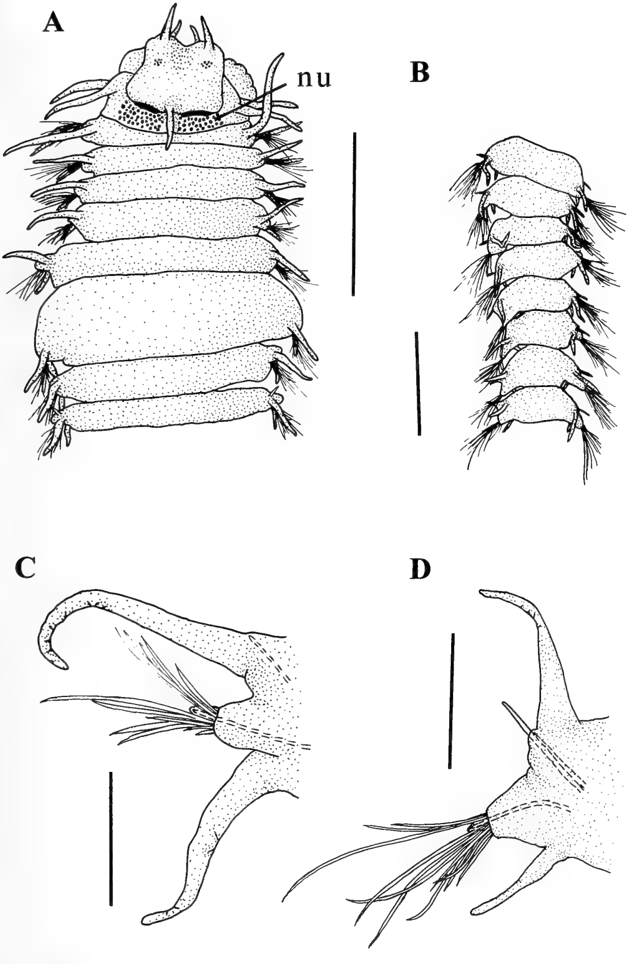

Fig. 1. *Glyphohesione nicoyensis,* new species: A. Anterior end, dorsal view (MCZ 4015); B. Mid body region, dorsal view (MCZ 4015); C. Parapodia, setiger one, posterior view (UCR 113-01-A); D. Median parapodia, posterior view (UCR ??1). Scale bar A & B = 100 μm; C & D = 500 μm. Abbreviation.—nu, nuchal organ (pigmented bulging area).

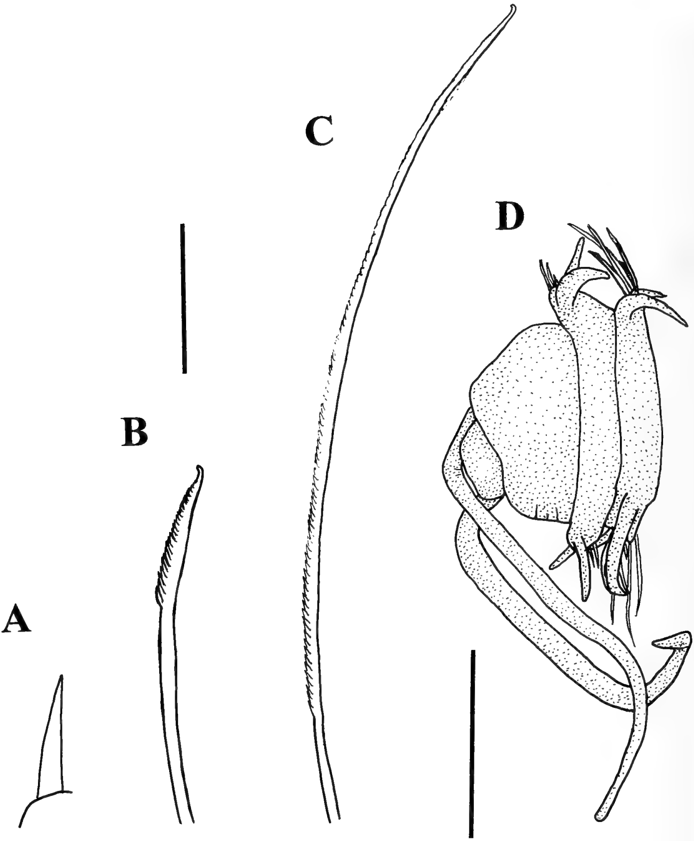

Fig. 2. *Glyphohesione nicoyensis,* new species: A. Notopodial spine, posterior setiger (UCR 113-01-A); B. Short neuroseta, setiger 12 (UCR 113-01-A); C. Long neuroseta, setiger 12 (UCR 113-01-A); D. Pygidium, dorsal view (MCZ 4015). Scale bar A, B & C = 40 μm; D = 500 μm.

cirri, less robust, extending slightly beyond neuropodial lobe.

Pygidium with rounded anal hood dorsally, two long, filiform, lateral anal cirri (Fig. 2D).

Distribution.—Glyphohesione nicoyensis, new species, is known from the Gulf of Nicoya, Costa Rica in mud, muddy sand, and sandy sediments from the intertidal to 35 m.

Remarks.—This species is placed within the genus *Glyphohesione* based on its simple setae, emergent notopodial spines, palpophores fused with the prostomium, elongate palpostyles, and the location of the three slender antennae. *Glyphohesione nicoyensis,* new species, differs from *G. klatti* in the presence of paired eyespots and the first appearance of emergent notopodial spines, beginning at setigers 7–10 in *G. nicoyensis* and setigers 5–8 in *G. klatti. G. nicoyensis* also has fewer neurosetae per parapodium than *G. klatti,* with the maximum number of neurosetae per notopodium being 25 in *G. klatti* and 14 to 18 in *G. nicoyensis.* Finally, the dorsal and ventral parapodial cirri of the mid and posterior body region extend beyond the tip of the neuropodial lobe in *G. nicoyensis* while in *G. klatti* the ventral cirri extend beyond the neuropodial lobe only in the anterior region.

Glyphohesione nicoyensis differs from *G. longocirrata* in the presence of paired eyespots and the first appearance of the emergent notopodial spines, those of *G. nicoyensis* first appear at setigers 7–10 as compared to setigers 10–15 in *G. longocirrata.* The maximum number of neurosetae per setiger is 14–18 in *G. nicoyensis* and 8–14 setae in *G. longocirrata. G. nicoyensis* and *G. longocirrata* also differ in the length of the dorsal cirri in the anterior body region. In *G. longocirrata* the anterior dorsal cirri are almost equal in length to the body width while they are much shorter relative to body width in *G. nicoyensis* (Fig. 1A). Lastly, the neurosetae of *G. longocirrata* are more bladelike and coarsely toothed (see below) than those of *G. nicoyensis.*

Examination of specimens identified as *G. klatti* from the English Channel (USNM 58901) and *G. longocirrata* from Massachusetts, off Cape Cod (USNM 91310) revealed some inconsistencies with the species descriptions by Licher 1994. There is a distinct separation between the prostomium and the first segment in both of these species while the figures of Licher (1994, Figs. 1A, B, 3A, B) show them to be dorsally fused. Also, the neurosetae of *G. longocirrata* are wider and more blade-like with longer, coarser teeth than those of both *G. nicoyensis* and *G. klatti.* Finally, Licher describes the tips of the neurosetae of *G. longocirrata* as being "minutely bidentate" but close examination disclosed that all the neurosetae had complete, slightly crooked, tips similar to those seen in *G. nicoyensis.*

Etymology.—This species is named for the type locality, the Gulf of Nicoya on the Pacific coast of Costa Rica.

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Laperocheres koorius, a new genus and species (Copepoda: Siphonostomatoida: Asterocheridae) associated with the sponge *Amphimedon* in Australia

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Abstract.—Both sexes of *Laperocheres koorius,* associated with the littoral sponge *Amphimedon* sp. (Porifera: Demospongiae: Haplosclerida: Niphatidae) in Australia (vicinity of Sydney), are described. The new genus can be distinguished from the 44 genera of the family Asterocheridae by the formula of legs 1–4: the third segment of the endopod of leg 3 with 1,I,1; the first segment of the exopod of legs 1–4 with 1-0; the third segment of the exopod of legs 2–4 with 4 spines. One of the outer spines (the middle) on the third exopodal segment of leg 2 is sexually dimorphic.

The family Asterocheridae Giesbrecht, 1899 is the most specious family of siphonostomatoid copepods associated with marine invertebrates, including about 146 species in 44 genera. The known hosts of asterocherids are bryozoans, cnidarians, echinoderms, sponges, and credibly ascidians (Ivanenko & Smurov 1997). The Australian copepods of this family are poorly known. Nicholls (1944) discovered a number of siphonostomatoids from Southern Australia apparently associated with littoral invertebrates including sponges. In this paper representatives of four genera currently recognized as asterocherids were described (*Acontiophorus* Brady, 1880, *Australomyzon* Nicholls, 1944, *Discopontius* Nicholls, 1944, *Scottocheres* Giesbrecht, 1897). Humes (1987, 1991) found a group of asterocherids from Northern Australia associated with crinoid echinoderms (*Collocheres* Canu, 1893, *Glyptocheres* Humes, 1987) and scleractinian corals (*Hetairosyna*, Humes, 1991; *Tychomyzon,* Humes, 1991). Despite the fact that asterocherids are common and abundant inhabitants of sponges (Humes 1996, Ivanenko 1997), the Australian fauna is virtually unknown, though other copepods associates of Australian sponges have been described: entomolepidid siphonostomatoids (McKinnon 1988b), harpacticoids (Huys 1990) and artotrogid siphonostomatoids (McKinnon 1988a) which may have originated from sponges.

This paper describes *Laperocheres koorius,* new genus, new species, associated with the littoral sponge *Amphimedon* sp. from the vicinity of Sydney, Australia.

Materials and Methods

The sponge *Amphimedon* sp. (Porifera: Demospongiae: Haplosclerida: Niphatidae) was collected by hand, isolated and then washed in freshwater. After passing the water through a fine-mesh net, the copepods were picked from the residue. Small fragment of the sponge, which is likely a new species, was identified by John N. A. Hooper. Two fragments are deposited in the collections of the Zoological Museum of Moscow State University and the Queensland Museum (QMG 313154).

Measurements and dissections were made in lactic acid, generally following the method proposed by Humes & Gooding

(1964). Specimens were stained by adding a solution of chlorazol black E dissolved in 70% ethanol/30% fresh water. The drawings were made using a camera lucida mounted on a ocular microscope.

In the formula for the armature of legs 1–4, Roman numerals indicate spines and Arabic numerals—setae; left numerals indicate lateral, middle—terminal, right—medial elements.

Asterocheridae Giesbrecht, 1899

Laperocheres, new genus

Diagnosis.—Asterocheridae. Body cyclopiform; prosome of female more thickened dorsoventrally then in male; urosome 4-segmented in female, 5-segmented in male. Antennule 20-segmented in female with aesthetasc on segment 18; 17-segmented in male, geniculate, with aesthetasc on segment 16. Antennal exopod small with 3 setae, terminal segment of endopod with 3 setae (one much reduced) and claw. Oral siphon reaching base of maxillipeds. Mandible with needle-pointed gnathobase and 1-segmented long palp bearing 2 terminal setae. Maxillule with 4 setae on each lobe. Maxilla 2-segmented. Maxilliped 6-segmented plus terminal claw. Legs 1–4 biramous, 3-segmented. Inner seta on coxa and first exopodal segment of legs 1–4 absent. Third segment of exopod in leg 1 with III,4, legs 2–3 with III,I,4, leg 4 with III,I,3. Third segment of endopod in leg 1 with 1,5, leg 2 with 1,4, legs 3–4 with 1,I,1. Leg 5 with free distal segment bearing 3 setae and proximal segment separated from somite only dorsally. Sexual dimorphism not expressed in maxilliped but shown for legs 2–5.

Type species.—Laperocheres koorius, new species.

Etymology.—The generic name is a combination of the name of the area where the copepods were collected ("La Perouse" region) and "cheres", apparently derived from the Greek "achtheros" meaning distressing or troublesome to.

Remarks.—The asterocherid genera are combined in one family on the basis of the presence of mandibular palp, the situation of the aesthetasc on the antennule and the form of tergite of metasomites (Stock 1987, 1992). The new species of *Laperocheres* possesses the peculiarities of asterocherids but can not be referred to known genera because of the unique setation of its legs. The third segment of endopod of leg 3 with formula 1,I,1 unreported for other asterocherids (although three elements have been indicated for this segment in three genera: *Peltomyzon* Stock, 1975; *Meandromyzon* Stock, 1989, and *Siphonopontius* Malt, 1991). Although considerable variability exists in leg setation, only this new copepod and five other asterocherid genera (*Psilomyzon* Stock, 1965, *Tuphacheres* Stock, 1965, *Inermocheres* Boxshall, 1990, *Sinopontius* Boxshall, 1990, *Siphonopontius* Malt, 1991), also described from sponges, lack inner seta on the first exopodal segment of legs 1–4. However, *Laperocheres* has four spines on the third exopodal segment of legs 2–4, while the representatives of the other five indicated genera have three spines or one spine. This genus also has the less reduced setation of legs 1–4 in the group of indicated genera. The only exception is the third endopodal segment of leg 3, in *Psilomyzon* which has four setae on this segment (*Laperocheres*—1,I,1).

The remarkable characteristics of the new genus are the only partial, dorsal separation of the proximal segment of leg 5 and the sexual dimorphism in leg 2 previously not clearly shown for other asterocherids.

The dorsoventral thickening of the female prosome observed for *Laperocheres* can be explained by the result of an intercalary growth along the lateral margins of the cephalothorax shield and the tergite of the following somite in a similar to that observed by Smurov & Ivanenko (1993) in the female of the asterocherid *Scottomyzon gibberum* (Scott & Scott, 1894).

Laperocheres koorius, new species
(Figs. 1–4)

Type material.—Two females, 6 males from a gray sponge, depth approximately 1 m, Cape Banks Marine Research Area (La Perouse), vicinity of Sydney, Australia, 34°00′S, 151°15′E, 17.05.1997. K. A. Mikrjukov collector. Holotype (no 1193), allotype (no 1194) and 2 paratypes (males) (no 1194–95) deposited in the Zoological Museum of Moscow State University. One paratype male placed in both the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM 285499), and the Museum of Natural History, London (BMNH 1997.911). One paratype male was presented to the Australian Museum, Sydney.

Male.—(Fig. 1A, B). Body cyclopiform, dorsoventrally flattened. Total length, excluding caudal setae, 0.53 mm (0.51–0.54 mm); greatest width 0.22 mm (0.22–0.23 mm), based on 5 specimens. Dorsoventral thickness of figured specimen on the level of ventral projection between maxilliped and first leg 0.12 mm; ratio of length of prosome to that of urosome 1.4:1; ratio of length to width of prosome 1.36:1. Prosome consisting of 4 articles: cephalothorax and 3 metasomites bearing legs 2–4, respectively. Position of prosomal appendages as in Fig. 1c. Shield of cephalothorax and metasomal tergites with numerous pores and sensillae. Lateral margin of shield ornamented with pores on ventral surface. Tergite of metasomites with heavily sclerotized ventrolateral margins (Fig. 1C). Urosome (Fig. 1D, E) consisting of 5 somites: somite with leg 5 having posterodorsal projection, genital somite bearing leg 6 and 3 abdominal somites; all somites with pores and sensilla.

Caudal ramus (Fig. 1F): ratio of outer length to greatest width 3:1, armed with 6 setae.

Rostral area (Fig. 1C): triangular in ventral view. One pore in posterior angle and two sensillae in anterior angles.

Antennule (Fig. 2A, B): geniculate, 17-segmented. Armature of segments is as follows: 2, 2, 2, 2, 2, 2, 2, 2, 7, 1, 2, 2+2, 2, 2, 2, 3+1 aesthetasc, and 10 setae, respectively. Aesthetasc on segment 16. Segment 10 reduced, partly overlapped by segment 9 armed with 7 setae, one of which reduced. Segment 12 with 2 pairs of setae, one of which in middle part of segment.

Antenna (Fig. 2C): a small coxa, elongate basis ornamented with row of scales anteriorly, 1-segmented exopod and 3-segmented endopod. Exopod short, longer than wide, armed with 3 setae: 2 terminal and 1 subterminal. First segment of endopod elongate, with setules along outer and inner margins. Second segment short, triangular, with one distal seta. Third segment with terminal claw and 3 setae, one of which reduced.

Oral siphon (Fig. 2E): formed by labrum and labium joined laterally, reaching nearly to base of maxillipeds.

Mandible (Fig. 2D): a gnathobase and palp. Gnathobase with needle-pointed apex, toothed subapically. Palp long, 1-segmented, with scales and 2 unequal terminal setae.

Maxillule (Fig. 2F): bilobed. Inner lobe about 2.5 times longer than outer lobe, armed with 4 terminal setae, and ornamented medially with spinules. Outer lobe with 4 setae, one of which hardly observed.

Maxilla (Fig. 5G): 2-segmented. Proximal part of first segment anteriorly with row of scales, ventrally with aesthetasc-like element. Distal claw-like segment serrated medially.

Maxilliped (Fig. 3A, B): 6-segmented. First segment with medial seta and ventral pore. Second segment long, unarmed. Segments 3–5 short, armed posterodistally with 2, 1, 1 setae. Segment 6 long, with distal claw and seta.

Legs 1–4 (Fig. 3C, D, E, G, J): biramous, each ramus 3-segmented. Protopods 2-segmented, intercoxal sclerites present in all legs. Formula for armature is as follows:

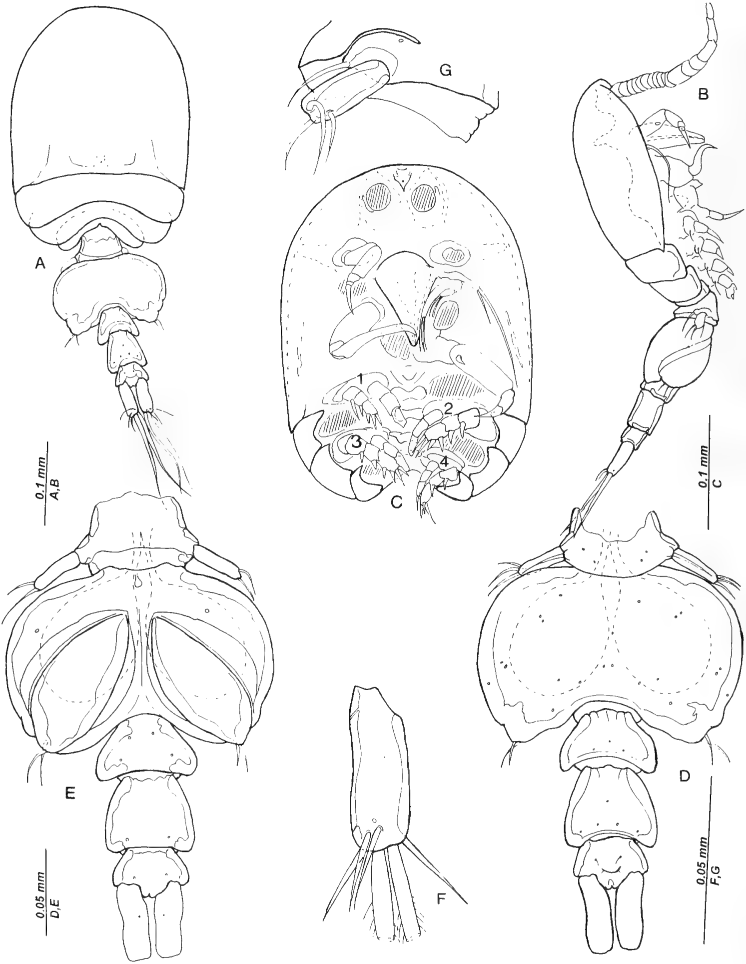

Fig. 1. *Laperocheres koorius* n. gen. n. sp. Male. A, Habitus, dorsal; B, Habitus, lateral; C, Prosome, ventral (1–4 - legs 1–4); D, Urosome, dorsal; E, Urosome, ventral; F, Left caudal ramus, dorsal; G, Leg 5, lateral.

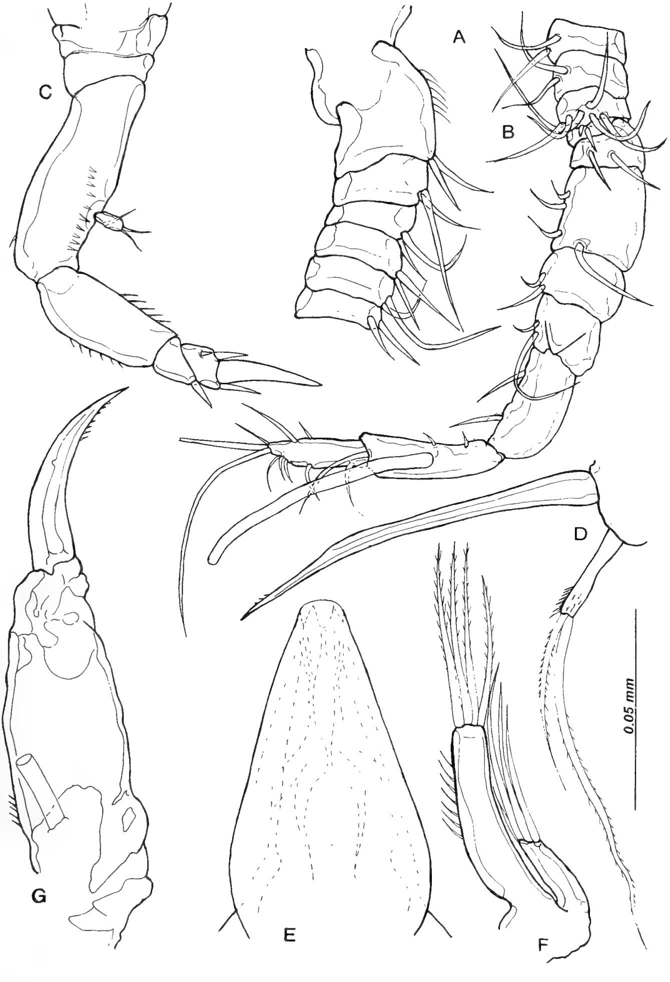

Fig. 2. *Laperocheres koorius* n. gen. n. sp. Male. A, Antennule, segments 1–6, lateral; B, Antennule, segments 7–17, anterior; C, Antenna, anterior; D, Mandible; E, Oral siphon, anterior; F, Maxillule; G, Maxilla.

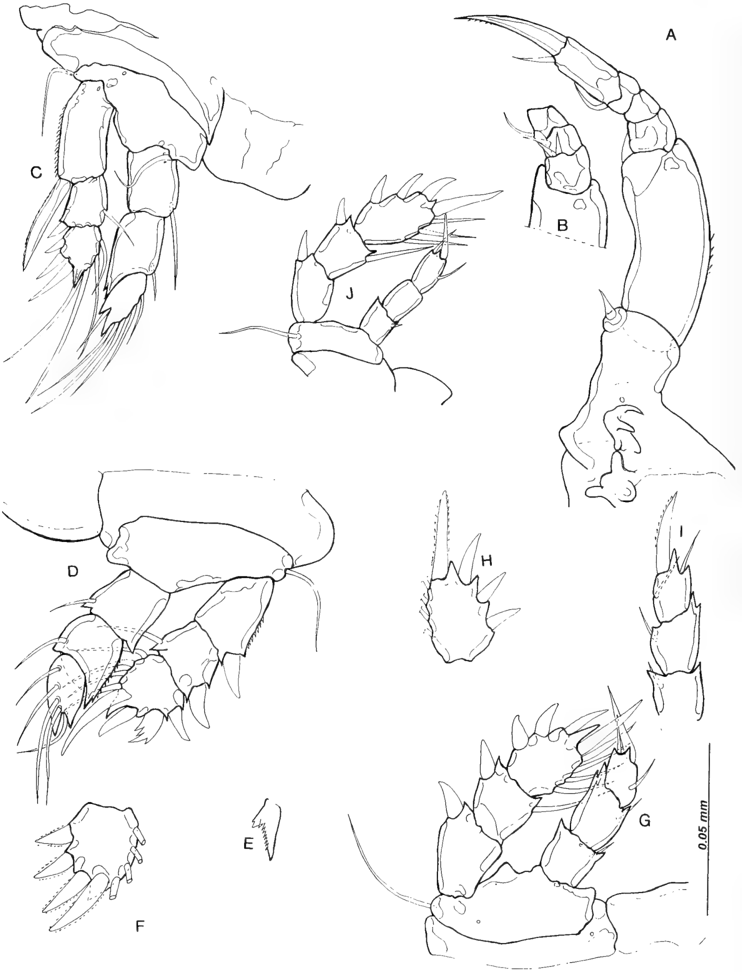

Fig. 3. *Laperocheres koorius* n. gen. n. sp. A, Male, maxilliped, anterior; B, Male, maxilliped, detail of segments 3–5, posterior; C, Male, leg 1, anterior; D, Male, leg 2, posterior; E, Male, leg 2, modified outer spine on distal segment of exopod, lateral; F, Female, leg 2, distal segment of exopod, posterior; G, Male, leg 3, anterior; H, Female, leg 3, distal segment of exopod; I, Female, leg 3, endopod; J, Male, leg 4, posterior.

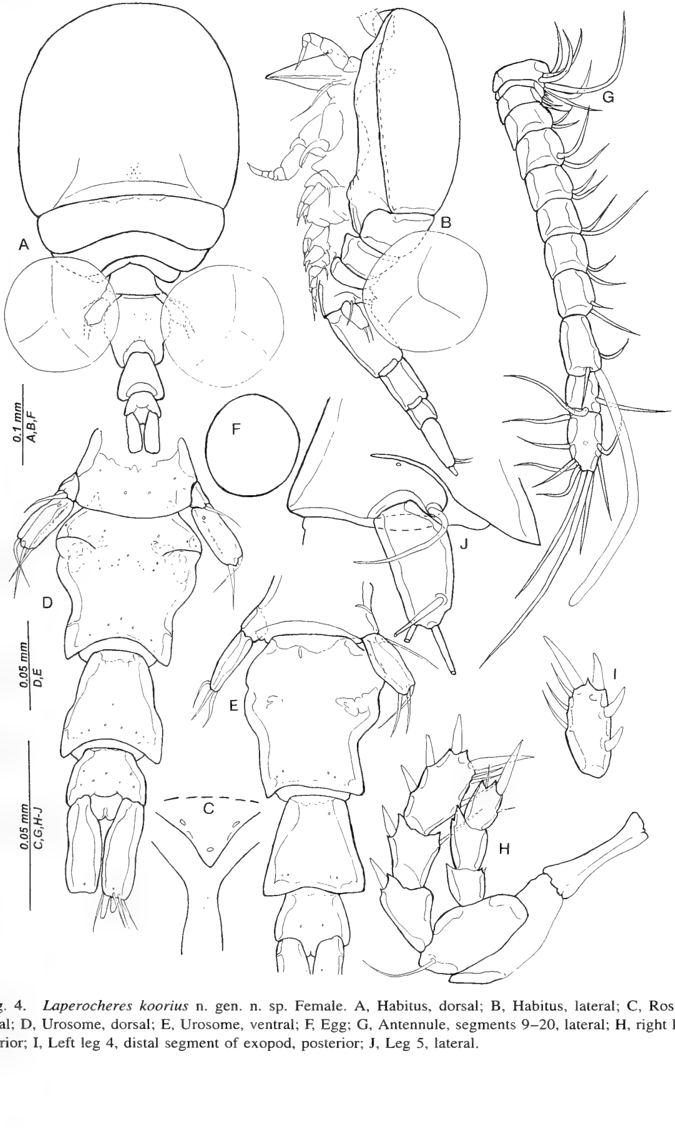

Fig. 4. *Laperocheres koorius* n. gen. n. sp. Female. A, Habitus, dorsal; B, Habitus, lateral; C, Rostrum, ventral; D, Urosome, dorsal; E, Urosome, ventral; F, Egg; G, Antennule, segments 9–20, lateral; H, right leg 4, posterior; I, Left leg 4, distal segment of exopod, posterior; J, Leg 5, lateral.

	coxa	basis	exopod	endopod
Leg 1	0-0	1-1	I-0;I-1;III,4	0-1;0-1;1,5
Leg 2	0-0	1-0	I-0;I-1;III,I,4	0-1;0-1;1,4
Leg 3	0-0	1-0	I-0;I-1;III,I,4	0-1;0-1;1,I,1
Leg 4	0-0	1-0	I-0;I-1;III,I,3	0-1;0-0;1,I,1

Distal segment of exopod of leg 2 with modified lateral spine (Fig. 3E).

Leg 5 (Fig. 1G): 2-segmented. First segment fused only ventrally with somite, armed with one lateral seta. Second segment free, elongate, with 3 setae.

Leg 6 (Fig. 1E): represented by posteroventral flap with 2 posterior setae. Color of living specimens unknown.

Female.—Body cyclopiform (Fig. 4A, B). Total length, excluding caudal setae, 0.55–0.58 mm; greatest width 0.27–0.28 mm, based on 2 specimens. Dorsoventral thickness of figured specimen on the level of ventral projection between maxilliped and first 0.49 mm; ratio of length of prosome to that of urosome 1.4:1; ratio of length to width of prosome 1.2:1. Prosome more thickened dorsoventrally than in male. Lateral edge of cephalothorax shield ornamented with pores on dorsolateral surface. Urosome (Fig. 4D, E) consisting of 4 articles ornamented with pores and sensilla: somite with leg 5, genital double-somite and two abdominal somites. Genital areas located dorsolaterally in anterior half of second urosomal somite. Copulatory pores situated ventrally beneath genital areas.

Rostrum (Fig. 4C): weakly developed, with pore and two sensillae, as in male.

Egg sacs (Fig. 4A, B): round, with 3 eggs. Egg as in Fig. 4F. Oral siphon, caudal ramus, antennae, mandible, maxillule, maxillae, maxilliped, and leg 1 like those of male.

Antennule (Fig. 4G): 20-segmented. Segments 1–10 as in male. Armature of segments is as follows: 2, 2, 2, 2, 2, 2, 2, 2, 7, 1, 2, 2, 2, 2, 2, 2, 2, 2+1 aesthetasc, 2, and 10 setae, respectively. Aesthetasc on segment 18, segment 10 reduced.

Leg 2 (Fig. 3F): same as in male, but differs in having unmodified spines on distal segment of exopod.

Leg 3 (Fig. 3H, I): differs from male in having less developed spiniform terminal tip on third exopodal segment.

Leg 4 (Fig. 4H, I): differs from male in asymmetrical position of inner setae on distal segment of exopod and two spiniform outerdistal points of second segment of endopod.

Leg 5 (Fig. 4J): differs from male in proportions of free segment being more broad.

Leg 6: without setae on genital area.

Etymology.—The specific name is derived from the name of Australian indigenous people living in the area around the sampling site, referring themselves as "koori".

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Pseudione humboldtensis, a new species (Isopoda: Bopyridae) of parasite of *Cervimunida johni* and *Pleuroncodes monodon* (Anomura: Galatheidae) from the northern coast of Chile

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Abstract.—*Pseudione humboldtensis,* a new species of bopyrid parasite of the squat lobsters *Cervimunida johni* and *Pleuroncodes monodon,* from the Northern coast Chile is described. This increases to six the number species of the genus *Pseudione* in Chile. *P. humboldtensis* clearly differs from the other species in the presence of smooth edges of the coxal plates, laterals and barbules, the large pleopods and the development of the female pereiopods. This new record increases the total number of bopyrid species in Chilean waters to nine.

The Family Bopyridae includes 500 described species in the world, only 29 of them recorded from Eastern Pacific coast and 7 from Chile (Markham, 1992): *Pseudione galacanthae* Hansen, 1897, parasite of *Munida subrugosa* on the east Patagonian coast; *Pseudione tuberculata* Richardson, 1904, parasite of *Neolithodes diomedeae* from Port Ortway; *Pseudione pausicecta* Richardson, 1904 parasite of *Munida curvipes* from the same locality; *Stegophryxus thompsoni* Nierstrasz & Brender à Brendis, 1931, parasite of pagurids; *Ionella agassizi* Bonnier, 1900, and *Ione ovata* Shiino, 1964, from Puerto Montt, both parasites on *Neotripaea uncinata*; and *Pseudione brattstroemi* described by Stuardo et al. (1986a) from Coliumo Bay, also parasitizing *C. uncinata.* Finally, Román-Contreras & Wehrtman, (1997) added a new species to this list describing *Pseudione chiloensis* a parasite of the caridean *Nauticaris magellanica.*

During a fisheries biology study off the northern-central Chilean coast, numerous specimens of the squat lobster *Cervimunida johni* Porter, 1903 were found parasitized by a new bopyrid species present in the gill chambers. The morphology of the male and female of this species are described and some aspects of the host-parasite relationship are discussed.

Order Isopoda
Suborder Epicaridea
Family Bopyridae
Genus *Pseudione*
Pseudione humboldtensis, new species
Figs. 1–2

Material examined.—1530 specimens of *Cervimunida johni* collected from 12 different fishing grounds along the north central Chilean coast from 26°58′56″S to 32°01′81″S from August to October 1994.

Type series.—Holotype ovigerous female, Museo Nacional de Historia Natural de Chile (MNHNC) 11151; Allotype adult male MNHNC 11152; bottom trawling, 26°59′56″S, 70°57′90″W; 19 Aug 1994.

Female.—Oval body 7.7 ± 0.7 mm in length and 6.4 ± 0.6 mm in wide ($n = 12$). Cephalon, pereion and pleon clearly detectable, symmetric or slightly asymmetric (Fig. 1a, 1b).

Cephalon round trapezoid, dorsal side

convex, wide and well developed frontal lamina, eyes absent.

Antennule with 3 articles completely covered by scales, article 1 massive subcubic; article 2 truncated, cone shape, with some subapical setae and a crown of apical setae; article 3 conical with 8 distal setae (Fig. 1c).

Antenna with 5 articles all with scales on surface; article 1 rectangular; article 2 conical with 1 subapical seta; article 3 similar in shape but thinner, with 2 subapical setae; article 4 cylindrical with medial and terminal setae; terminal article an ovoid flagellum with 8 distal setae (Fig. 1d).

Maxilliped of 2 articles, smaller article rounded and with irregular margin, inserted into larger endite; endite with simple palp with 13 apical and 4 basal setae (Fig. 1e, 1f).

Posteroventral edge of cephalon or barbula with 2 elongate lateral projections with smooth edges, internal margin with small digitiform projections (Fig. 1g).

Pereon of 7 pereomeres clearly detectable, coxal plates with smooth edges.

Pereopods covered by scales; increasing in size posteriorly; basis wide and well developed, ischium cylindrical with tubercles on lateral margin, increasingly conspicuous in posterior pereopods; meri subquadrate; carpi conical with group of distal setae; propodi ovoid and terminating in claw-like dactyli (Fig. 1h, i, j).

Five pairs of marsupial oostegites, first pair bilobed and separated by horizontal band with numerous digitiform projections (Fig. 1k). Posterior lobe with marginal or posterolateral round projection (sensu Markham, 1985). Other oostegites lamellar, concave with setose posterior edges (Fig. 1l), except second completely surrounded by setae.

Pleon of 5 pleomeres and pleotelson. Pleotelson with central lobe. Pleopods biramous, well-developed, with globular elongate sac-like shape of smooth edges, reaching almost entire body length, with small tubercles randomly located (cellular group). Uropods uniramous and of similar shape to pleopods, but smaller (Fig. 1m). Lateral plates of same shape of pleopods.

Male.—Body elongate, 5.8 ± 0.6 mm long and 1.8 ± 0.4 mm broad ($n = 12$). Cephalon, pereomeres and pleomeres completely differentiated, maximal width at the fourth pereomere (Fig. 2a, b).

Cephalon trapezoidal with two dorsal cephalic fissures, and two slightly pigmented anterior areas. Oral cone behind antennas and simple oral palps.

Antennulas of 3 articles; ovoid antennular base, second segment cylindrical, apex with 8 setae reaching the flagellum or last segment; flagellum with 10 central setae distally (Fig. 2c).

Antenna of 5 articles, massive base with distal portion wider than proximal; segment 2 of similar shape but shorter and thinner; segment 3 cylindrical distally setose; segment 4 cylindrical with a subapical constriction, the terminal edge of the segment with a crown of setae; segment 5 ovoid with 8 apical setae (Fig. 2d).

Pereon of 7 pereomeres clearly detectable, all rectangularly rounded united by a marked constriction.

Pereiopods covered by scales, similar in size; basis cylindrical and decreasing in size posteriorly; ischium tubular without tubercles; meri and carpi similar to those of female; propodi ovoid and larger posteriorly; dactyli prominent, claw-like and setose on internal edges (Fig. 2e, f, g).

Pleon of 5 pleomeres besides pleotelson; first 4 pleomeres similar in shape to pereiomeres, but thinner; fifth pleomere of fanlike shape like pleotelson, latter with a central sharp in its lower edge. No pleopods or tubercles.

Etymology.—The specific names is in reference to the Humboldt current off of the Chilean coasts.

Distribution.—Off the northern Chilean coast from 25° to 32°S, in a depth range between 137 and 408 m.

Hosts.—*Pseudione humboldtensis* is found parasitizing two galatheid species,

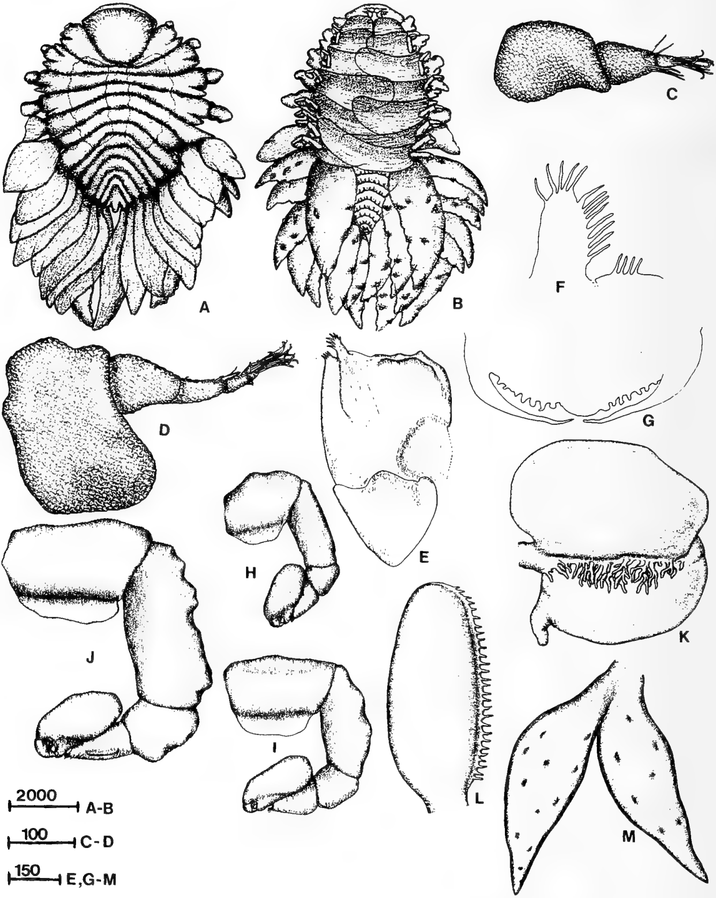

Fig. 1. *Pseudione humboldtensis,* new species, holotype female. A. Dorsal view. B. Ventral view. C. Antennula. D. Antenna. E. Maxilliped. F. Maxilliped palp. G. Barbules. H. First left pereiopod. I. Fourth left pereiopod. J. Seventh left pereiopod. K. First right oostegite. L. Last right oostegite. M. Uropods. Scale in microns.

Cervimunida jonhi Porter, 1903 with a prevalence of 5.8% ($n = 1530$) and *Pleuroncodes monodon* (H. Milne Edwards, 1837) with an prevalence of 0.4% ($n = 144$). In both squat lobsters, the bopyrid occupies the gill chambers with a density of 1–8 parasites per host in *C. jonhi* and 1–2 in *P. monodon.*

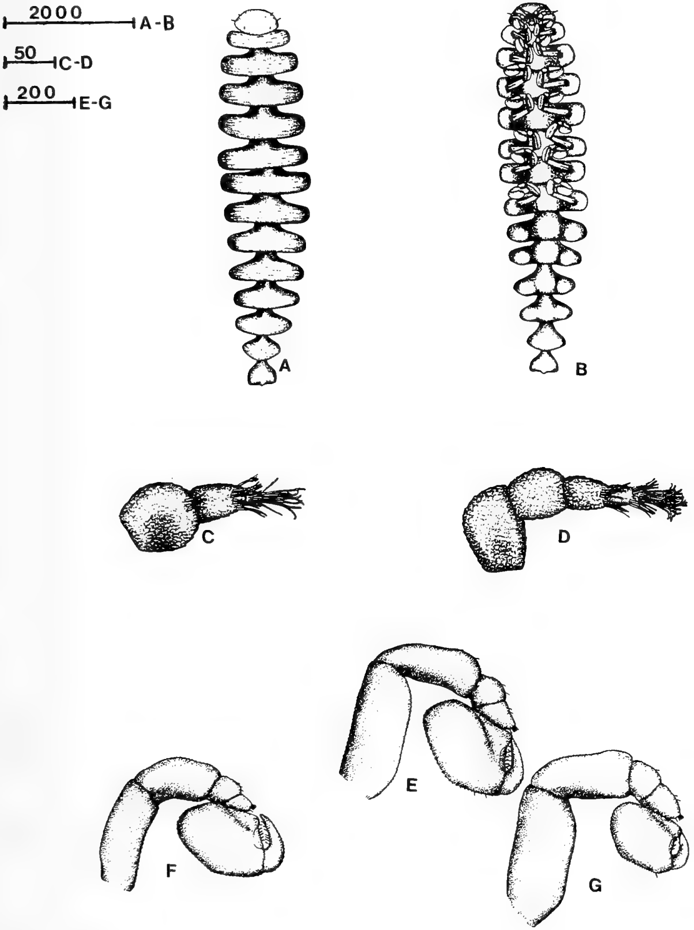

Fig. 2. *Pseudione humboldtensis*, new species, holotype male. A. Dorsal view. B. Ventral view. C. Antennula. D. Antenna. E. First left pereiopod. F. Fourth left pereiopod. G. Seventh left pereiopod. Scale in microns.

Discussion

Species of the genera *Pseudione* and *Munidion* are the main bopyrid parasites in galatheids of the American coast of the Pacific, differing in the presence of a maxillar palp in *Pseudione* female and the fusion of the pleomers of *Munidion* male (Markham, 1975, 1985).

Cervimunida johni and *Pleuroncodes monodon* are two new hosts of this parasitic isopod group. Only the presence of *Munidion pleuroncodis* on the squat lobster *Pleuroncodes planipes* in the coast of California had been previously recorded (Markham 1975).

Pseudione humboldtensis is similar to *P. brattstroemi* and differs clearly from *P. galacanthae, P. tuberculata* and *P. pausicecta* in the larger size of female pleopods. However, there also are important morphological differences between both bopyrids. *P. humboldtensis* possesses smooth edges in the lateral coxal plates and barbulas, is larger in size, all pereiopods are similar, and lateral plates extremely extended in the female. *P. brattstroemi* has some segments of its pereiopods reduced or atrophied, and lateral plates and pleopods less developed. The males differ mainly in the shape of the pleotelson, it is similar to the pleomeres in *P. brattstroemi* and is fanlike in *P. humboldtensis.*

Pseudione brattstroemi infests *Neotripaea uncinata,* which lives mainly in the shallow subtidal (Stuardo et al. 1986a). The hosts of *P. humboldtensis,* the squat lobsters *C. johni* and *P. monodon,* occur between 130 and 400 m deep where dissolved oxygen and temperature are lower. This could explain the larger development of female pleopods of this bopyrid, since these are respiratory in function (Shultz 1969).

With the discovery and description of *P. humboldtensis,* the number of species of bopyrids recorded in Chilean waters now is nine, six in the genus *Pseudione.*

Acknowledgments

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Ekleptostylis heardi (Diastylidae), a new cumacean species from South Atlantic waters

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Abstract.—A new species of Diastylidae in the genus *Ekleptostylis* was discovered among cumacean specimens collected at two stations in the South Atlantic by the R/V *Eltanin* in 1962. The new species, *E. heardi,* features a smooth, unornamented carapace, a rounded distal process on the basis of the second peraeopod of males, and a telson which is shorter than the telsonic somite and which, in males, exhibits a flattened dorsal process strongly produced posteriorly over the terminal part. The characteristic telson process is shared by its only other congener, *E. walkeri* (Calman, 1907) and by the similar *Diastylis pseudinornata* Ledoyer, 1977, which also occurs in the South Atlantic. Both sexes of *E. heardi* differ from the preceding two species and from other similar species of *Diastylis* by the spination of the telson, uropods, and third maxilliped, and by other aspects of the carapace.

We were recently given the opportunity to examine specimens of an unidentified cumacean in the family Diastylidae collected from extreme South Atlantic and Antarctic waters and made available for study by the Smithsonian Oceanographic Sorting Center. Characteristics of the specimens place them in the obscure genus *Ekleptostylis* (Stebbing, 1912) previously reported mainly in the north Atlantic and Mediterranean. The specimens were obtained from two samples collected in December 1962 by the R/V *Eltanin* one from very deep water (3474–3590 m) north of the Antarctic Peninsula, and the other from relatively shallow water (119 m) on the Patagonian Shelf south of the Falkland Islands and east of Tierra del Fuego. Although many other samples were examined from collections made at various depths from these areas, no other specimens of the new species were found. Type specimens of the new species are deposited in the U.S. Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.; additional material is deposited in the museum of the Gulf Coast Research Laboratory (GCRL), Ocean Springs, MS.

The cumacean family Diastylidae includes an extensive group of somewhat loosely related genera, most of which, like the type genus *Diastylis,* have two terminal spines on the telson. Among the genera of Diastylidae, the formerly monospecific genus *Ekleptostylis,* has characteristics similar to *Diastylis* except that it has a telson shorter than the telsonic somite (sixth abdominal segment) and similar to *Leptostylis* except that the flagellum of the second antenna of males greatly exceeds the end of the body. Similarities to *Leptostylis* also include the first antenna of males with the third peduncular article bearing a brush-like tuft of setae and the endopods of the uropods being longer than the exopods. Stebbing (1912: 153) erected the genus to include the single species *E. walkeri* (Calman, 1907), formerly of the genus *Leptostylis,* in which the male has a telson with "a lobe uniquely produced over the narrow distal portion." His meager generic diagnosis induced Fage (1951) to provide a more thorough description of *E. walkeri,* to which he added to the generic diagnosis the important feature of a rounded apical process on the basis of the second peraeopod of males. The new species described herein, *E. heardi,* extends the range of this genus to the South Atlantic.

Genus *Ekleptostylis* Stebbing, 1912
Ekleptostylis heardi, new species
Figs. 1–5

Holotype.—Adult non-ovigerous (incubatory) female (USNM 230401). Type locality: Station 363, 600 km north of Antarctic Peninsula (57°09′S, 58°58′W), 3590 m depth, 7–8 Dec 1962, R/V *Eltanin* Cruise 6.

Paratypes.—From same sample: 1 male, damaged, P1 removed, abdominal half missing (USNM 230402); 8 males, 11 ovigerous females, 10 subadult females, 7 juveniles (USNM 230403); 1 ovigerous female, remnants of dissection (USNM 230404).

Additional material examined.—Station 344, 500 km east of Tierra del Fuego (54°04′S, 58°46′W), 119 m depth, 4 Dec 1962, R/V *Eltanin* Cruise 6: 6 males, 10 incubatory females, 8 ovigerous females (GCRL 1372).

Description of adult incubatory female.—Total body length 5.7–8.5 mm (17 individuals measured, mean = 7.3 mm). Carapace (Fig. 1D, E) less than 1.5× longer than deep, greater than 1.5× longer than broad, with fine granular ornamentation. Antennal notch well developed. Anterolateral margin of carapace finely serrate immediately posterior to antennal notch. Pseudorostrum moderately produced, frontal lobe broad; ocular lobe small, eyes absent. Thorax approximately 0.4× carapace length; all segments visible dorsally; fifth segment narrow, with rounded posterolaterally produced corners. Cephalothorax about 0.8× length of abdomen.

First antenna (Fig. 2A): First article of peduncle stout, approximately same length as second and third articles combined, with large plumose seta at distal end; third article longer and narrower than second. Main flagellum with 3 articles; article 2 with 2 multiarticulate aesthetascs emerging from near distal end, aesthetascs approximately as long as 3 flagellar articles combined. Accessory flagellum less than half length of main flagellum, with 3 articles; second article longer than other 2 combined; third article with 2 aesthetascs and 1 hair seta of approximately equal lengths at distal end; seta shorter than combined articles of flagellum.

Second antenna (Fig. 2B): composed of 2 articles, first slightly longer than second. First article with stout plumose seta at distal end; second article with long plumose seta emerging at mid-length, short plumose seta at distal end. Total length of second antenna approximately one third length of first antennal peduncle.

Mandible (Fig. 2C): Large, boat-shaped, with well-developed pars molaris and pars incisiva, latter with 4 teeth; well-developed lacinia mobilis on left mandible, with 3–4 teeth. Each mandible bearing 11–13 plumose setae between incisor and molar processes, with small recurved spine at proximal end of setal row.

First maxilla (Fig. 2D): 2 endites twice as long as broad; smaller endite with 4 thick and 1 slender distal setae. Palp with 2 distal setae (filaments) of equal length.

Second maxilla (Fig. 2E): 2 endites slightly longer than broad, each with 3–4 distal pectinate spines. Setose lateral (flagellum exopod) with short, 2-articulate palp at distal end.

First maxilliped (Fig. 3A): Composed of 6 articles; basis broad, longer than remaining articles combined, with row of 5 short plumose setae on inner margin. Endite with specialized structures consisting of 3 curved spines, 1 tri-dentate spine, 2 coupling hooks, and 2 plumose setae located near base. Ischium short, wider than long,

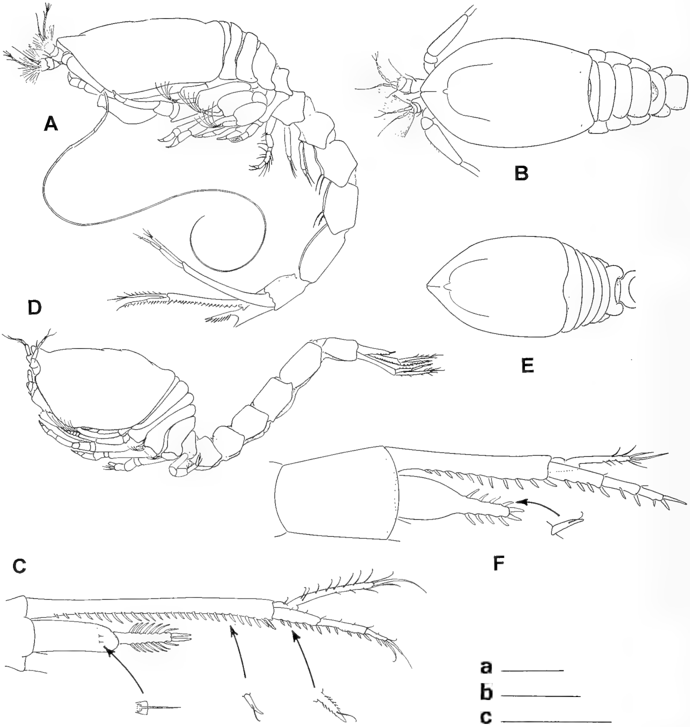

Fig. 1. *Diastylis heardi,* n. sp. Male: A, lateral view of whole animal; B, dorsal view of cephalothorax; C, telson and uropod, dorsal view, insets showing spinal detail. Female (incubatory): D, lateral view of whole animal; E, dorsal view of cephalothorax; F, telson and uropod, inset showing spinal detail. Scales: a = 1.0 mm (A, B, D, E); b = 0.5 mm (C); c = 0.5 mm (F).

with 2–3 short plumose spinules on distal third of inner margin; outer margin naked. Merus, inner margin with 2 rows of denticulate spines and hair setae, distally with short plumose seta and 2 partially fused plumose setae on inner and outer margins respectively. Carpus inner margin with row of fine hair setae; outer distal margin with 1 apical and 1 subapical long plumose setae, 1 subproximal simple seta, 2 comb setae adjacent to base of propodus. Propodus with thick distal spine setae and 2–3 simple setae. Dactylus in the form of a thick spine approximately same length as propodus.

Second maxilliped (Fig. 3B): Composed of 6 articles; basis slightly less than half total length of appendage, distal end with 4 large plumose setae on inner margin, 3 stout hair setae near outer margin. Ischium with 2 large plumose setae on inner margin. Merus with 7 stout plumose setae on inner margin, 3 longer plumose setae on outer

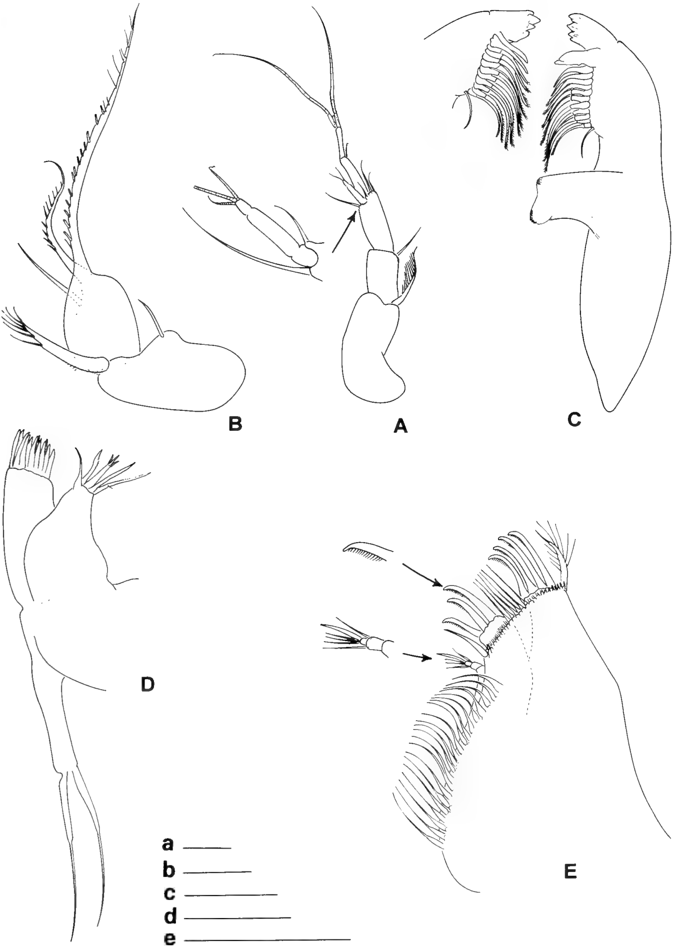

Fig. 2. *Diastylis heardi,* n. sp. Incubatory female: A, first antenna, inset showing accessory flagella; B, second antenna; C, mandibles; D, first maxilla; E, second maxilla, insets showing pectinate spine detail and palp. Scales: a = 0.1 mm (C); b = 0.1 mm (D); c = 0.1 mm (E); d = 0.1 mm (B); e = 0.5 mm (A).

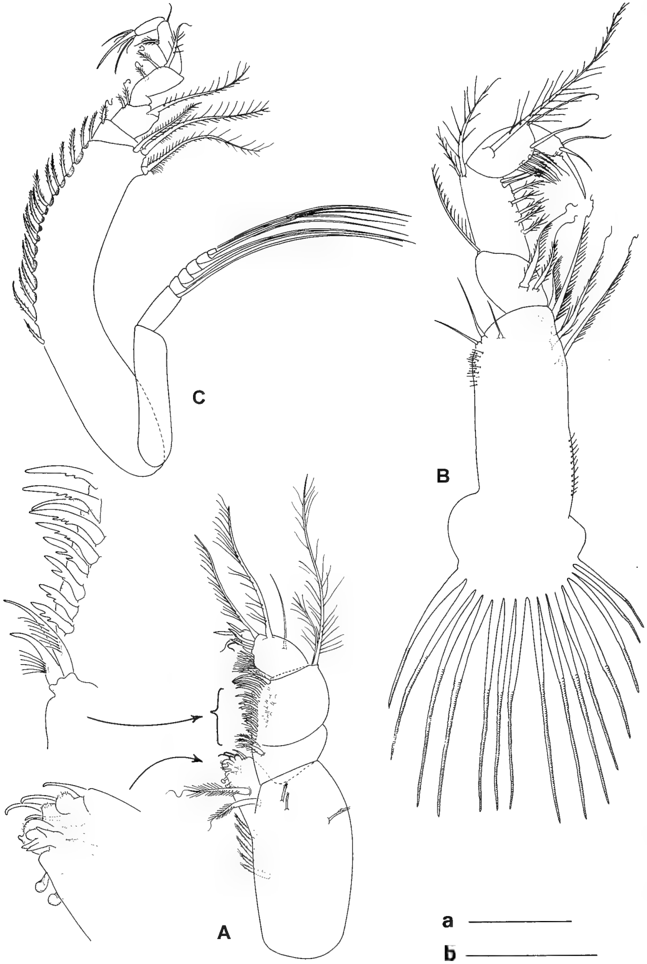

Fig. 3. *Diastylis heardi,* n. sp. Incubatory female: A, first maxilliped, insets showing denticulate spines on carpus and detail of endite; B, second maxilliped; C, third maxilliped. Scales: a = 0.2 mm (A, B); b = 0.5 mm (C).

margin, 1 at proximal end and 2 at distal end. Carpus with 1 large mesial plumose seta near proximal end, row of small plumose setae on inner margin, 2 hair setae, 1 at each distal corner. Propodus shorter than carpus, with 2 hair setae at distal end. Dactylus in form of strong spine, bent back toward base of appendage; length exceeds that of propodus. Oostegite rudimentary, with 15–17 setae, each with annulations on distal half. All plumose setae end in coiled filaments.

Third maxilliped (Fig. 3C): Basis over twice length of remainder of appendage, curved, with 17 short plumose setae on exterior lateral margin, 3 large plumose setae at distal end of interior margin. Ischium short, wedge-shaped, inner margin with one short, plumose distal seta. Merus about as long as wide, with large, plumose distal seta on outer margin, 2 short, plumose distal setae on inner margin. Carpus approximately as long as ischium and merus combined, with 3 short plumose setae on distal half of inner margin. Propodus approximately as long as carpus, with 2 small plumose setae on middle of inner margin, 1 small hair seta on outer distal margin. Dactylus shorter than propodus, terminating in 1 long spine and several simple setae. Exopod composed of single peduncular article and 6-articulate flagellum, each flagellar article with 2 terminal setae.

First peraeopod (Fig. 4A): Basis curved nearly 90 degrees, approximately 0.7× length of remaining articles, lateral margins heavily setose on distal half. Propodus nearly as long as ischium, merus, and carpus combined. Dactylus approximately same length as ischium and merus combined, terminating with 3 thick simple setae. Exopod flagellum with 8 articles, otherwise similar to that of third maxilliped, approximately as long as basis of endopod.

Second peraeopod (Fig. 4B): Smaller than first peraeopod. Basis slightly curved, approximately as long as next 3 articles combined. Ischium very short, wedge-shaped. Carpus with 2 stout spines at distal end. Propodus with 1 stout spine at distal end. Dactylus with 3–4 thick terminal setae. Exopod longer than basis, otherwise similar to that of in peraeopod 1.

Third and fourth peraeopods (Fig. 4C, D): Basis long, straight, similar in both appendages except longer than remaining articles combined in peraeopod 3 and about ⅔ length of remaining articles combined in peraeopod 4. Ischium + merus equal to carpus + propodus in length. Exceptionally thick setae at distal ends of carpus (2) and propodus (1). Dactylus terminates in large stout spine twice as long as dactylus. Exopod rudimentary, with 2 articles.

Fifth peraeopod (Fig. 4E): Similar to peraeopods 3 and 4 except relatively shorter; basis about half length of remaining combined articles. Carpus and propodus each with single exceptionally thick seta, overreaching terminal spine of dactylus. Without exopod.

Telson and uropods (Fig. 1F): Telson 0.89× length of telsonic somite (6th abdominal segment), 0.75× length of uropodal peduncles; with 2 terminal spines, 4–5 pair of lateral spines. Peduncles with 11 lateral spines. Exopods 2-articulate, with nearly imperceptible articulation formed by 2 deep notches proximally, on dorsal and lateral margins. Endopods 3-articulate, bearing 4, 2, and 2 spines respectively in proximal to distal articles, entire endopod longer than exopod. Both rami terminate in a long spine. Each lateral spine on telson, peduncles and endopods with sub-terminal hair seta.

Description of mature male.—Males are distinctly sexually dimorphic from females in the following respects:

Total length 7.5–9.1 mm. (9 individuals measured, mean = 8.5 mm.) Carapace (Fig. 1A, B) 2.5× longer than deep, 1.5× longer than broad. Antennal notch absent. Thorax approximately 0.5× carapace length; all segments visible dorsally; first segment reduced to narrow band, lateral margins obscured, overreached by carapace and anterolateral corners of second segment; pos-

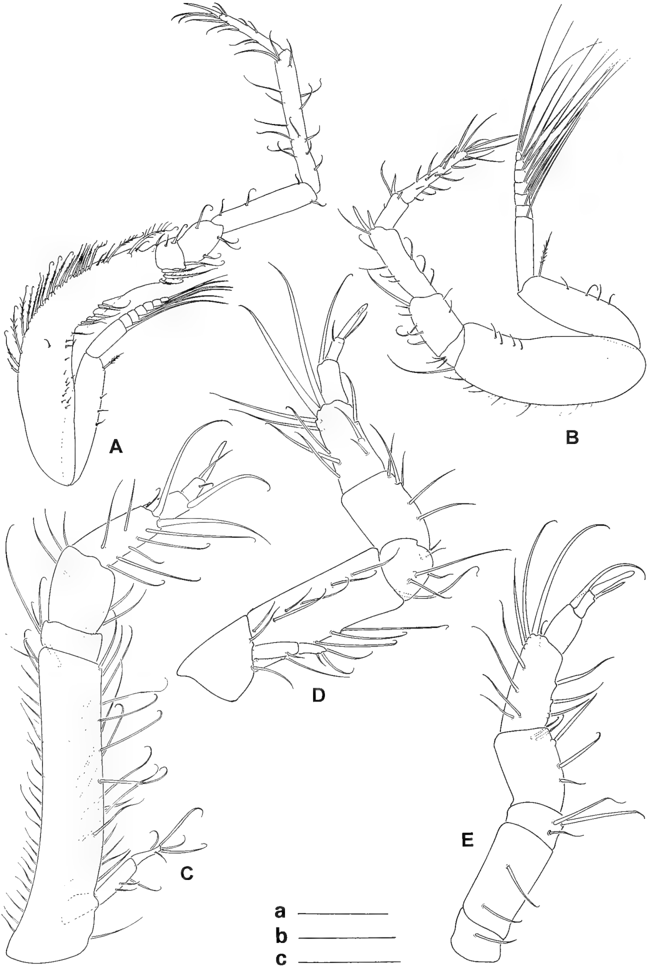

Fig. 4. *Diastylis heardi,* n. sp. Incubatory female: A, first peraeopod; B, second peraeopod; C, third peraeopod; D, fourth peraeopod; E, fifth peraeopod. Scales: a = 0.25 mm (C, D, E); b = 0.5 mm (A); c = 0.5 mm (B).

terolateral margins of segments 2–5 produced, visible dorsally. Cephalothorax about 0.8× length of abdomen.

First antenna (Fig. 5A): Third article with conspicuous, thick brush-like tuft of hair filaments surrounding flagella, 2-articulated accessory flagellum terminating in long hair seta, 5-articulated main flagellum terminating in 3 multiarticulate aesthetascs.

Second antenna (Fig. 5B): First and second articles with 1 and 2 plumose setae respectively. Fifth article wide, tapering distally, longer than preceding four articles combined. Flagellum long, extending past ends of uropods.

Peraeopods (P1—Fig. 5C; P2—Fig. 5D): Exopods present on peraeopods 1–5; endopods and exopods with enflated bases; otherwise similar to female except peraeopod 2 with conspicuous apical rounded process on basis and distal plumose seta on first article of exopod flagellum.

Abdomen: Pleopods (Fig. 5E, F) present on first and second segments; third and fourth segments with pleopods replaced by single plumose setae.

Telson and Uropods (Fig. 1C): Telson 0.69× length of telsonic somite, 0.54–0.59× length of uropodal peduncles; with 2 terminal spines, 5–7 pairs of lateral spines; with flattened dorsal process strongly produced posteriorly over the terminal part; with pair of ventral anal valves. Dorsal process with row of closely spaced "scales" on lateral margin, extending from base of telson, around end of process and back to base; scales pointed near base of process, becoming rounded at distal end. Pair of small, slender spines located near distal end of process lying flat against dorsal surface (see inset, Fig. 1C), each with pair of short, broad companion setae situated laterally at base. Uropodal peduncles 1.6× length of exopods, with 20–27 medial spines. Endopods with 3 articles, with 6–8, 4–5, and 2–3 medial spines respectively. Exopods slightly shorter than endopods; 2-articulate with proximal notches as in female. Spines toward distal end of peduncle and on endopod barbed, possessing hair setae as in female.

Distribution.—Known only from the type locality, north of the Antarctic Peninsula, and from the nearby southern tip of South America.

Etymology.—Named for Richard W. Heard in honor of his numerous contributions to the study of Cumacea and other crustaceans.

Remarks.—*Ekleptostylis heardi* differs from its congenitor, *E. walkeri* mainly by spination of the telson and uropods. Fage (1951:125) described females of *E. walkeri* as having a telson with 14–15 lateral spines, the uropod peduncle with about 20 lateral spines, and the the endopod of the uropod with 7-1-1 spines respectively on its three proximal to distal articles. Conversely, the females of *E. heardi* have 4–5 telson spines, 11 uropodal peduncle spines, and 4-2-2 spines on the three endopodal articles of the uropod. The female telson of *E. walkeri* is about 0.75× and 0.47× the lengths of the 6th abdominal somite and uropodal peduncles respectively, whereas in *E. heardi* these proportions are 0.89× and 0.75×. The males of *E. walkeri,* while not thoroughly described by Fage, appear to have a telson similar in appearance and spination to that of *E. heardi*; the second peraeopods, however, differ in that the dactylus is much longer in comparison to that of *E. heardi,* being about the same length as the carpus, whereas in *E. heardi,* the dactylus is shorter, about 0.7× the length of the carpus.

Ekleptostylis heardi appears also to be very similar to *Diastylis pseudinornata* Ledoyer, 1977, described from Kerguelen Island, in the far southern Indian Ocean. Ledoyer's description of the male of this species did not mention the second peraeopod nor features of the first antennae. However, his figure 4a shows the brush-like tuft of hair filaments on the third article of the male first antennae and a dorsal telson structure similar to that of *E. heardi.* These characteristics suggest that *D. pseudinor-*

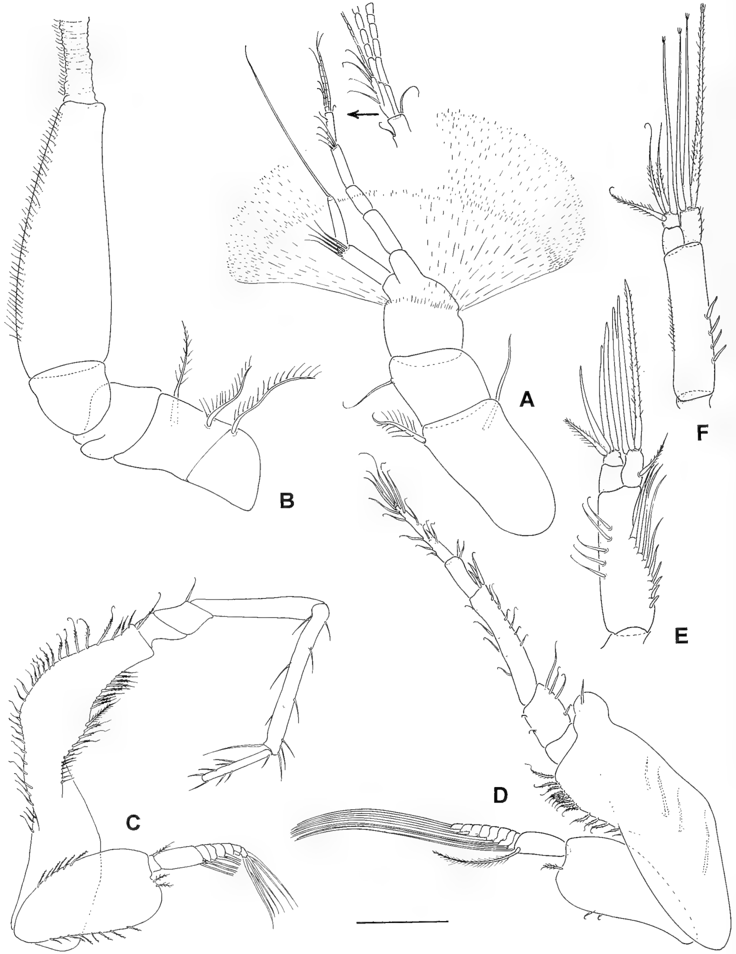

Fig. 5. *Diastylis heardi,* n. sp. Male: A, first antenna, inset showing distal end detail of main flagellum; B, second antenna; C, first peraeopod; D, second peraeopod; E, first pleopod; F, second pleopod. Scale = 0.25 mm (A, B, D, E, F), 0.5 mm (C).

nata may in fact belong in the genus *Ekleptostylis.* The male telson of the two species differ in the number of lateral spines, 3 pairs on *D. pseudinornata,* as opposed to 5–7 pairs respectively on *E. heardi*; no data are given on the male uropod characteristics of *D. pseudinornata.* According to Ledoyer's description, the females of *D. pseudinornata* are also very similar to those of *E. heardi*; however, the first two thoracomeres of the female *E. heardi* lack anterior prolongations, a determining characteristic of *D. pseudinornata,* and the first four articles of the third maxilliped in *D. pseudinornata,* especially the merus, bear 1–3 large teeth, whereas these teeth are lacking in *E. heardi.*

The prominent dorsal process on the male telson of *E. heardi* is also present in *Diastyloides carpinei* as illustrated by Băcescu (1969:164); however this species, from the Mediterranean, differs generically from other members of Diastylidae by virtue of its broad, truncate mandibular base (boat-shaped in *Diastylis* and others).

Diastylis inornata Hale, 1937, another similar Antarctic species with a smooth carapace, is distinguished from *E. heardi* by the near absence of an antennal notch and by having fewer (3) lateral telson spines. The male of *D. inornata* is unknown.

Because of the large disparity in depths between the two stations where *Ekleptostylis heardi* occurred (3490 and 119 m), it is likely that the species is distributed widely in the South Atlantic and Antarctic region.

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Taxonomy and distribution of the parasitic isopod *Progebiophilus bruscai* Salazar-Vallejo & Leija-Tristán, 1990 (Crustacea: Bopyridae)

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Abstract.—*Progebiophilus bruscai* Salazar-Vallejo & Leija-Tristán, 1990 parasitizing the mud shrimps *Upogebia dawsoni* Williams, 1986 and *U. macginitieorum* Williams, 1986 is redescribed, reillustrated and its synonymy is updated. We point out those characters that permit separation from its congeners. The updated distribution of this species is: Mexican Pacific, Gulf of California, from San Felipe, Baja California (BC) to La Paz Bay, Baja California Sur (BCS) and west coast of the BC Peninsula at Tortugas Bay, BCS, and Todos Santos Bay (Estero Punta Banda), BC.

Epicaridean isopods of the family Bopyridae are holoparasites of crustaceans (Markham 1985). Hosts include carideans, penaeoids, brachyurans, anomurans and thalassinoids (Markham 1986). Campos & Campos (1989a), Markham (1992) and Román-Contreras (1993, 1996) have recorded 14 described species along the Pacific coast of Mexico. Of these, the only branchial parasite of thalassinoid shrimps of the genus *Upogebia* (Family Upogebiidae) is *Progebiophilus bruscai* Salazar-Vallejo & Leija-Tristán, 1990. A second species parasitic on mud shrimps is *Phyllodurus abdominalis* Stimpson, 1857; it is an abdominal parasite of *U. macginitieorum* Williams, 1986 and *U. pugettensis* (Dana, 1852) (Markham 1977; Campos-González & Campoy-Favela 1987).

Collection of *Upogebia* spp. along the Gulf of California and on the west coast of the Baja Peninsula at Tortugas Bay, Baja California Sur and Todos Santos Bay, Baja California, produced additional material of *P. bruscai.* The host animals were collected intertidally in burrows. *Upogebia macginitieorum* was collected by hand, under rocks, and *U. dawsoni* Williams, 1986 in soft sediments using a Yabby pump (see Manning 1975). The study of the new material of *P. bruscai* allows us to recognize unrecorded shared morphological features among this species, *P. upogebiae* (Hay, 1917) and *P. sinicus* Markham, 1982, that call to question their generic assignment. Regarding *P. bruscai* we recorded new taxonomically important characters and/or morphological variants that were not considered in the original description. Moreover, some inaccuracies in the original description and figures are herein corrected. Two of the three features recomended by Salazar-Vallejo & Leija-Tristán (1990) to separate *P. bruscai* from *P. upogebiae* do not permit separation of these species. The redescription of *P. bruscai* permits us to provide four new diagnostic features for this species. These new features and the above noted shared traits permit for the first time a reliable separation of *P. bruscai* from its congeners. Furthermore, two juvenile stages of *P. bruscai* are described and illustrated. These stages are so different from the adult male and female that a positive identification is almost impossible using the description for adults. All specimens have been deposited in the Colección de Invertebrados, Universidad Autónoma de Baja California. The following abbreviations are used: BC, Baja

California; BCS, Baja California Sur; SON, Sonora.

Progebiophilus bruscai Salazar-Vallejo & Leija-Tristán, 1990
Figs. 1A–O; 2A–I

Aporobopyrus sp.; Leija-Tristán & Salazar-Vallejo, 1987: 179, infesting *U. dawsoni.*
Pseudione sp.; Campos & Campos, 1989a: 33; 1989b: 177, infesting *U. macginitieorum.*
Progebiophilus bruscai Salazar-Vallejo & Leija-Tristán, 1990: 423–432, infesting *U. dawsoni*; Leija-Tristán & Salazar-Vallejo, 1991: 1–5, infesting *U. dawsoni*; Campos et al., 1992: 753, 756–757, infesting *U. macginitieorum*; Markham, 1992:3 (listed).

Type locality.—El Comitán, Laguna de La Paz, Bahía de La Paz, BCS, Mexico. Infesting *U. dawsoni* Williams.

Previous distribution.—La Paz, BCS, infesting *U. dawsoni*; west coast of Baja California at Tortugas Bay, BCS (Campos et al., 1992).

Material examined.—2 males, 2 females, El Pescador Camp, 4.5 km north of San Felipe, BC (31°04′11″N, 114°04′11″W), Jun 1991, infesting *U. dawsoni*; 3 males, 4 females, Los Angeles Bay, BC (28°56′N, 113°32′N), 27 Jul 1996, infesting *U. dawsoni*; 2 juvenile female, Tormento Point, Tiburon Island, SON (29°N, 112°24′W), Jan 1986, infesting *U. dawsoni*; 5 males, 5 females, topotypes (24°07′N, 110°24′W), infesting *U. dawsoni*; 11 males, 11 females, La Bajada beach, Tortugas Bay, BCS (27°41′N, 114°53′W), Apr 1987, Sep 1989, Dec 1989, infesting *U. macginitieorum*; 1 male, 1 female, Punta Banda estuary at Estero Beach Hotel, Todos Santos Bay, Ensenada, BC (31°43′N, 116°38′W), 23 Nov 1996, infesting *U. macginitieorum.*

New distribution.—Gulf of California, from San Felipe, BC to La Paz, BCS, infesting *U. dawsoni*; west coast of Baja California at Tortugas Bay, BCS and Todos Santos Bay, Ensenada, BC, infesting *U. macginitieorum.*

Redescription of female.—Length 4.5 to 12 mm. Body (Fig. 1A) whitish-transparent to opaque-red, dorsally flat, ventrally convex. Outline subelliptical, body axis distorted only 15° to 30°. Head oval, set flush with anterior margin of pereon, dorsally slightly biconvex. Frontal lamina moderately long, slightly broader than head, produced into subacute points. Eyes present. Antennae of 3 and 5 articles respectively (Fig. 1B–C), each antenna distally setose. Barbula (Fig. 1D) with two deeply digitate projections on each side and middle region produced into similar but shorter projections. Maxilliped (Fig. 1E–F) with scaly integument, bearing extended, subtriangular, articulated, anteromesially placed, sometimes setose palp and subacutely pointed somewhat setose plectron.

Pereon of 7 pereomeres, widest across pereomere 3–4. Pereomeres 1–4 with ovoid coxal plates and dorsolateral bosses (Fig. 1G). Pereomeres 5–7 with lateral margins expanded. Ventral margin of pereomere 1 convoluted, those of pereomeres 2–7 smooth (Fig. 1D). Oostegites completely enclosing brood pouch; oostegite 1 (Fig. 1H–I) with anterior lobe rounded, posterior one produced into rounded posterolateral point; outer ridge smooth (Fig. 1H), inner ridge deeply digitate (Fig. 1I). Oostegite 5 (Fig. 1J) ovoid, outer face with row of tuberculiform processes, inconspicuous in shorter (less than 10 mm) adult female. Pereopods (Fig. 1K–M) larger from 1 to 7. Bases of pereopods of shorter side of body with scaled and slightly tubercular carinae; ischia ventrally tubercled; each merus with rounded and marginally scaled projection extending far beyond proximal margin of distally setose carpus; propodus 7 twice as long as wide; dactyli curved, subtruncate.

Pleon (Fig. 1N) of 5 pleomeres and pleotelson, ventral surface of pleomeres covered with numerous prominent longitudinal ridges (Fig. 1N). Lateral plates produced, cordiform, their margin sinuous. Five pairs of

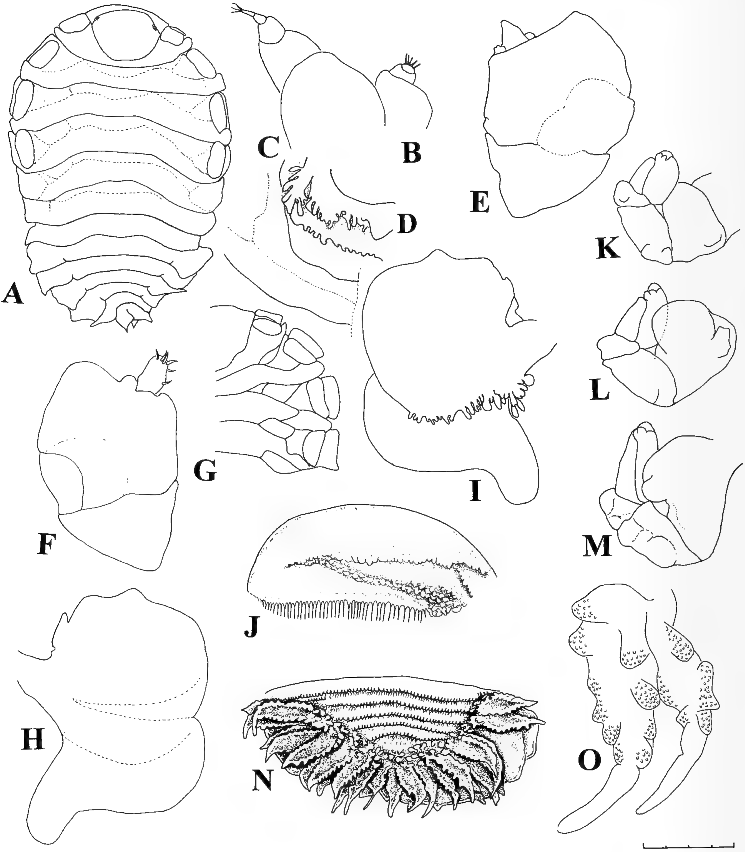

Fig. 1. *Progebiophilus bruscai* Salazar-Vallejo & Leija-Tristán, 1990. A–D, F–I, K–M, O, female, length 10.5 mm; J, N, female, length 11.3 mm; E, female, length 14.4 mm: A, Dorsal view; B, left antenna 1; C, left antenna 2; D, barbula and ventral margins of pereomeres 1–3; E–F, left maxilliped; G, pereomeres 1–4; H–I, right oostegite I, external and internal view respectively; J, oostegite 5, external view; K–M, pereopods 1, 4, 7 respectively; N, pleon ventral view; O, left pleopod 5. Scale bar, A = 3.36 mm; B–C = 0.48 mm; D = 1.21 mm; E = 1.22 mm; F, H–I, K–M, O = 0.99 mm; G = 0.21 mm; J = 2.51 mm; N = 2.54 mm.

lanceolate, marginally strongly tuberculate and biramous pleopods (Fig. 1O). Uniramous uropods lanceolate, marginally strongly tuberculate.

Male.—Length 1.5 to 3.9 mm. Body (Fig. 2A) with suboval outline; length about twice width. All body regions and segments distinctly separated. Head suboval, some-

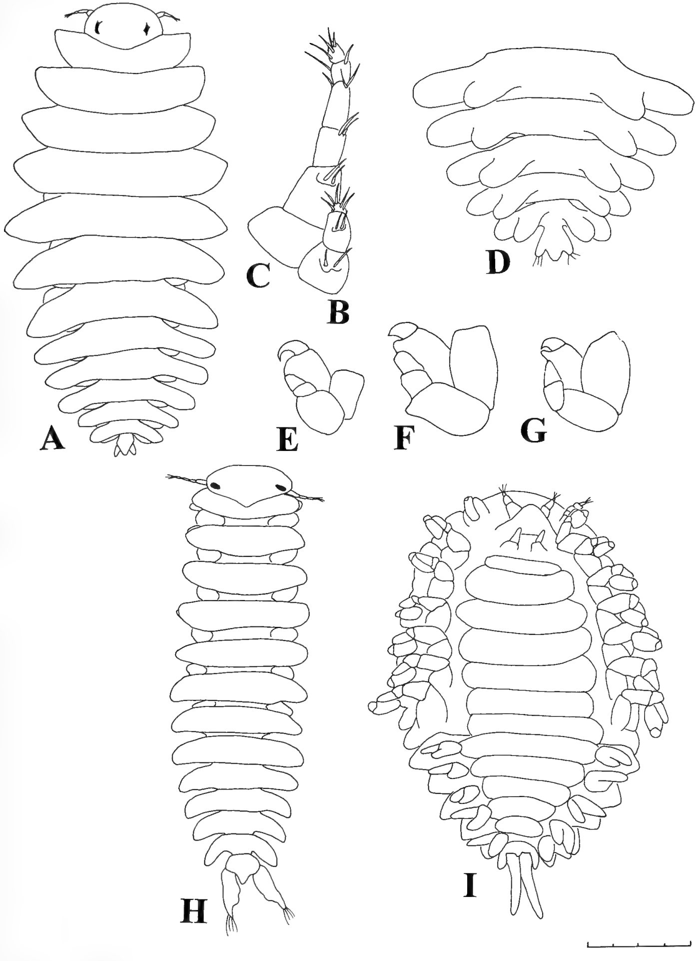

Fig. 2. *Progebiophilus bruscai* Salazar-Vallejo & Leija-Tristán, 1990. A–G, male, length 3.7 mm: A, dorsal view; B, left antenna 1; C, left antenna 2; D, pleon, ventral view; E–G, left pereopod 1, 4, 7; H, juvenile female, dorsal view, length 1 mm; I, juvenile female, ventral view, length 1.2 mm. Scale bar, A = 0.86 mm; B–C = 0.17 mm; D = 0.69 mm; E–G = 0.51 mm.

times medially fused to and always narrower than pereomere 1. Two small dark eyes near posterior margin of head. Antennae of 3 and 6 articles respectively (Fig. 2B–C), with tuft of setae on distal end of all but basal article of antenna 2; antenna 1 less than half as long as antenna 2; distal 4 articles of antenna 2 extending far beyond distal margin of head.

Pereon widest at pereomere 5–6; all pereomeres sharply pointed laterally; pereopods small (Fig. 2E–G), not visible in dorsal view; pereopod 1 shortest, others progressively longer to pereopod 4 and then shorter to pereopod 7. Articles of all pereopods easily visible, meri and carpi distally setose; dactyli progressively less sharp on pereopods 1 to 7. Mid-ventral tubercles on pereomeres 2–7, that of pereomere 6 best-defined.

Pleon of 5 pleomeres and pleotelson. Pleomeres 1–5 rounded laterally. Each pleomere with pair of flaplike, uniramous pleopods (Fig. 2D); pleotelson with prominent central anal cone and terminally setose uniramous uropods, sometimes completely fused to pleotelson like two lateral digitiform lobes.

Juvenile female.—Two juvenile females were studied. The smaller one (Fig. 2H) resembles the adult male except in the slender body shape and presence of two larger, uniramous uropods. The larger one (Fig. 2I) resembles the adult female; however, it lacks oostegites, and tubercles and ridges on body somites and appendages as observed in adult female. This female has five pairs of undeveloped, bare and biramous pleopods and a pair of uniramous, digitiform uropods.

Remarks.—The genus *Progebiophilus* comprises nine species, all branchial parasites of mud shrimps of the genus *Upogebia* (Table 1). The taxonomic knowledge of this genus has increased since its original description; however, some doubt about the generic diagnostic features and proper placement of species within it remains (see Markham 1982, Bourdon 1985). In partic-

Table 1.—Worldwide list of species of *Progebiophilus* Codreanu & Codreanu, 1963.

Species	Distribution	Hosts	References
Progebiophilus brevis Bourdon, 1981	Sierra Leone, West Africa	*Upogebia contigua* Bozic & de Saint Laurente	Bourdon, 1981
P. bakeri Hale, 1929	Gulf of Saint-Vicent, Australia	*U. bowerbankii* (Miers)	Hale, 1929
P. bruscai Salazar-Vallejo & Leija-Tristán, 1990	Gulf of California and West coast of Baja California, Mexico	*U. dawsoni* (Williams) and *U. macginitieorum* (Williams)	this work
P. chapini (van Name, 1920)	Banana river, Congo, West Africa	*U. furcata* (Aurivillius)	van Name, 1920; Bourdon, 1981
P. euxinicus (Popov, 1927)	Black Sea, Mediterranean and French coasts of Atlantic and Manche	*U. pusilla* (Pentagns) *U. deltaura* Leach	Bourdon, 1968
P. filicaudatus (Shiino, 1958)	Mie Prefecture, Japan	*U. issaeffi* Balss	Shiino, 1958
P. sinicus Markham, 1982	Hong Kong	*U. major* de Haan	Markham, 1982; in litt.
P. upogebiae (Hay, 1917)	North Carolina, U.S.A. to Ceará, Brazil	*U. affinis* (Say)	Markham, 1988
P. villosus (Shiino, 1964)	Amami, Japan	*U. pugnax* de Man	Shiino, 1964

ular, adult females of *P. bruscai, P. upogebiae* and *P. sinicus,* differ from other species in *Progebiophilus* in the broadly oval body and large and cordiform lateral plates, while males have mid-ventral tubercules on the pereomeres. In our opinion, these shared features call into question their generic assignment and suggest a future study to determine if these species should be removed from *Progebiophilus.* In the meantime, the following shared features among these three species and *P. euxinicus* (type species of *Progebiophilus*) conservatively support their retention within this genus. Adult females share: all oostegites amply enclosing brood pouch; first oostegite with extended rounded posterolateral point and inner ridge strongly digitate; fifth oostegite externally tuberculate and its posterior margin very setose; pereopodal meri extending beyond margins of carpi, and bases, ischia and meri tuberculate; pleomeres longitudinally ridged ventrally; pleopods biramous, sharply pointed, densely overlapping and with strongly tuberculate margins.

Progebiophius bruscai is very similar to the Atlantic species *P. upogebiae.* These two species can be separated from their congeners by the following shared features: females have the head set flush with anterior margin of pereon, pleon of 5 pleomeres and pleotelson, and margin of both sides produced into indistinct demarcated lateral plates. Males have mid-ventral tubercles on pereomeres, tuberculiform pleopods, pereomeres sharply pointed laterally and pleotelson with a well-defined anal cone. Salazar-Vallejo & Leija-Tristán (1990) separated *P. bruscai* from *P. upogebiae* as follows: female without tubercles on the ostegite 5; uropods in the male well developed; and male pleotelson distally pointed. However the adult female of *P. bruscai* always has tubercles on ostegite 5 although they are inconspicuous in females shorter than 10 mm of length. The uropods in the male may be articulated or fused to pleotelson like two lateral digitiform lobes of variable length (Fig. 2A, D). From Markham's (1988) redescription of *P. upogebiae* we obtained two diagnostic features for this species. Antennae of the male of 5 articles (6 in *P. bruscai*) and female with the palp of the maxilliped fused (articulated in *P. bruscai*). However, Bourdon (in litt.) pointed out that these features should not be considered diagnostic since the antennae of *P. upogebiae* may have 6 articles and the palp may be articulated. The more expanded anal cone in *P. bruscai* (= pleotelson pointed) recorded by Salazar-Vallejo & Leija-Tristán (1990) seems to separate it from *P. upogebiae,* which has a much shorter and rounded anal cone (see Markham 1988). Additional features that separate these species are: in the female of *P. bruscai,* eyes present, antennae of 5 articles and ventral margin of pereionites 2–7 smooth (Fig. 1D). Male has antennulae of 3 articles. Female of *P. upogebiae* has no eyes, antennae of 4 articles, and ventral margin of pereomeres greatly convoluted. Male has antennulae of 4 articles.

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A new species of *Cassidinidea* Hansen (Isopoda: Sphaeromatidae) and first record of the genus from the eastern tropical Pacific

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Abstract.—*Cassidinidea mexicana,* a new species, is described from an abundant material from the southeastern Gulf of California, on the west coast of Mexico. The species is closely related to the type species of the genus, *C. ovalis* (Say) with which it shares a very similar appendix masculina, and an almost similar arrangement of trifid serrated spines on the distal margin of the carpus of pereopod 7. The absence of dorsal nodules on pereonites (very weak, almost wanting, in *ovalis*) and the presence of a single, median elevation on the pleotelson are other similarities between the two species. It differs from this Atlantic species, however, by the presence of a pair of weak ridges almost parallel to the lateral margin of the pleotelson, the presence of another pair of ridges, inverted "v"-shaped, running from the anterior part of the median elevation of the pleotelson towards its posterior margin, and the absence of a clear indentation on the distal margin of the exopod of pleopod 1. The new species is the first record of the genus *Cassinidinea* in the east Pacific region.

The subfamily Cassidininae Hansen was recently reviewed by Bruce (1994). Species of this subfamily of Sphaeromatidae Latreille are small and usually associated with shallow water, estuarine or coastal lagoonal habitats. Although he indicates that ". . . the resolution of the status of the Cassidininae must wait until further data are available on the [two other subfamilies] Sphaeromatinae and Dynameninae" Bruce (1994:1083) implicitly accepted the validity of the Cassidininae by providing synonymy and diagnosis. Bruce (1994) further divided the genera of Cassidininae into three groups: the "*Cassidina*" group, the "*Leptosphaeroma*" group, and the "*Cassidinidea*" group. The material on which this study is based clearly belongs to the *Cassinididea* group (containing only two genera) for the following reasons: the lateral margins of the cephalon are expanded (not expanded in the *Leptosphaeroma* group) and the pleon has only one segment (three segments in the *Cassidina* group). It is distinct from *Syncassidina* Baker, the second genus belonging to the "*Cassidinidea*" group, in having non-flattened first and second antennule peduncle articles. Its affinity with the genus *Cassidinidea* Hansen is confirmed by the presence of the very long and acute appendix masculina set on a proximal directed expansion of the endopod of male pleopod 2, the absence of a rostral point, pleon without sutures and a relatively wide epistome. Dorsal nodules are apparently very weak or wanting (as in *Naesa ovalis* Say, 1818, the type species of *Cassidinidea*), except on the pleotelson.

The exact composition of the genus *Cassidinidea* Hansen is still to be confirmed. According to Bruce (1994), several Atlantic species are probably synonyms of previously described species [e.g., *C. ovalis* (Say, 1818)]. All together, there seems to be 10 valid species, none from the east Pacific. The presence of the herein described new species along the coast of western Mexico, represents the first record of the genus *Cassidinidea* for the west coast of America.

Abbreviations used in this paper are: TL, total length; coll., collector; EMU, Estación Mazatlán UNAM Invertebrates Reference Collection; USNM, United States National Museum, Smithsonian Institution, Washington D.C., U.S.A.; QM, Queensland Museum, Brisbane, Australia.

Family Sphaeromatidae Latreille, 1825
Genus *Cassidinidea* Hansen, 1905
Cassidinidea mexicana, new species
Figs. 1–4

Type material.—Holotype, 1 male (TL 3.0 mm), Estero Sirena (23°09.03′N, 106°19.00′W), Mazatlán, Sinaloa, Mexico, 24 Apr 1997 (EMU-4072). Paratype, 1 female (TL 3.7 mm), same locality, 24 Apr 1997 (EMU-4073). Paratypes, 2 males (TL 2.5 and 2.8 mm) and 2 ovigerous females (TL 4.0 and 4.2 mm), same locality, 24 Apr 1997 (USNM 285513). Paratypes, Estero el Infiernillo, Mazatlán, Sinaloa, Mexico, 14 Mar 1996, 1 male (TL 3.2 mm) and 1 female (TL 2.9 mm) (QM W22716). Paratypes, 3 males (TL 2.7–3.1 mm) and 8 females (TL 1.6–3.7 mm), same locality, 24 Apr 1997 (EMU-4074) (All specimens, coll. J. Salgado-Barragán and M. C. Espinosa-Pérez).

Additional material.—Estero el Infiernillo, Mazatlán, Sinaloa, Mexico, 06 Sep 1995, 1 male (TL 2.8 mm), 1 female (TL 3.4 mm), and 1 ovigerous female (TL 3.1 mm) (EMU-4432) (coll. J. Salgado-Barragán and M. C. Espinosa-Pérez). Same locality, 14 Mar 1996, 3 males (TL 2.7–3.1 mm), and 3 females (TL 2.8–3.5 mm) (EMU-4433) (coll. J. Salgado-Barragán and M. C. Espinosa-Pérez). Estero Caiman (23°09.20′N, 106°19.93′W) 1 female (TL 3.5 mm) (EMU-4434) (coll. J. Salgado-Barragán). Estero el Verde (23°25′N, 106°34′W), Sinaloa, Mexico, 10 Feb 1979, 2 ovigerous females (TL 4.0–4.3 mm) (coll. M. E. Hendrickx) (EMU-4435). Estero Barron (23°08.87′N, 106°18.78′W), 24 Feb 1994, 1 male (TL 3.0 mm) (EMU-4436) (coll. J. Salgado-Barragán). Estero Sirena (23°09.03′N, 106°19.00′W), Mazatlán, Sinaloa, Mexico, 24 Apr 1997, 1 male (TL 2.5 mm), 6 females (TL 1,4–2.7 mm), and 2 ovigerous females (TL 3.4 mm) (EMU-4630).

Description of male.—Body ovate, about 1.8 times as long as wide; pereonites 1–7 without sub-median nodules (Fig. 1A). Pleotelson with a median elevation and a pair of lateral ridges; another pair of inverted 'V'-shaped ridges running from the anterior part of the median elevation towards posterior margin of the pleotelson. Epistome (Fig. 3F) anterior margin almost straight, reduced, less than half the length of cephalon in dorsal view. Epistome in ventral view subrectangular, slightly longer than broad, lateral and posterior sides strongly concave. Cephalon without rostral point. Antennule peduncle (Fig. 2A) with 3 articles; flagellum with 7 articles, long, extending slightly beyond half of pereonite 2. Antenna peduncle (Fig. 2B) with 5 articles; flagellum with 8 articles, slightly longer than antennular flagellum.

Mandible palp (Fig. 3B) articles 1 and 2 with 5 serrated spines each. Left mandible with incisor tooth 3-dentated (an inconspicuous fourth) and lacinia mobilis (3-dentated); setal row of 3 serrated setae; molar process with a straight serrated margin. Right mandible similar in shape, with only one 3-dentated (an inconspicuous fourth) incisor tooth; setal row made of 3 serrated setae and one bifid serrated setae; molar process as in left mandible. Apex of the lateral lobe of maxillula (Fig. 3D) with 8 non-plumose, non-serrated spines, and 2 serrated spines; medial lobe with 4 plumose spines. Maxilla (Fig. 3C) lateral lobe with 4 serrated spines, middle with 4, and medial lobe with 5 plumose spines (the inner one mounted on a short lobular process) and two slender non-plumose spines. Maxilliped palp (Fig. 3E) with only 4 distinguishable articles; about 7-8-6-7 setae on articles 1–4, respectively.

All pereopods with setules on margins. Pereopod 1 (Fig. 2C) merus about half as

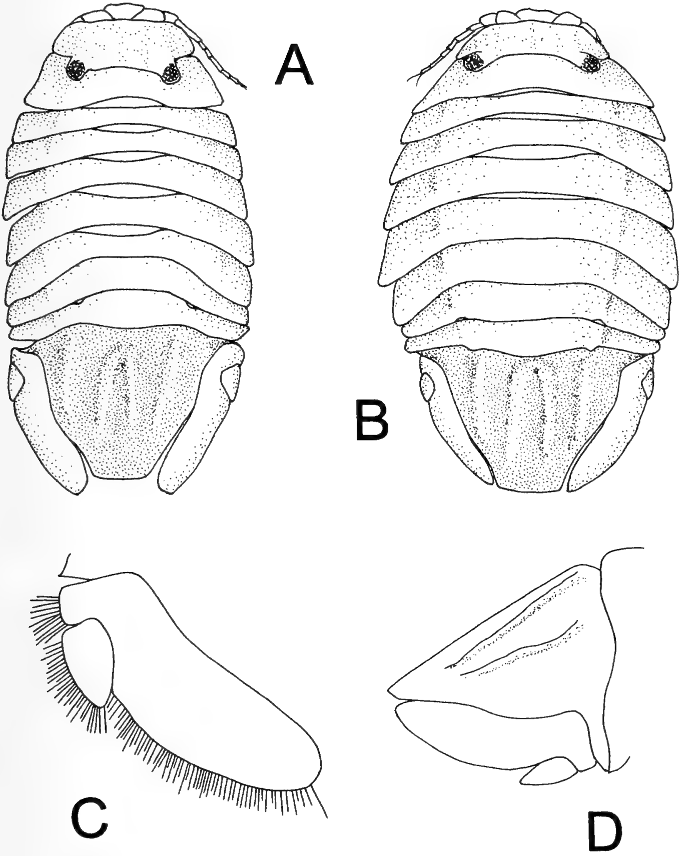

Fig. 1. *Cassidinidea mexicana,* new species. A, Paratype, male, dorsal view (EMU-4074); B, Paratype, female, dorsal view (EMU-4074); C, left uropod, male, dorsal view; D, pleotelson, female, lateral view.

long as ischium; merus with one serrated spine at superior distal angle; carpus triangular, short, about half length of merus; propodus and ischium sub-equal in length; dactylus more than half the length of propodus, with one subterminal spine on the lower margin; 2 serrated scales near base of this sub-terminal spine. Pereopod 2 (Fig. 2D) about 15% longer that pereopod 1, carpus stronger and longer than in pereopod 1, provided with three large trifid serrated spines on superior distal margin; merus

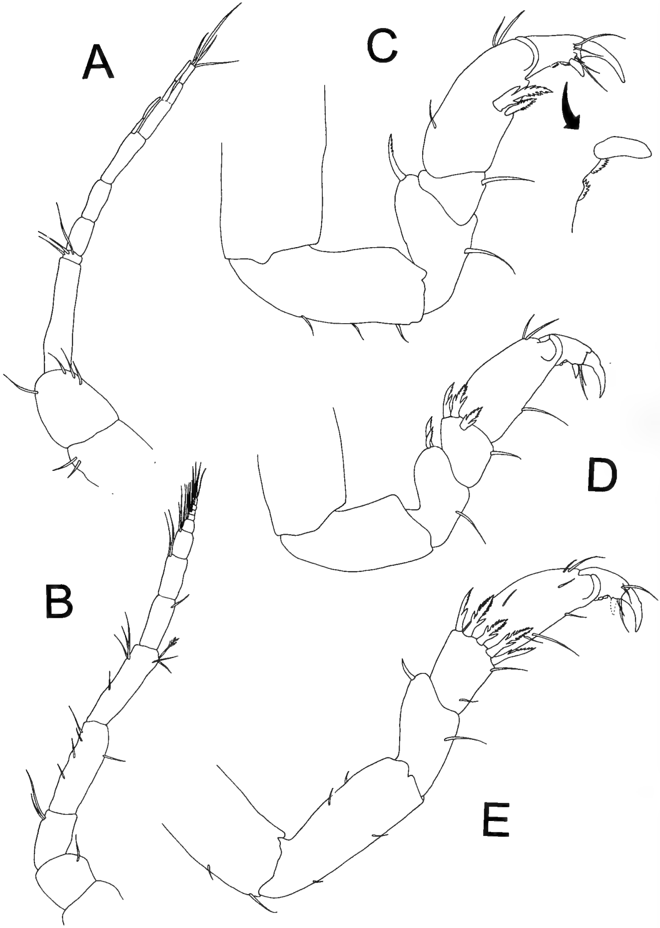

Fig. 2. *Cassidinidea mexicana*, new species, male holotype (EMU-4072). A, right antennula; B, right antenna; C, right pereopod 1; D, right pereopod 2; E, right pereopod 7.

with a pair of serrated spines at superior distal angle; inferior margins of merus, carpus and propodus each with 1 setae. Pereiopods 3–4 similar in shape and spination to pereiopod 2, slightly longer, the 4th the longest. Pereopod 7 (Fig. 2E) more slender and longer than pereopod 2; carpus distal margin with 5 large trifid serrated spines; is-

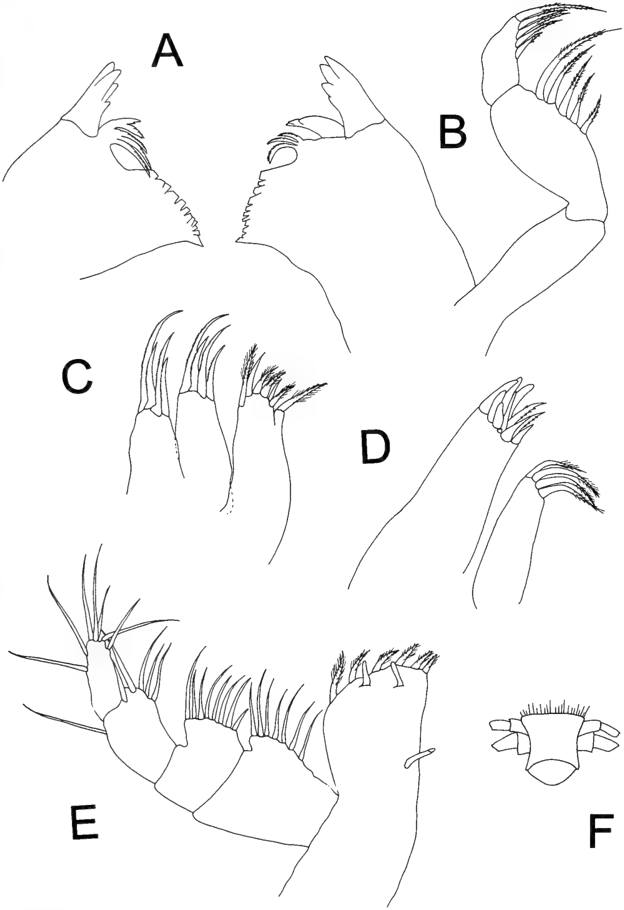

Fig. 3. *Cassidinidea mexicana,* new species, male holotype (EMU-4072). A, right mandible; B, left mandible; C, right maxilla; D, right maxillula; E, right maxilliped; F, epistome and upper lip, ventral view.

chium, merus and carpus with 1–2 setae on the inferior margin; merus with one setae at the superior distal angle. Pereiopods 5–6 similar in shape and spination to pereiopod 7; these pereiopods slightly increasing in size from 5th to 7th.

Penial process subtriangular, ca. 1.3 times longer than wide (Fig. 4F).

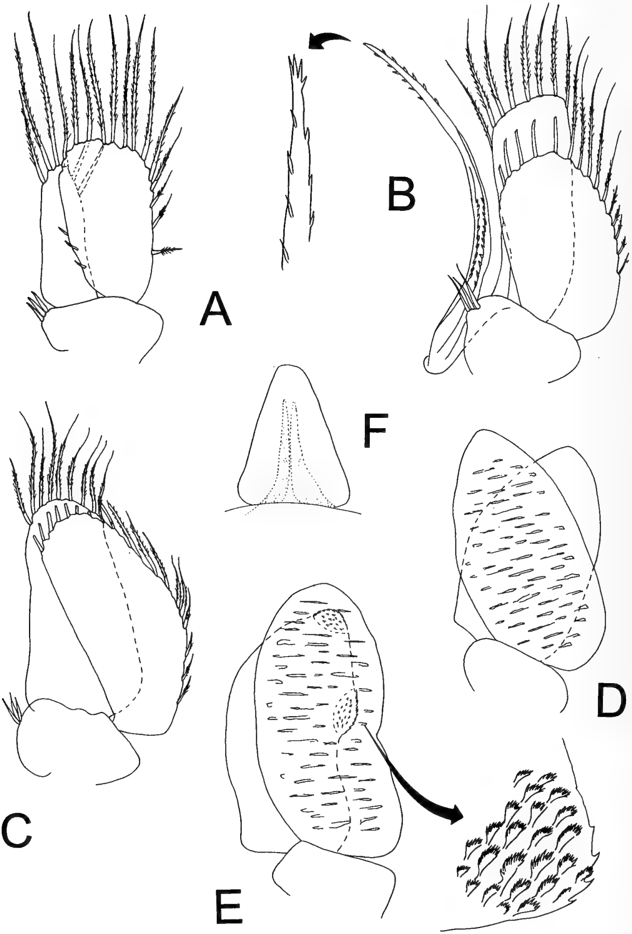

Fig. 4. *Cassidinidea mexicana,* new species, male holotype (EMU-4072). A, right pleopod 1; B, pleopod 2; C, pleopod 3; D, pleopod 4; E, pleopod 5; F, penial process.

Pleopods 1–3 (Fig. 4A–C) endopod and exopod with plumose marginal setae. Distal margin of pleopod 1 endopod almost rounded, with no clear distal identation. Appendix masculina of pleopod 2 elongate, slender, twice (or a little more than twice) as long as distance from the distal margin of peduncle to distal margin of endopod, curved in its distal half; shaft with marginal spines almost throughout its length; tip four-spined. Pleopod 4 (Fig. 4D) without marginal setae; exopod almost entirely covered with transverse folds. Pleopod 5 (Fig. 4E) without marginal setae; exopod with two scaled patches, scales with 5–12 spinules of sub-equal length; endopod entirely covered with transverse folds.

Uropod exopods as in other species of Cassidinidea (Fig. 1C).

Female.—Body ovate, wider than in male, about 1.6 times as long as wide. All characters agree closely to male, including all pereiopods. No variation of mouthparts in ovigerous females.

Etymology.—The epithet refers to the west coast of Mexico where the new species was first recorded.

Habitat.—Most specimens of *C. mexicana* were collected from the aerial roots of *Rhizophora mangle* L., in Estero de Urias, where they live among epifauna: the mussel *Mytella strigata* (Hanley), the oyster *Crassostrea corteziensis* (Hertlein), and the barnacles *Balanus inexpectatus inexpectatus* Pilsbry and *Balanus eburneus* Gould. Specimens from Estero el Verde were found under a piece of dead wood. Specimens of presumably the same species were also collected under twigs, on an intertidal mudflat, at Caimanero coastal lagoon, south of Mazatlán (ca. 22°55′N, 106°05′W) but were no longer available for comparison. Search for material of *Cassidinidea* in another coastal lagoon located much northern, in the central part of the Gulf of California (Estero el Soldado, San Carlos, Guaymas), were unsuccessful. The general habitat ("mangroves") of *C. mexicana* is similar to the habitat reported for *C. arndti* (Ortiz & Lalana, 1980) from Cuba. Bruce (1994: 1151) erroneously used the same specific name for two *Cassidinidea:* "*C. monodi* (Carvacho, 1977)" [sic] and *C. monodi* (Barnard, 1951). The species of Carvacho is in fact *C. barnardi,* found in mangrove of Guadeloupe (". . . sur les racines de *Rhizophora mangle*"). A fourth species occasionally living on mangrove is *C. korpie* Bruce, 1994 (tidal *Rhizophora*).

Geographic distribution.—The species is currently known only from the southeast coast of the Gulf of California.

Remarks.—The new species is strikingly similar to *C. ovalis,* the type species of the genus. It shows a very similar appendix masculina, and similar arrangement of trifid serrated spines on the distal margin of the carpus of pereopod 7. The absence of distinguishable dorsal nodules on pereonites (very weak, almost wanting, in *C. ovalis*) and the presence of a single, median elevation on the pleotelson are other similarities between the two species. Male and female of *C. mexicana* show a weak but distinct lateral carina on both sides of the pleotelson elevation, and another pair of ridges (inverted "v"-shaped) running from the anterior part of the median elevation of the pleotelson towards its posterior margin; none of these ridges have been reported in *C. ovalis* by Bruce (1994). *Cassidinidea mexicana* also differs from this Atlantic species by the absence of a marked indentation on the distal margin of the exopod of pleopod 1. Two species of *Cassidinidea* present ridges on pleotelson: *C. monodi* (Barnard, 1951), known from South Africa and *C. korpie* Bruce, 1994, from Australia. *Cassidinidea mexicana* differs from the former by its widely truncate pleotelson tip (narrower and rounded in *C. monodi*), the size and shape of the epistome (large, subquadrangular and broader than long in *C. monodi*) and the shape of the penial process on 7th sternite (much narrower in *C. monodi*); it differs from the latter by the absence of submedian nodules on pereonites 1–7, the absence of a clear notch on distal margin of exopod of pleopod 1, the shape of the edge of the molar process of mandibles and, as in the case of *C. monodi,* by the size and shape of the epistome (large, subquadrangular and broader than long in *C. korpie*) and the shape of the penial process on 7th sternite (much narrower in *C. korpie*).

According to Bruce (1994: 1083), the lacinia mobilis is usually present on left mandible of Sphaeromatidae but ". . . it is not always clear if the distal most spine of the spine row [on the anterior margin of mandible] is a reduced lacinia mobilis or not when a distinct lacinia mobilis is not present". In the new species the lacinia mobilis is clearly present.

Acknowledgments

The authors thank the CONABIO (Comisión Nacional para el Estudio y Uso de la Biodiversidad, Mexico) for supporting the research on isopods of the Pacific coast of Mexico (CONABIO project H-170) and the people who helped during the present study. José Salgado-Barragán provided useful information regarding the habitat of the new species and helped during the collections. The habitus drawings are by Graciano Valenzuela.

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A new species of *Excorallana* Stebbing (Crustacea: Isopoda: Corallanidae) from the Pacific coast of Mexico, and additional records for *E. bruscai* Delaney

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Abstract.—The genus *Excorallana* Stebbing is represented in the Mexican Pacific by four species. A fifth species, *E. conabioae* is recognized among material collected offshore from a depth range of 28–70 m. *Excorallana conabioae* is readily separated from Atlantic and Pacific species of this genus without horns on cephalon and/or pereonite 1. Among the "horned" species, *E. conabioae* most closely resembled *E. bruscai,* from which it differs by the size and orientation of cephalic horns-like processes, the presence of 3 pairs of small horns-like processes or tubercles on pereonite 1, its much longer antenna, and the presence of a sub-lateral cluster of tubercles on each side of the telson. New records of *E. bruscai* indicate that it is distributed throughout the Gulf of California area from the intertidal to at least 55 m.

The genus *Excorallana* Stebbing, 1904, belongs to the family Corallanidae (Bruce et al. 1982). It is represented in the Mexican Pacific by four species (one as a subspecies): *E. truncata* (Richardson, 1899), *E. tricornis occidentalis* Richardson, 1905, *E. bruscai* Delaney, 1984 and *E. houstoni* Delaney, 1984. In addition to this, Brusca (1980) reported specimens of an undescribed species of *Excorallana* from the entire Gulf of California. Brusca (1980) also reported *E. kathyae* Menzies, 1962, from the Gulf of California, but this species has since been synonymized with *E. truncata* (Delaney, 1982). In its review of the family Corallanidae, Delaney (1989:32) reported 18 species (one with two subspecies) of *Excorallana.* In all, the genus *Excorallana* contains 22 species, including those cited by Delaney (1989), *E. bicornis* Lemos de Castro & Lima, 1976, *E. yamamuroae* Nunomura, 1988, and *E. delaneyi* Stone & Heard, 1989. Except for one record of *E. oculata* (Hansen, 1890) at Annobon Island, West Africa, the genus is known only from the coasts of America (Delaney 1989). In addition to the four above-mentioned Mexican species, only one other member of the genus is known from the East Pacific: *E. meridionalis* Carvacho & Yañez, 1971, from Chile.

Recent collection of invertebrates along the Pacific coast of Mexico (Espinosa-Pérez & Hendrickx, 1997, Hendrickx & Espinosa-Pérez, 1998) led to the capture of large series of intertidal and sub-tidal isopods, among which a new species of *Excorallana* was recognized. The new species is close to *E. bruscai,* yet it contains distinctive characters that separate it from this species and from any other previously known species of *Excorallana.*

Abbreviations used in this paper are: St., sampling station; TL, total length; coll., collector; EMU, Estacion Mazatlan UNAM Invertebrates Reference Collection; USNM, United States National Museum, Smithsonian Institution, Washington D.C., U.S.A.; SEM, Scanning Electronic Microscope; CEEMEX P4, research cruise in the Gulf of Tehuantepec (1991); CORTES 1, 2 and 3, research cruises in the Gulf of California

(1982 and 1985); BBMAZ C, monthly research cruises in the Bay of Mazatlan, Mexico (1979–1981). All specimens reported herein were collected by the staff of the Laboratorio de Invertebrados Bentónicos, Estación Mazatlán, ICML, UNAM.

Corallanidae Hansen, 1890
Excorallana Stebbing, 1904
Excorallana conabioae, new species
Figs. 1–5

Type material.—Holotype, 1 male (TL 10.0 mm), CORTES 2 Cruise, St. 8, San Marcial Point (25°02.03′N, 108°30.08′W), Baja California Sur, Mexico, 11 Mar 1985 (EMU-4942). Paratype, 1 female (TL 11.4 mm), CORTES 1 Cruise, St. 8, Carmen Island (25°34.06′N, 111°58.07′W), Baja California Sur, Mexico, 4 May 1982 (EMU-4943). Paratypes, 1 male (TL 13.0 mm), CORTES 3 Cruise, St. 8, San Marcial Point (25°33.04′N, 110°59.08′W), Baja California Sur, Mexico, 30 Jul 1985 and 1 female (TL 9.0 mm), CORTES 1 Cruise, St. 8, Carmen Island (25°34.06′N, 111°58.07′W), Baja California Sur, Mexico, 4 May 1982 (mounted for SEM photography) (EMU-4944). Paratypes, 1 male (TL 10.0 mm) and 1 female (TL 9.8 mm), CORTES 1 Cruise, St. 8, Carmen Island (25°34.06′N, 111°58.07′W), Baja California Sur, Mexico, 4 May 1982 (EMU-4945). Paratypes, 1 male (TL 10.4 mm) and 1 female (TL 12.4 mm), CORTES 1 Cruise, St. 8, Carmen Island (25°34.06′N, 111°58.07′W), Baja California Sur, Mexico, 4 May 1982 (EMU-4946). Paratypes, 1 male (TL 10.5 mm), CORTES 3 Cruise, St. 8, San Marcial Point (25°33.04′N, 110°59.08′W), Baja California Sur, Mexico, 30 Jul 1985 (USNM 239375), and 1 female (TL 11.7 mm), CORTES 1 Cruise, St. 8, Carmen Island (25°34.06′N, 111°58.07′W), Baja California Sur, Mexico, 4 May 1982 (USNM-239374) (all specimens collected aboard the R/V *El Puma*).

Additional material.—CORTES 1 Cruise, St. 8, Carmen Island (25°34.06′N, 111°58.07′W), Baja California Sur, Mexico, 4 May 1982, 6 females (TL 8.1–12.4 mm) (EMU-4947). CORTES 3 Cruise, St. 19, San Miguel Cape (28° 06.04′N,112° 47.01′W), Baja California, Mexico, 1 Aug 1985, 1 ovigerous female (TL 10.6 mm) (EMU-4948) (all specimens collected aboard the R/V *El Puma*).

Description.—Male. Body elongate, with nearly sub-parallel margins, about 3.3 times as long as wide. Anterior margin of cephalon slightly produced in dorsal view, forming a very small rostral point. Cephalon with a pair of conspicuous, anterior hornlike processes between eyes, a smaller pair between anterior pair and anterior border of pereonite 1; distance between tubercles of second pair about ½ distance between tubercles of anterior pair. Eyes large, extending somewhat obliquely over the entire length of cephalon (Fig. 1C). Antennule (3 peduncular articles) containing 7–9 flagellar articles, almost reaching anterolateral angle of pereonite 1 (Fig. 2A). Antenna with 29–34 flagellar articles, all with fringe of short or long setae; flagellum long, reaching about midlength of fourth pereonite (Fig. 2B). Frontal lamina with anterior margin narrowing to rounded apex (Fig. 1A). Right mandible with elongate incisor, with 1 apical and 1 shorter sub-apical cusps; lacinia reduced, represented by a small 2-spined lobe. Left mandible with elongate incisor, with one apical and two shorter sub-apical cusps; lacinia reduced, represented by a small 2-spined lobe; small molar process present on left mandible only; middle and distal articles of palp of both mandibles with few plumose (right) and non-plumose (both) setae. Maxilla with trilobed, spinose apex. Maxilliped with a 5-segmented flagellum; last 3 articles of palp with numerous setae, antepenultimate article longer than the combined length of last two articles (Fig. 3).

Pereonite 1 with 2 pairs of dorsal hornlike processes, set on transverse line, inner pair larger, of about same size as anterior cephalic, outer pair considerably smaller;

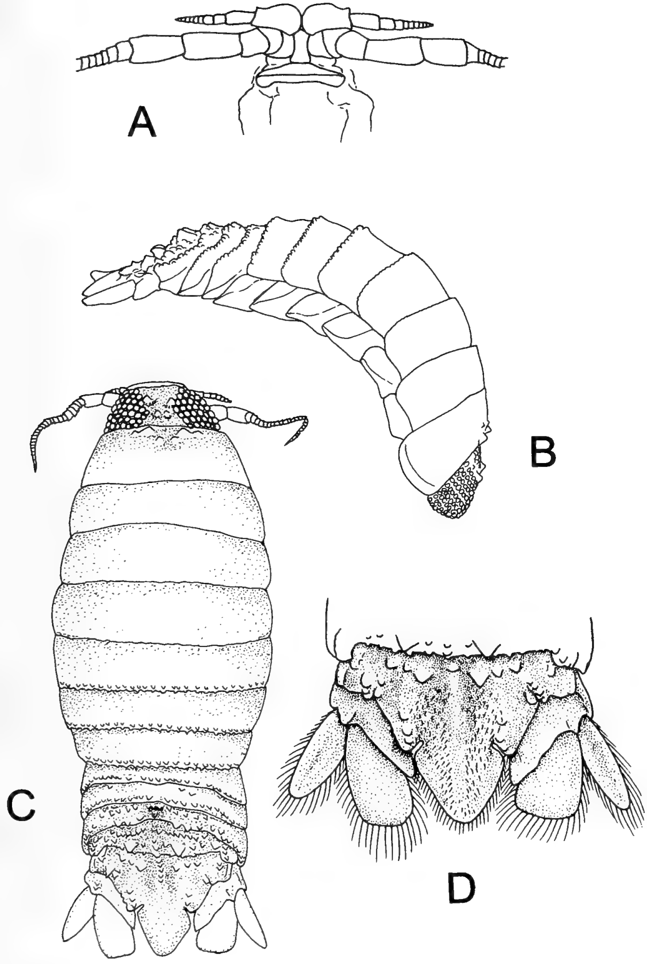

Fig. 1. *Excorallana conabioae*, new species, male holotype (EMU-4942). A, frontal lamina, clypeus and labrum; B, lateral view; C, dorsal view; D, pleotelson. (Total length, 10.0 mm).

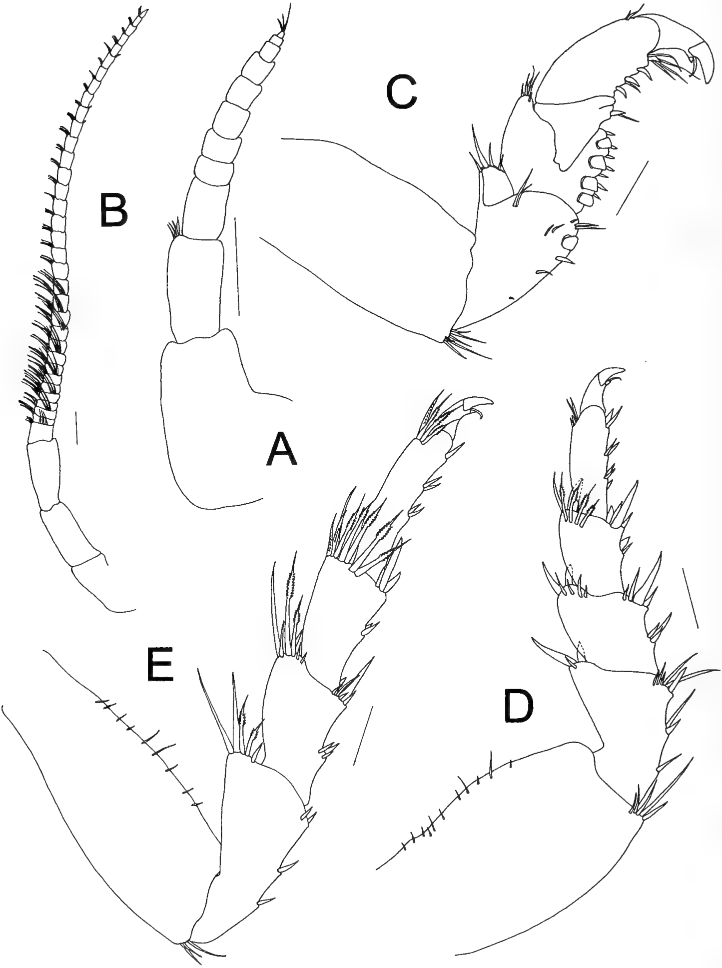

Fig. 2. *Excorallana conabioae,* new species, male holotype (EMU-4942). A, right antennula; B, right antenna; C, right pereiopod 1; D, right pereiopod 2; E, right pereiopod 7. Scale bar = 0.25 mm.

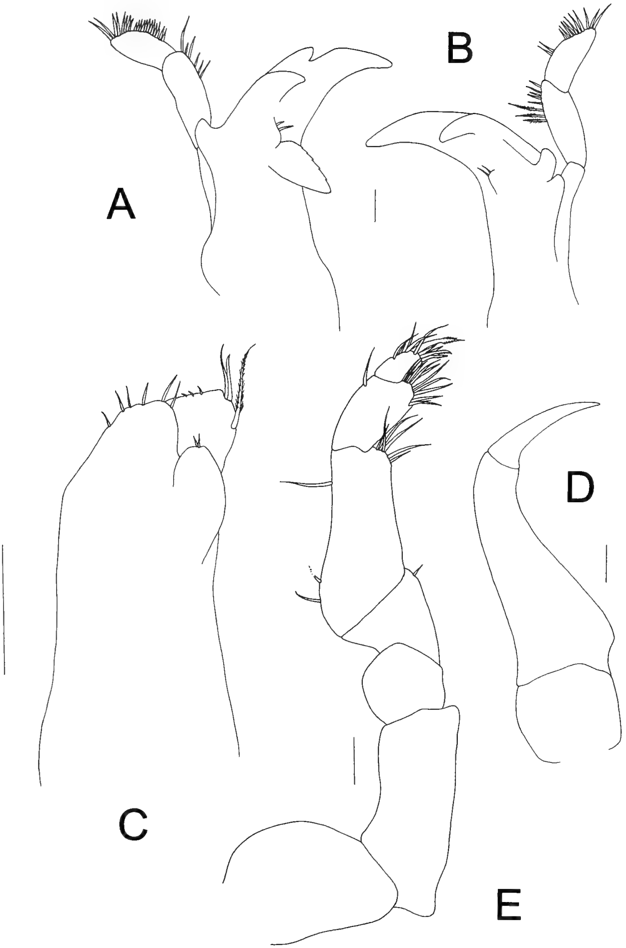

Fig. 3. *Excorallana conabioae,* new species, male holotype (EMU-4942). A, right mandible; B, left mandible; C, right maxilla; D, right maxillula; E, right maxilliped. Scale bar = 0.1 mm.

pair of closely set smaller, median tubercles, just beyond 2 pairs of anterior horns. Anterolateral angle of pereonite 1 produced, partly covering posterior part of eyes. Posterior margin of pereonites 2–5 without conspicuous ornamentation; posterior margin of pereonite 6 crenate, that of pereonite 7 with a crenate section overhanging a lower margin with sub-marginal row of tubercles (Fig. 5A, B, C).

Pleonites 1 and 4 with sub-marginal row of tubercles, median and sub-median tubercles slightly larger on pleonite 1, larger in posterior segments; sub-median tubercles fused in 2 large posteriorly produced submedial cluster. A second row of smaller tubercles visible close to anterior margin of each pleonic segment (Fig. 1B). Pleotelson triangular, apex rounded; deep, large notch at about midlength of lateral margin; a row of 6 (3 pairs) sub-basal tubercles, median pair much larger than other 2; a cluster of tubercles above the insertion of uropods; a sub-triangular cluster of strong sub-median bifid setae extending longitudinally on each half of telson, from base of largest sub-basal tubercle to posterior margin; a sub-lateral cluster of tubercles between each patch of setae and lateral margin of telson (Fig. 1D).

Uropods slightly longer than pleotelson, fringed with long setae. Uropodal endopod broad, posteriorly sub-truncate, distal lateral angles rounded with lateral spines, easily lost on preserved specimens. Uropodal exopod less than half width of endopod, also with easily lost marginal spines (Fig. 1D).

Pleopods 1–5 fringed with plumose marginal setae, except endopod of pleopod 5. Appendix masculina rodlike, with simple pointed apex (Fig. 4).

Female. Relatively wider than male (about 2.5 times as long as wide). Anterior pair of cephalic horn-like processes less than half the size of males, posteriormost smaller pair wanting. Largest sub-median pair, clearly visible on anterior half of male first pereonite, reduced to an obsolete pair of small conical tubercles in female; the other dorsal tubercles on pereonite 1 are wanting. Ornamentation of pereonites 6–7 and of pleotelson similar in male and female, tubercles somewhat smaller in female (Fig. 5D, E, F).

Remarks.—*Excorallana conabioae* is readily separated from most Atlantic species of the genus and from *E. houstoni* and *E. truncata* by the presence of cephalic processes. Among the "horned" species, *E. conabioae* most closely resembled *E. bruscai,* from which it differs by the following characteristics: in *E. conabioae* the cephalic processes are pointing upwards, and the pereonite 1 horns are not strongly produced forwards (with upturned apex) as in *E. bruscai*; the anterior median cephalic margin of *E. bruscai* is strongly produced, while *E. conabioae* features a small rostral point; number of flagellar articles in antennula and antenna of *E. bruscai* is 6–8 and 22–25, respectively, 7–9 and 29–34 in *E. conabioae*; in *E. conabioae* pereonite 1 processes are smaller yet more numerous (three pairs instead of one, very large, in *E. bruscai*); the antenna is much longer and with more numerous flagellular articles in *E. conabioae*; there is no sub-lateral cluster of tubercles on each side of the dorsal side of telson in *E. bruscai*; females of *E. bruscai* lacks horns, while in the new species these features are reduced, yet distinguishable as tubercles on cephalon and on first pereonite (one pair on each).

Other "horned" species of the genus have two large (*E. bicornis* Lemos de Castro & Lima, 1976) or three horns on cephalon [*E. berbicensis* Boone, 1919, and *E. tricornis* (Hansen, 1890)], no lateral incision on pleotelson (*E. longicornis* Lemos de Castro, 1960), or presented four or 6 horns on the cephalon [*E. meridionalis, E. quadricornis* (Hansen, 1890), *E. mexicana* Richardson, 1905, and *E. sexticornis* (Richardson, 1901)].

Etymology.—The new species is named for CONABIO (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México), in recognition of the support re-

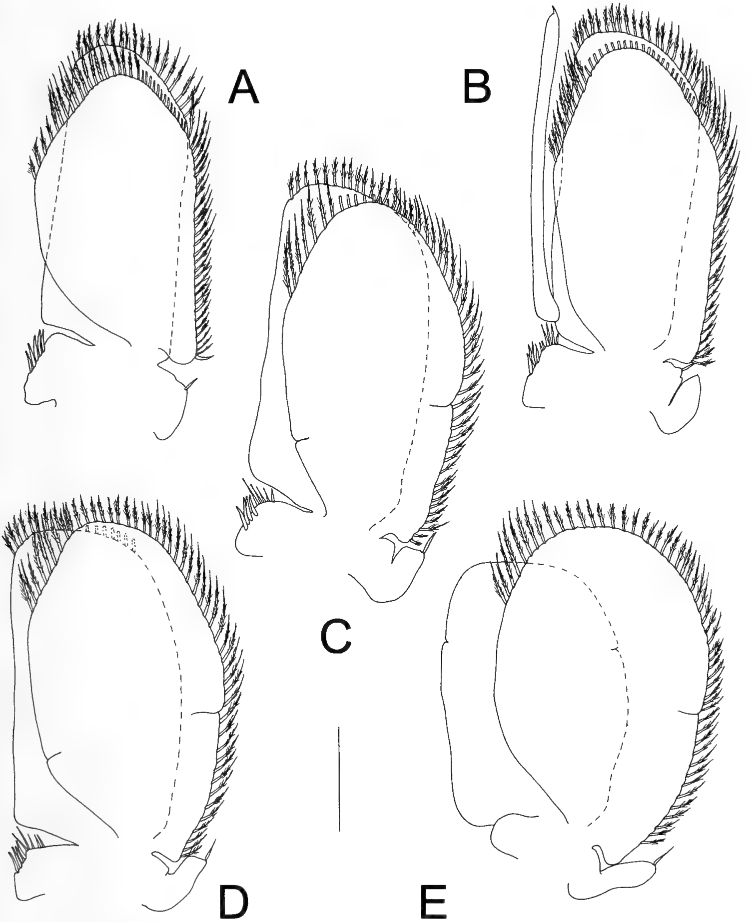

Fig. 4. *Excorallana conabioae,* new species, male holotype (EMU-4942). A, right pleopod 1; B, right pleopod 2; C, right pleopod 2; D, right pleopod 4; E, right pleopod 5. Scale bar = 0.5 mm.

ceived during our study of isopods of the Pacific coast of Mexico.

Habitat.—Excorallana conabioae was taken in grab and dredge between 25 and 70 m. Environmental data available at the moment of sampling indicate epibenthic temperature range from 14.2 to 19.8°C and dissolved oxygen concentration always

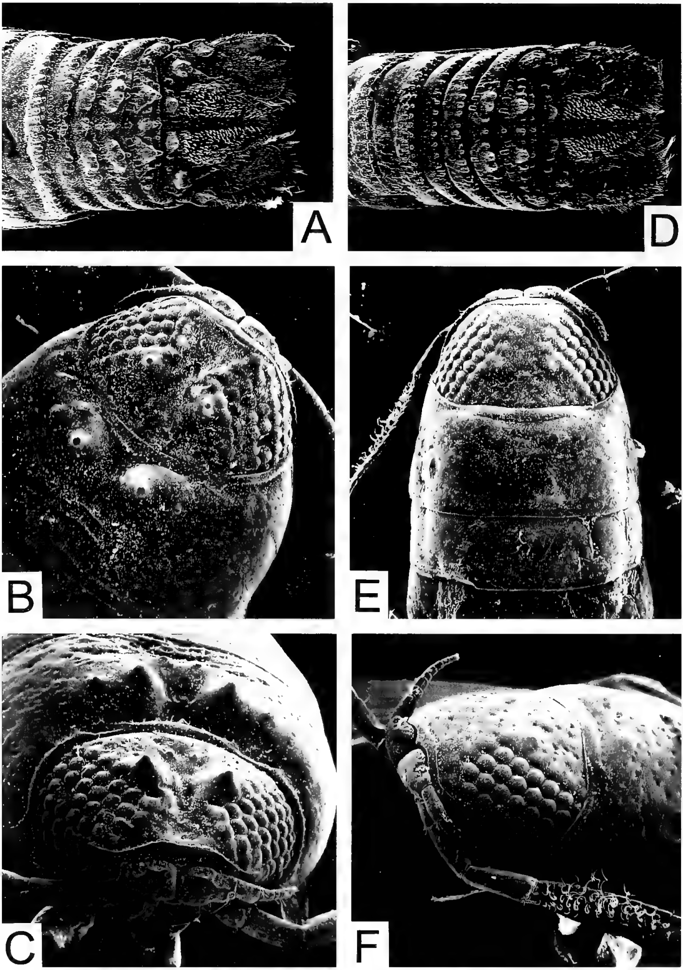

Fig. 5. *Excorallana conabioae*, new species, male (A–C) and female (D–F) paratypes (EMU-4944). A–D, dorsal view of pleotelson; B, dorsal view of cephalon and pereonite 1; C, frontal view of cephalon and pereonite 1; E, dorsal view of cephalon and pereonites 1–2; F, fronto-lateral view of cephalon and pereonite 1 (SEM).

Table 1.—Environmental data available for the captures of *Excorallana conabioae* and *E. bruscai.* Dissolved oxygen and temperature measured at bottom level. S, sand; L, lime; C, clay; VFS, very fine sand; FS, fine sand; MS, medium sand.

Cruise	Station	Depth (m)	O_2 (ml/l)	Temp. (°C)	Sediments SLC	Grain size
E. conabioae						
CORTES 1	8	55	2.5	16.0	GRAVEL	—
CORTES 2	8	64–70	3.5	17.5	99--	FS
CORTES 3	8	42	3.4	19.5	97--	FS
CORTES 3	19	28	3.5	14.2	100--	MS
E. bruscai						
BBMAZ-C14	8	8	—	—	—	—
BBMAZ-C16	10	4	—	—	—	—
CORTES 1	8	55	2.5	16.0	GRAVEL	—
CORTES 2	47	37	1.5	13.5	---	—
CORTES 3	16	22	4.5	—	87--	VFS
CORTES 3	47	28	4.0	29.4	96--	FS
CEEMEX-P4	10	23–24	4.8	27.5	—	—

higher than 2.4 ml/l O_2; sediments were mostly sandy, with one capture associated with gravels (Table 1).

Geographic distribution.—The new species is restricted to the continental platform along the east coast of Baja California Peninsula, between Carmen Island and San Miguel Cape.

Excorallana bruscai Delaney, 1984

Excorallana sp. Brusca, 1980: 229.

Excorallana bruscai Delaney, 1984: 5, figs. 1–4, 14–17, 22; 1989: 8, 31, 33, figs. 1D, 19, 21, 24.—Wetzer et al. 1991: 25.

Material examined.—CORTES 3 Cruise, St. 16, Punta Arboleda (26°52.02′N, 110°01.05′W), Sonora, Mexico, 31 Jul 1985, 3 males (TL 5.2–7.4 mm), 1 female (TL 5.9 mm) and 2 ovigerous females (TL 7.4–7.5 mm) (EMU-4949). CORTES 2 Cruise, St. 47, Estero Tastiota (28°17.08′N, 111°37.03′W), Sonora, Mexico, 18 Mar 1985, 1 male (TL 10.4 mm) and 2 females (TL 10.5–11.4 mm) (EMU-4950). CORTES 3 Cruise, St. 47, Estero Tastiota (28°20.08′N, 111°41.04′W), Sonora, Mexico, 6 Aug 1985, 1 male (TL 8.6 mm) (EMU-4951). CORTES 1 Cruise, St. 8, Carmen Island (25°34.06′N, 111°58.07′W), Baja California Sur, Mexico, 4 May 1982, 1 male (TL 5.7 mm) (EMU-4952). BBMAZ 16 Cruise, St. 10, Bay of Mazatlan (23°13.00′N, 106°27.00′W), Sinaloa, Mexico, 27 Nov 1980, 1 female (TL 7.5 mm) (EMU-4953). BBMAZ 14 Cruise, St. 8, Bay of Mazatlan (23°13.00′N, 106°27.00′ W), Sinaloa, Mexico, 27 Nov 1980, 2 males (TL 6.9–7.0 mm) and 7 ovigerous females (TL 6.8–9.6 mm) (EMU-4954). CEEMEX P4 Cruise, St. 10, Boca de San Francisco (16°10.00′N, 94°58.09′W), Oaxaca, Mexico, 30 Mar 1991, 1 female (TL 9.0 mm) (EMU-4955). Ensenada de Litigu (20°47.04′N, 105°31.09′W), Nayarit, Mexico, 9 Apr 1996, 1 male (TL 7.6 mm) (EMU-4633). Playa el Tesoro (24°18.00′N, 110°19.00′W), Baja California Sur, Mexico, 17 Jul 1996, 6 males (TL 5.7–8.2 mm) and 16 females (TL 4.7–8.2 mm) (EMU-4634) (CORTES and CEEMEX Cruises specimens collected aboard the R/V *El Puma*).

Remarks.—The present records extend the distribution of this species from Punta Lobos (27°20′N, 110°40′W), Sonora, to Boca de San Francisco (16°10.00′N, 94°58.09′W), Oaxaca, along the east coast of the Gulf of California and western Mexico, and from Concepcion Bay (26°50′N, 111°55′W), Baja California, to the area of

La Paz, Playa el Tesoro (24°18.00′N, 110°19.00′W), Baja California Sur. Collection of isopods were also made in the area of Colima, Jalisco and Michoacan, in western Mexico, during this survey but no specimens of *E. bruscai* were found.

Habitat.—According to Delaney (1984, 1989), *E. bruscai* is found in the intertidal and shallow sub-tidal benthic habitats. Our records for this species, however, indicate that *E. bruscai* is also found in deeper water, on the continental shelf, at least to 55 m, thus sharing a similar lower bathymetric limit with *E. conabioae*. Both species are occasionally sympatric. They co-occurred in one sample, obtained in the Carmen Island area (CORTES 1, St. 8). Environmental conditions indicate an epibenthic temperature range of 13.5–29.4°C and dissolved oxygen concentrations quite variable (1.5 to 4.8 ml/l). Sediments were predominantly sandy (Table 1).

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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A new isopod species from Key Largo, Florida (Crustacea: Isopoda: Holognathidae)

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Abstract.—*Cleantioides verecundus* is described from *Thalassia* seagrass rootmats found at Key Largo, Florida. The species, the third from the western Atlantic, is characterized by the possession of a maxillipedal palp of five articles, three complete and one incomplete pleonite, and a subcircular posterior pleotelson bearing two rounded longitudinal ridges.

A single specimen of a holognathid isopod was serendipitously collected during a class field trip conducted by the second author, while searching for gastropods along the *Rhizophora* mangle fringe of Lake Surprise, Florida. The habitat is a soft-bottomed mangrove lagoon of exceptional water clarity and rapid *Thalassia* growth. In late summer, rapid photosynthesis by *Thalassia* creates sufficient buoyancy to pull large clumps of seagrass loose from the bottom. These clumps gradually die and release large quantities of detritus, including seagrass rhizome fragments. The isopod was found within the hollow core of such a fragment. Additional collecting efforts at the type locality in July, August, and September 1997 focussed on *Thalassia* fragments, but failed to yield further specimens.

Suborder Valvifera
Family Holognathidae Thomson, 1904
Cleantioides Kensley & Kaufman, 1978
Cleantioides verecundus, new species
Figs. 1–3

Material examined.—Holotype, USNM 253361, male tl 16.2 mm, from *Thalassia* root mat adjacent to mangrove, 0.25 m, north shore of Lake Surprise, Key Largo, Florida, 25°10′26″N, 80°23′15″W, water temperature 20°C, coll. Harry Yamalis, 29 Mar 1997.

Description.—Male: Body elongate-cylindrical, parallel-sided, about 5.2 times longer than greatest width, not noticeably setose, fine dense setae most visible on antennae and pereopods. Anterior margin of cephalon sinuous, with shallow midline notch. Eyes dorsolateral, reniform. Coxa of pereopod 1 demarked but fused with tergum; coxae 2–4 narrow, elongate; coxae 5–7 ovate, posteriorly narrowly rounded. Pleonites 1–3 complete, 4 incomplete, lacking free ventrolateral margin. Posterior pleotelsonic margin semicircular, oblique, bearing 2 submedian longitudinal rounded ridges best seen in lateral view, ridges not reaching posterior margin.

Antennular flagellum of single short article less than half length of peduncle article 3, bearing about 9 or 10 aesthetascs. Antennal flagellum of single tapering article, strongly setulose, especially ventrally. Mandible lacking palp; incisor of 3 cusps; spine row of 6 or 7 spines; molar stout, distally broad, flattened. Maxilla 1, inner ramus having 3 circumplumose setae distally; outer ramus having 9 or 10 distal spines. Maxilla 2, both lobes of outer ramus bearing numerous pectinate setae; inner ramus bearing numerous sparsely circumplumose setae. Maxillipedal endite bearing 3 coupling hooks; palp of 5 articles, 4 distal articles mesially setose. Pereopod 1, merus with 3 posterodistal spines; carpus with very short free anterior margin, about 10 spines on posterior margin; propodus with 7 spines on posterior margin; dactylar unguis with strong accessory claw. Pereopod 2 and 3 similar, longer than pereopod 1, carpi rectangular, with free anterior margin, with about 7 spines on posterior margin; propodi about 3 times longer than wide, with irregular clumps of spines on posterior margin. Pereopod 4 short, equal in length to propodus, carpus, and merus of pereopod 3; ischium with 2 posterodistal spines; merus with 4 posterodistal spines and single anterodistal spine; carpus with 8 spines on posterior surface; propodus with about 9 spines on posterior surface; dactylus reduced to single stout corneous spine. Pereopods 5–7 increasing in length posteriorly; merus with 2 or 3 spines on posterior surface, 1 or 2 anterodistal spines; carpus with 3–7 spines on posterior surface; propodus with 4 or 5 clumps of spines on posterior surface; dactylus hooked, having strong accessory unguis. Penes near base of uropod, on ventrum of pereonite 7, rami separate, tapering to rounded apices. Pleopod 1, sympod bearing 4 retinaculae; exopod shorter than endopod, both bearing numerous plumose marginal setae. Pleopod 2, both rami bearing plumose marginal setae, copulatory stylet strongly grooved, tapering to acute apex, reaching to distal margin of endopod, articulating at about proximal third of endopodal mesial margin. Pleopod 3, sympod bearing 4 retinaculae; rami subequal, only exopod bearing plumose marginal setae. Pleopods 4 and 5 similar, rami subequal, only exopod bearing sparse simple marginal setae. Uropodal sympod having longitudinal groove near mesial margin, curving laterally near base, about 2.5 times length of single ramus.

Color pattern.—Strong red-brown pigment anteriorly in dense band, posteriorly in 6 longitudinal bands on cephalon; antennules and antennae uniformly pigmented except for unpigmented antennal flagella. Pereon and pleon somites each bearing 6 longitudinal pigment stripes; subcircular pleotelson having medial pigment stripe and 5 slightly more dense patches submarginally.

Remarks.—Four species of *Cleantioides* are now known from the Western Atlantic: *C. verecundus,* from Key Largo, Florida, described here; *C. planicauda* (Benedict, 1899), from Georgia and Florida to the broad Caribbean region, as well as Oaxaca, Pacific Mexico (see Brusca & Wallerstein 1979); *C. bruscai* (Kensley, 1987) from Belize; and *C. occidentalis* (Richardson, 1899) from Lower California to Ecuador and the Galapagos Islands, as well as Atlantic Colombia (see Carvacho 1983, Müller 1988). These species can easily be distinguished by the structure of the subcircular part of the pleotelson (Fig. 1): unadorned in *C. planicauda,* with two narrow submedian lobes basally in *C. bruscai,* with two submedian longitudinal ridges in *C. verecuncus,* and with two broadly rounded submedian lobes in *C. occidentalis.* In addition to the two amphi-Panamic species mentioned above, *C. vonprahli* Ramos & Rios, 1988, has been recorded from the eastern Pacific (Colombia). In this species the pleotelson is unadorned, but not as concave as in *C. planicauda.* These five aforementioned species of *Cleantioides* can be distinguished using the features provided in Table 1. Although *C. bruscai* possesses two complete and two incomplete pleonites, Poore & Lew Ton (1990) did not consider this difference from most other species of *Cleantioides,* which have three complete and one incomplete pleonites, to be sufficient to warrant generic separation. Poore & Lew Ton (1990) redefine *Cleantioides,* and list all the species included in it.

All four species of *Cleantioides* from the western Atlantic live in the specialized habitat of hollow seagrass stems, with their brown coloration perfectly matching the stolons. While kept alive in an aquarium, the holotype of *C. verecundus* would not leave its stolon fragment unless forced to

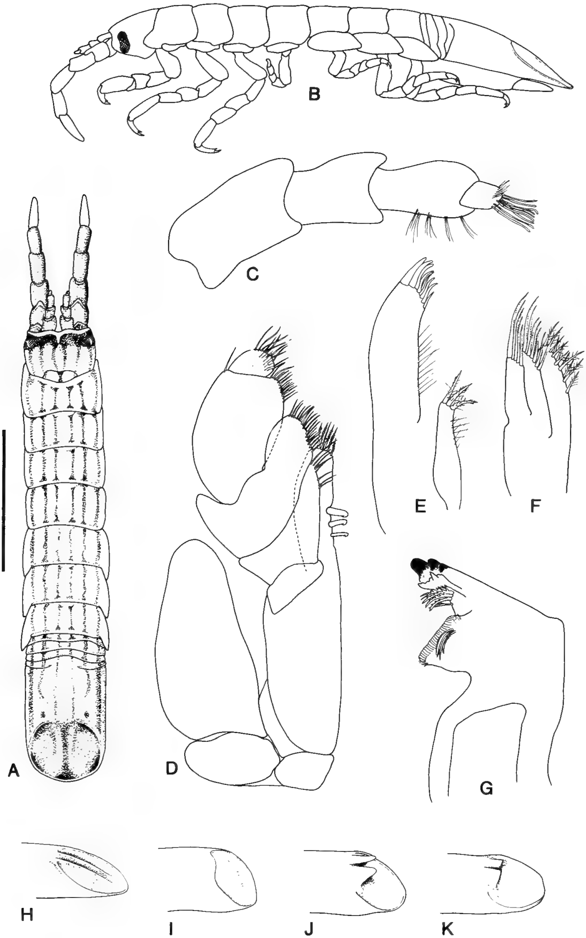

Fig. 1. *Cleantioides verecundus,* holotype. A, Dorsal view, scale = 5 mm; B, Lateral view; C, Antennule; D, Maxilliped; E, Maxilla 1; F, Maxilla 2; G, Mandible; H, Oblique-lateral view of pleotelson; I, Oblique-lateral view of pleotelson of *Cleantioides planicauda*; J, Oblique-lateral view of pleotelson of *Cleantioides bruscai*; K, Oblique-lateral view of pleotelson of *Cleantioides occidentalis.*

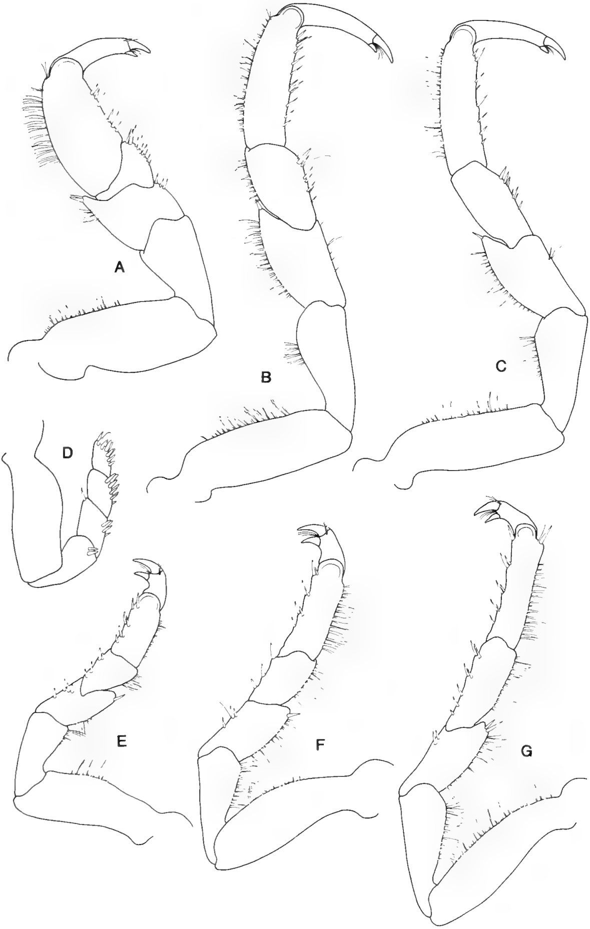

Fig. 2. *Cleantioides verecundus,* holotype. A, Pereopod 1; B, Pereopod 2; C, Pereopod 3; D, Pereopod 4; E, Pereopod 5; F, Pereopod 6; G, Pereopod 7.

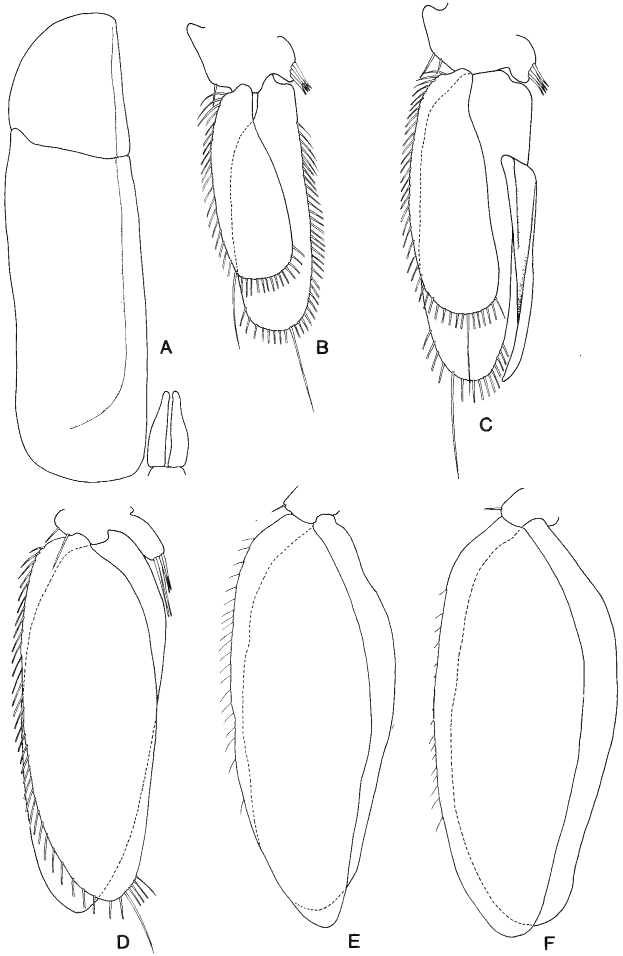

Fig. 3. *Cleantioides verecundus,* holotype. A, Uropod and penes; B, Pleopod 1; C, Pleopod 2; D, Pleopod 3; E, Pleopod 4; F, Pleopod 5.

Table 1.—Summary of four distinguishing features in western Atlantic and eastern Pacific species of *Cleantioides.*

	C. verecundus	*C. bruscai*	*C. planicauda*	*C. occidentalis*	*C. vonprahli*
Maxillipedal palp articles	5	4	5	4	4
Maxillipedal endite hooks	3	3	3	2	3
Pereonite 7 setal border	absent	present	absent	present	? absent
Pleonites: complete/incomplete	3/1	2/2	3/1	3/1	3/1
Posterior pleotelson	2 ridges	2 strong lobes	unarmed	2 short lobes	unarmed

do so; when released, it would immediately re-enter the hollow stem.

Etymology.—The specific name is from the Latin *verecundus,* shy, and refers to the holotype's reluctance to leave its tubular home while yet alive.

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We thank Mr. Harry Yamalis, Department of Oceanography, Florida Institute of Technology, who collected the holotype and brought it to our attention.

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Systematics of the Raninidae (Crustacea: Decapoda: Brachyura), with accounts of three new genera and two new species

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Abstract.—Reexamination of the Raninidae reveals revised relationships of raninid genera, both fossil and Recent. *Symethis* Weber is removed from the Raninidae and placed in the newly erected Symethidae under the Raninoidea. One subfamily is reestablished, Palaeocorystinae, and several subgenera are elevated to generic status: *Notopocorystes* McCoy, *Eucorystes* Bell, and *Cretacoranina* Mertin within the Palaeocorystinae. *Lysirude* Goeke, within the Lyreidinae, is distinguished as a discrete genus rather than as a subgenus of *Lyreidus* De Haan. Additionally, three new genera are described: *Macroacaena,* within the Lyreidinae and *Carinaranina* and *Quasilaeviranina* within the Raninoidinae. Two new raninid species, *Laeviranina goedertorum* and *Carinaranina marionae,* from the Eocene Hoko River Formation of Washington, U.S.A., are established. Descriptions of three species previously described by Rathbun are emended based upon new fossil material: *Carinaranina willapensis* (Rathbun) new combination, *Laeviranina lewisanus* (Rathbun) and *L. vaderensis* (Rathbun). The description of *Eumorphocorystes sculptus* Binkhorst is emended.

Phylogenetic relationships within the Raninidae are explored using parsimony analyses. A hypothetical phylogeny is established for the Raninidae, including fossil and extant genera. One result of these analyses is the importance of using character states from the oldest recognized species for fossil genera, while continuing to use character states of the type for extant genera.

Reexamination of the Raninidae was initiated as a result of an investigation of fossil decapods recovered from the Eocene Hoko River Formation, Olympic Peninsula, Washington, U.S.A. Two new species of raninids were discovered and are described from this locality. In addition, many new specimens of fossil raninids described by Rathbun (1926) also were collected, adding greatly to the understanding of those species. Three of Rathbun's descriptions are emended herein, those of *Carinaranina willapensis* (Rathbun, 1926) new combination, *Laeviranina lewisanus* (Rathbun, 1926), and *L. vaderensis* (Rathbun, 1926). It has been recognized for some time that specimens from the Pacific coast of North American, which Rathbun (1926, 1932) referred to *Eumorphocorystes* Binkhorst, 1857, were incorrectly placed. In order to resolve this problem, it was necessary to reexamine *Eumorphocorystes* and emend the original description.

In order to make complete comparisons of fossil raninids from Washington State, it was found essential to examine many other extant and fossil forms. That effort demonstrated the need to provide an arrangement that would include fossil and Recent species. To accomplish this, species were studied employing traditional systematic procedures, and were arranged in genera defined by mutually exclusive characteristics. The generic-level and subfamily-level arrangements were tested using cladistic methods.

The Raninidae was subdivided into six subfamilies by Guinot (1993): Ranininae De Haan, 1841; Notopodinae Serène & Umali, 1972; Symethinae Goeke, 1981; Raninoidinae De Haan, 1841; Lyreidinae Guinot, 1993; and Cyrtorhininae Guinot, 1993. The present work agrees with five of these designations, and suggests (as did Guinot 1993) that the Symethinae should be elevated to family rank within the Superfamily Raninoidea. The Cyrtorhininae should be retained within the Raninidae and not be placed as a subfamily of the Symethidae, as suggested by Guinot (1993).

The systematic treatment of the Raninidae that follows includes descriptions of subfamilies that contain genera or species that are newly recognized, or genera that were elevated from subgeneric rank. In cases where no noteworthy changes within a subfamily were made, that subfamily was not described. In addition, Palaeocorystinae is re-established to embrace three of the earliest fossil members of the Raninidae.

Methods.—When possible, specimens representing each species were borrowed for study. When it was not possible to borrow specimens, photographs were used to determine pertinent characteristics for those species. As a last resort, drawings were used.

All specimens in this paper are identified by collection or museum numbers. Institutions and their acronyms are: California Academy of Science, San Francisco, California (CAS); Institut Royal des Sciences Naturelles de Belgique (IG); Museum für Naturkunde Zentralinstitut der Humboldt-Universität zu Berlin, Institut für Paläontologie (MNZH); Kent State University (KSU); New Zealand Geological Survey, Lower Hutt (NZGS AR); and National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Localities for the specimens from the Hoko River Formation are identified by numbers assigned by Ross Berglund (RB) who collected most of those specimens.

Systematic Paleontology

Order Decapoda Latreille, 1803
Superfamily Raninoidea De Haan, 1841
Family Raninidae De Haan, 1841

Raninoidea De Haan, 1841:136–137.

Key to subfamilies of the Raninidae

1. Carapace with distinct cervical and branchiocardiac grooves; 2 or more anterolateral spines; longitudinal carina present, often centrally nodose; rostrum bifid; carapace anterior of cervical groove often tuberculate or lingulate . . . . Palaeocorystinae Lörenthey (*in* Lörenthey & Beurlen 1929)

1′. Carapace rarely bearing cervical groove, branchiocardiac groove faint, rarely complete; usually no more than 2 anterolateral spines; longitudinal carina sometimes present, never nodose; rostrum variable, never bifid; carapace anterior of cervical groove variable, never tuberculate or lingulate 2

2. Carapace often quite rounded, broad, ovate in outline; surface of dorsal carapace variable; front margin variable . . 3

2′. Carapace elongate oval; surface of dorsal carapace almost always smooth; front margin always toothed 4

3. Orbits straight, directed forward; outer margin of extraorbital spines often quite convex; chelipeds with elongate propodus, tip of dactylus sometimes extending beyond margin of propodus; rostrum extending as triangular process, sometimes trifid 5

3′. Orbits often oblique, directed obliquely downward; outer margin of extraorbital spines never very convex; chelipeds with short flattened propodus, dactylus very short and bent against margin of propodus; rostrum present as triangular process, or absent . . . . Notopodinae Serène & Umali, 1972

4. Fronto-orbital margin equal to or more than ½ extreme width of carapace; 2 orbital fissures; medial supraorbital tooth always present, though not always produced beyond orbital rim; never more than 1 anterolateral spine . . . . Raninoidinae De Haan, 1841

4′. Fronto-orbital margin somewhat narrow, often less than ½ extreme width of carapace; 1 or 2 orbital fissures; medial supraorbital tooth sometimes absent; 1 or 2 anterolateral spines, though often reduced in size . . Lyreidinae Guinot, 1993

5. Dorsal surface of carapace either scabrous or terraced; front margin of carapace wide; rostrum often trifid, base with sides parallel, or produced triangle; chelipeds with short, flattened propodus, dactylus very short and bent against margin of fixed finger; sternal thoracic shield quite broad, especially between first pereiopods . . Ranininae De Haan, 1841

5′. Dorsal surface of carapace granulate in front and anteriorly, smoother medially; front margin of carapace narrow; rostrum never trifid, short produced triangle; chelipeds with elongate swollen or subcircular propodus, dactylus long so that tip often crosses propodus; sternal thoracic shield narrow, nearly linear between first pereiopods . . . . Cyrtorhininae Guinot, 1993

Subfamily Lyreidinae Guinot, 1993

Lyreidinae Guinot, 1993:1325.

Key to *Lyreidus, Lysirude* and *Macroacaena*

The three genera included within Lyreidinae, *Lyreidus, Lysirude,* and *Macroacaena,* are often difficult to distinguish from one another. The following key is provided only as an aid in identification, and should be used with caution.

1. Tridentate fronto-orbital margin with 2 pairs orbital fissures; 2 pairs orbital teeth, outer teeth as long, or longer than the rostrum; inner teeth small, barely protruding; carapace typically with distinct longitudinal ridge; 1 pair of hypertrophied anterolateral spines, and additional obsolete anterolateral spine often present at midpoint of anterolateral border; no spines on abdominal somites; no spine or lobe on lancelate propodus of fourth pereiopods . . . . *Macroacaena*, new genus

1′. Tridentate fronto-orbital margin with single pair orbital fissures; single pair extraorbital teeth, no inner orbital teeth; carapace sometimes with indistinct longitudinal ridge; carapace with 1 or 2 pairs anterolateral spines; spine on abdominal somites 3 and/or 4; sternite 4 about as wide anteriorly as posteriorly; fourth pereiopods with spine or lobe on propodus of fourth pereiopods 2

2. Carapace with not more than 1 pair of anterolateral spines; anterolateral spines sometimes reduced or absent; anterolateral margins smooth or beaded; extraorbital teeth typically as long as wide, about as long as rostrum; sternal plate about as wide at anterior sternite 4 as process between sternites 4 and 5; propodus of fourth pereiopods with spine carrying a spine . . . *Lyreidus* De Haan, 1841

2′. Carapace with 2 pairs of anterolateral spines or anterolateral margin coarsely corrugated; anterolateral spines often hypertrophied; anterolateral margins typically bearing an obsolete spine; extraorbital teeth as long as rostrum, often elongated; sternal plate distinctly widest between sternites 4 and 5; propodus of fourth pereiopods with expanded lobe . . . . *Lysirude* Goeke, 1985

Lyreidus De Haan, 1841

Lyreidus De Haan, 1841:138

Figs. 1(1–2), 2(10–13)

Type species.—*Lyreidus tridentatus* De Haan, 1841:140, by monotypy. Gender: Masculine.

Diagnosis (modified from Feldmann 1992:943).—Carapace fusiform, much longer than wide, fronto-orbital region narrow, between ¼ to ½ maximum width of carapace; extraorbital spines about equal in length to rostrum; orbits with single, diminutive fissure; marginal spines, if present, at anterolateral corner; anterolateral margin straight, smooth or slightly granulate; surface of carapace smooth or very finely pitted, regions not clearly defined.

Remarks.—There has been some difficulty placing certain species referred to *Lyr-*

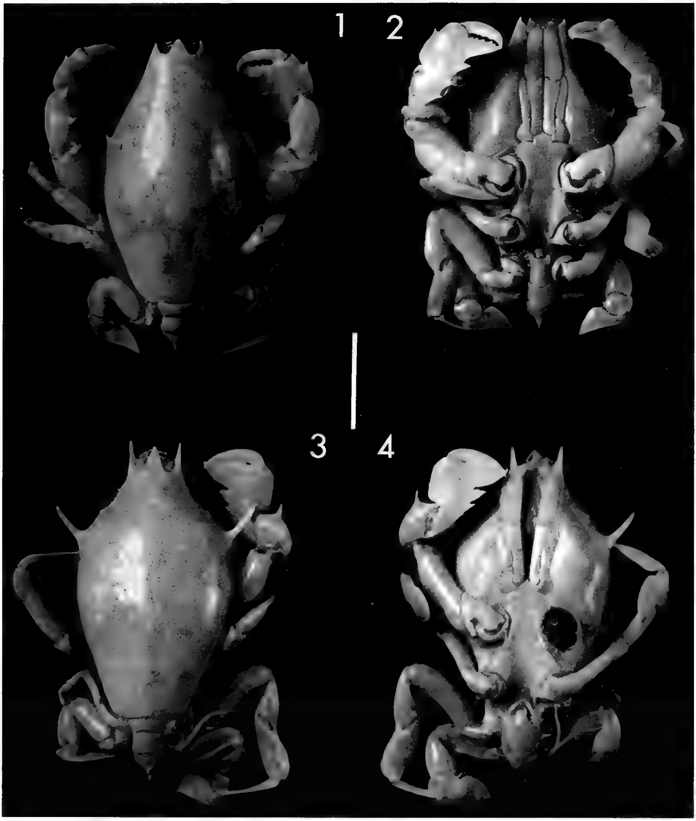

Fig. 1 *Lyreidus tridentatus* De Haan, 1841, USNM 18848: 1, dorsal view; 2, ventral view showing sternites. *Lysirude channeri* (Wood-Mason, 1885), USNM 216686: 3, dorsal view; 4, ventral view. Scale bar equals 1 cm.

eidus De Haan, 1841, and *Lysirude* Goeke, 1985, into their proper systematic positions. Among the most problematic are *Lyreidus succedanus* Collins & Rasmussen, 1992; *Lyreidus rosenkrantzi* Collins & Rasmussen, 1992; *Lyreidus bispinulatus* Collins & Rasmussen, 1992; and *Lyreidus alseanus* (Rathbun, 1932). These four species are placed in a new genus (see *Macroacaena,* new genus). There are several characteristics that are useful taxonomic indicators for species within *Lyreidus*; these were expressed in some detail by Feldmann (1992).

Generic differences between *Lyreidus* and *Lysirude* species often are quite subtle. Goeke (1985) erected the genus *Lysirude* for two species formerly assigned to *Lyreidus,* based upon the lobate nature of the

Table 1.—Distributions and geologic ages of recognized species of *Lyreidus*.

Taxon	Age	Locality
Lyreidus tridentatus De Haan, 1841	Recent	Indopacific
Lyreidus antarcticus Feldmann & Zinsmeister, 1984	early to late Eocene	Antarctica
Lyreidus bennetti Feldmann & Maxwell, 1990	late Eocene	New Zealand
Lyreidus brevifrons Sakai, 1937	Recent	Indian Ocean; Philippines; Japan
Lyreidus elegans Glaessner, 1960	Micoene	New Zealand
Lyreidus lebuensis Feldmann & Chirono-Gálvez, 1992 in Feldmann, 1992	Eocene	Chile
Lyreidus stenops Wood-Mason, 1887	Recent	S. China Sea; Philippines; Japan
Lyreidus sp. Karasawa, 1993	early Pliocene	Japan

dactylus and propodus of fourth pereiopods and the rudimentary spine on the anterolateral margin of *Lysirude*. Feldmann (1992) subsequently united the two groups as subgenera of *Lyreidus*. Further observations yielded additional characters, which can be used to differentiate these two genera. The fronto-orbital margins of *Lyreidus* species in all cases are very narrow, much narrower than one-half the maximum width of the carapaces. *Lysirude* species typically have a fronto-orbital margin that is relatively wider than those of *Lyreidus*. Typically, the rostrum and orbital spines of *Lysirude* species are more produced than those of *Lyreidus*. These additional observations, when coupled with those provided by Goeke (1985:214), serve to distinguish members of *Lysirude* as a separate generic group. Table 1 provides a list of the geographic and stratigraphic positions of recognized species of *Lyreidus*.

Lysirude Goeke, 1985
Figs. 1(3–4), 2(6–9)

Lysirude Goeke, 1985:205–228.
Lyreidus (*Lysirude*) Feldmann, 1992:943–957.

Type species.—*Raninoides nitidus* A. Milne Edwards, 1880:34, by original designation. Gender: Masculine.

Diagnosis.—Fronto-orbital margin tridentate, equal to or slightly wider than posterior margin or ½ maximum width of carapace; rostrum and extraorbital spines often elongate; anterolateral margin typically not straight, usually corrugated, granular, or with rudimentary anterolateral spine at midlength; spine at anterolateral corner often hypertrophied.

Remarks.—Species of *Lysirude* (Table 2) share many traits with species of *Lyreidus*, including a narrow, tridentate fronto-orbital margin, a single orbital furrow, an abdominal spine on the third somite, and "ptery-

Table 2.—Distributions and geologic ages of recognized species of *Lysirude*.

Taxon	Age	Locality
Lysirude nitidus (A. Milne Edwards, 1880)	Recent	western N. Atlantic; Caribbean
Lysirude channeri (Wood-Mason, 1885)	Recent	Bay of Bengal; Philippines
Lysirude griffini Goeke, 1985	Recent	Philippines
Lysirude hookeri (Feldmann, 1992)	late early Eocene	Antarctica
Lysirude hungaricus (Beurlen, 1939)	middle Oligocene	Hungary
Lysirude paronae (Crèma, 1895)	Miocene	Italy
Lysirude waitakiensis (Glaessner, 1980)	middle Eocene	New Zealand

goid processes" (Bourne 1922) along the margin of the sternum between the fifth and sixth somites. These processes are used to lock the abdomen into the sternum, and they do not occur on any other known raninid except *Rogueus* Berglund and Feldmann 1989 and, possibly, *Macroacaena* new genus. In contrast, members of *Lysirude* typically have a much longer rostrum and orbital spines than do species of *Lyreidus.* Variations in the fronto-orbital width within some species of *Lysirude* (for example, *Lysirude nitidus* (A. Milne Edwards 1880)) can be attributed to ontogenetic changes, with juveniles exhibiting a relatively wider fronto-orbital margin (Goeke 1980) than adults. The anterolateral spine generally is hypertrophied in *Lysirude* species, and most species bear some evidence of an extra pair of smaller, rudimentary anterolateral spines at the midlength of the anterolateral margin. Typically, species of *Lysirude* also have a flattened dactylus and a propodus with a flattened flap, which is extended, along the outer margin. Finally, the sterna of *Lysirude* have a broad alate process separating the first and second pereiopods. These differences are significant enough to justify elevation of the subgenus *Lysirude* to generic status.

The earliest records of *Lysirude* are from rocks in high southern latitudes in Antarctica. Table 2 documents the occurrences of species of *Lysirude.*

Macroacaena, new genus

Fig. 2(1–5)

Type species.—*Lyreidus succedanus* Collins & Rasmussen, 1992:23, figs. 11A, B, C, 12, by present designation.

Diagnosis.—Fronto-orbital margin tridentate, wider than posterior margin with orbits bearing 2 fissures; anterolateral margin with or without small tubercle at midlength; spine at anterolateral corner typically hypertrophied; distinct, median, longitudinal ridge typically extending through cardiac region to posterior margin. Abdominal somites (where observed) smooth. Fourth pereiopods (where observed) without spine or extended propodus (Fig. 2).

Etymology.—"Macra", from Greek μακροζ (makros) = long + "acaena" from Greek ακαιγα (akaina) thorn or spine. Gender: Feminine.

Remarks.—Members of this genus appear superficially similar to *Lyreidus* and *Lysirudae.* The fronto-orbital margins of some species of *Lysirude* are just slightly wider than the posterior margins. This also is true of three taxa from Greenland assigned by Collins & Rasmussen (1992:23–30) to *Lyreidus.* However, the three species from Greenland have two orbital fissures, while members of *Lyreidus* and *Lysirude* typically bear only a single orbital fissure. This is a very important taxonomic character, based upon cladistic character analysis (see section on Phylogenetic Analysis and Fig. 22). The additional orbital fissure demarks a rudimentary mid-orbital tooth not observed in species within *Lyreidus* or *Lysirude.* Furthermore, the pronounced longitudinal ridge observed on *L. succedanus* and *L. alseanus* does not appear to be as prominent on species of *Lyreidus* or *Lysirude.* Two of the three species described by Collins & Rasmussen (1992), *Lyreidus rosenkrantzi* and *L. succedanus,* have portions of the abdomen preserved; no specimens appear to bear any abdominal spines, a character typical of species of *Lyreidus* and *Lysirude* (Fig. 2). Moreover, three species from Greenland have a lancelet dactylus on the fourth pereiopods, and show no protuberance, spine or flap on the propodus of the fourth pereiopods, as exhibited on *Lyreidus* species and *Lysirude* species. These species should be united within a distinct genus. Additionally, *Lyreidus alseanus* Rathbun, 1932, appear to have these same characteristics; thus, they also must be united under the new genus (Table 3). All four species referred to *Macroacaena* are discussed below.

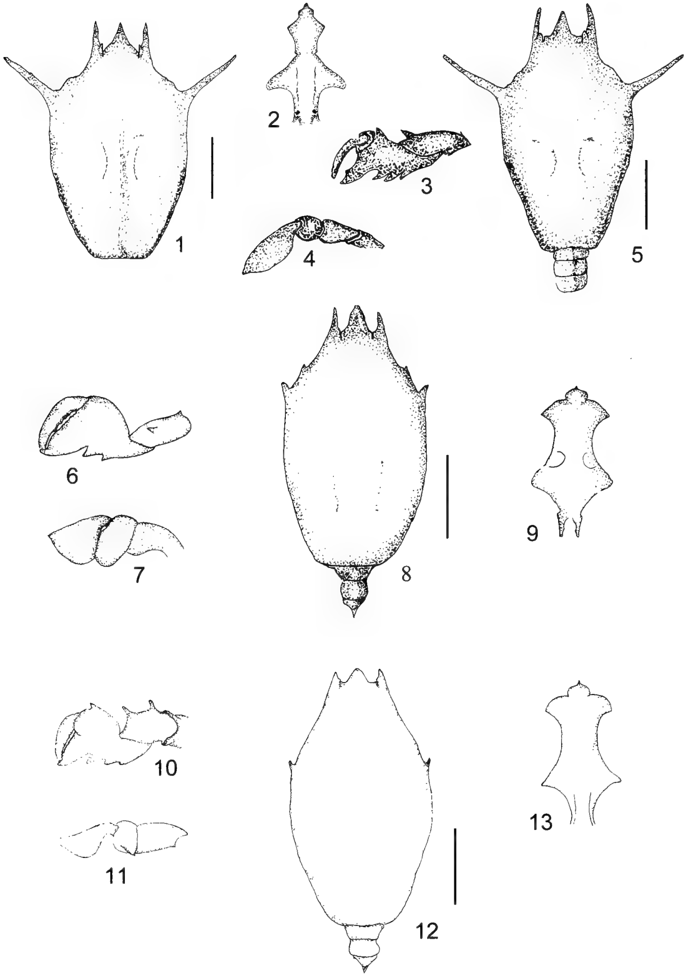

Fig. 2. *Macroacaena alseana* (Rathbun, 1932): 1, View of dorsal carapace; 2, sternum. *M. rosenkrantzi* (Collins & Rasmussen, 1992): 3, cheliped; 4, fourth pereiopod; 5, dorsal carapace. *Lysirude nitidus* (A. Milne Edwards, 1880): 6, cheliped; 7, fourth pereiopod; 8, dorsal carapace; 9, sternum. *Lyreidus tridentatus* De Haan, 1841: 10, Cheliped; 11, fourth pereiopod; 12, dorsal carapace; 13, sternum. Scale bar equals 1 cm.

Macroacaena succedana (Collins & Rasmussen, 1992), new combination

Lyreidus succedanus Collins & Rasmussen 1992:23, figs. 11A–C, 12.

Material examined.—Plastotype kindly supplied by J. H. S. Collins, Jr., supplemented with photographs and drawings by Collins & Rasmussen (1992).

Remarks.—The carapace is somewhat fusiform in outline; the fronto-orbital region is slightly wider than the posterior margin and bears two closed fissures and a medial tooth; the anterolateral margin is armed with two spines, one hypertrophied and positioned at the anterolateral corner, the other rudimentary tubercle and positioned at about the midlength of the anterolateral margin; the fourth pereiopod has a lancelet dactylus; and there is no spine observable on any abdominal somite such as occurs on species of both *Lyreidus* and *Lysirude.*

Occurrence.—*Lyreidus succedana* is represented by 192 carapaces from many localities ranging in age from Campanian to Maastrichtian, along the central western shores of Greenland (Collins & Rasmussen 1992).

Macroacaena alseana (Rathbun, 1932), new combination

Lyreidus alseanus Rathbun, 1932:239, 240, 242, figs. 3–4; Glaessner, 1960:17; Bennett, 1964:24; Feldmann, 1989:63–69, figs. 1.1–2, 3.1–8; text fig. 4.1–3.

Ranidina teshimai Fujiyama & Takeda, 1980:339–342, pl. 39, figs. 1–5, pl. 40, figs. 1–4.

Lyreidus (Lysirude) alseanus. Feldmann, 1992:951, figs. 4.10–11.

Material examined.—Fifteen specimens (USNM 431289–431303); 4 specimens, coll. R. Berglund (private collector affiliated with Burke Museum).

Remarks.—Specimens previously referred to *Macroacaena alseana* bear a midorbital tooth that protrudes just beyond the orbital rim, thus allowing this taxon to be distinguished from members of *Lyreidus* or *Lysirude.* The fronto-orbital margin is just slightly wider than the posterior margin, or one-half the extreme width of the carapace. Specimens of *M. alseana* have a very distinctive longitudinal carina, a character that is shared with some species of *Carinaranina,* a new genus assigned herein to the Raninoidinae. However, the three prominent frontal teeth, two extraorbital teeth and the rostrum, serve to distinguish this taxon from any other described from the Pacific northwest of North America. *Macroacaena alseana* also bears a rudimentary second anterolateral tooth or nubbin, which is not observed on any species of *Carinaranina* new genus. This last character also serves to distinguish *M. alseana* from species of *Carinaranina* when the fronto-orbital region is not well preserved.

Macroacaena alseana is most similar to *M. succedana,* but differs in the possession of a relatively wider carapace and a more well defined longitudinal ridge. The medial tooth is positioned a little closer to the extraorbital spine than in *M. succedana.*

As noted by Feldmann (1989:68, 1992: 951), *Ranidina teshimai,* recognized from the Oligocene Poronae Formation of Hokkaido, Japan, is a junior synonym of *Lyreidus alseanus* Rathbun. Photographs (Fujiyama & Takeda 1980, plates 39 & 40) indicate that specimens of *R. teshimai* have the same broad carapace as seen in specimens of *M. alseana,* and the anterolateral spines are positioned similarly and at a similar angle as specimens from Washington and Oregon.

Occurrence.—*Macroacaena alseana* is known from several localities in Washington and Oregon, U.S.A., in rocks that range in age from late Eocene to Oligocene (Feldmann 1989:951).

Macroacaena bispinulata (Collins & Rasmussen, 1992), new combination

Lyreidus bispinulatus Collins & Rasmussen, 1992:27, fig. 16A–D.

Material examined.—Several plastotypes supplied by J. S. H. Collins.

Remarks.—Upon inspection of photographs as well as several plastotypes, I agree with Collins & Rasmussen (1992) that this species should not be referred to *Hemioon* Bell, 1863, which it superficially resembles. Even though there is no extra anterolateral tooth or tubercle, this species is more correctly placed within *Macroacaena,* since the occurrence of a rudimentary anterolateral tooth seems to be quite variable within this genus. The front of *M. bispinulata,* however, appears to be exceptionally wide and the extraorbital tooth exceptionally short, when compared with other members of *Macroacaena.* In the description by Collins & Rasmussen (1992:28–29), the species is defined as possessing a medial orbital tooth and two orbital fissures, two very important characters for uniting *Macroacaena* species. The front margin is described as being rather narrow, and as possessing a rostrum that is broadly triangular with no median furrow. This observation serves to differentiate this species from those referred to *Hemioon* Bell, with which it could easily be confused.

Occurrence.—Macroacaena bispinulata is known from six incomplete carapaces collected from Paleocene age rocks on the western coast of Greenland.

Macroacaena rosenkrantzi (Collins & Rasmussen, 1992), new combination

Lyreidus rosenkrantzi Collins & Rasmussen (1992):23, figs. 11A–C, 12.

Material examined.—Plastotype supplied by J. S. H. Collins.

Remarks.—Macroacaena rosenkrantzi possesses all the characteristics of the genus, and is distinguished from *M. succedana* and *M. alseana* primarily by the lack of a longitudinal median ridge. *Macroacaena rosenkrantzi* is further distinguished from *M. succedana* by the possession of less deeply impressed cardiac furrows and by anterolateral spines that are positioned at a more acute angle with the carapace midline than those of *M. succedana.*

Occurrence.—Macroacaena rosenkrantzi is represented by 1240 carapaces from many localities, Maastrichtian in age, along the central western shores of Greenland.

Subfamily Notopodinae Serène & Umali, 1972

Notopinae [sic] Serène & Umali 1972:25, 29.—Notopodinae Goeke 1986:224, 226.—Notopodinae Guinot 1993:1324–1325, 1327–1329.

Diagnosis.—Carapace either elongate or quite rounded; front margin variable, often directed forward but sloping obliquely downward; median dorsal carina sometimes present; chelipeds, where known, with short flattened propodus, dactylus very short and bent against margin of propodus; rostrum present as triangular process, or absent.

Remarks.—Serène & Umali (1972:29) first erected the Notopinae [sic] and designated *Notopus* De Haan 1841 as the type genus. Subsequently, Manning & Holthuis (1981:7) corrected the name to Notopodinae. The genera that Serène & Umali referred to the Notopodinae included *Notopus* De Haan, *Cosmonotus* White, 1847, and *Ranilia* H. Milne Edwards, 1837. Eight additional genera are included within this subfamily: *Eumorphocorystes* Binkhorst, 1857, *Lianira* Beschin et al., 1991, *Lovarina,* Beschin et al., 1991, *Notopella* Lörenthey (*in* Lörenthey & Beurlen, 1929), *Pseudoraninella* Lörenthey (*in* Lörenthey & Beurlen, 1929), *Raniliformis* Jagt et al., 1993, and *Umalia* Guinot, 1993. *Umalia* is the only extant taxon; seven of the eight are fossil.

Genus *Eumorphocorystes* Binkhorst, 1857

Fig. 3

Type species.—Eumorphocorystes sculptus Binkhorst 1857, by monotypy:108, pl. VI, figs. 1–2. Gender: Masculine.

Diagnosis.—Carapace obovate, with anteriorly directed anterolateral spines. Ros-

Fig. 3. *Eumorphocorystes sculptus* Binkhorst, 1857, IG 6521-9.7: dorsal view of carapace. Scale bar equals 1 cm.

trum long, very narrow. Dorsal surface of carapace with narrow, raised median ridge extending entire length of carapace; surface covered with longitudinal and oblique raised, beaded ridges which are irregular in pattern, but somewhat symmetrical on each side of midline of carapace; surface very finely punctate.

Remarks.—See discussion under *Carinaranina,* new genus.

Eumorphocorystes sculptus Binkhorst, 1857
Fig. 3

Eumorphocorystes sculptus Binkhorst, 1857:108, pl. VI, figs. 1–2.–Binkhorst, 1861, pl. 9, fig. 2.—Straelen, 1923: 119.—Glaessner, 1929:170.—Lörenthey (*in* Lörenthey & Beurlen, 1929).—Tucker & Feldmann, 1990.

Raninella sculpta A. Milne Edwards, 1862: 493.—Pelseneer, 1886:174.

Diagnosis.—Same as for genus.

Description (emending E. sculptus*).*—Carapace longer than broad; widest at or just slightly posteriad anterolateral spines; extreme width, excluding anterolateral spines, about 75% length. Carapace slightly convex transversely, less so longitudinally; dorsal surface of carapace evenly covered by minute punctae. Dorsal surface with raised, almost bilaterally symmetrical longitudinal and oblique ridges with flattened tops lying on either side of raised median carina which extends entire length of carapace including rostrum. Median carina and ridges steep-sided and irregularly beaded along both margins.

Width of fronto-orbital margin about 66% extreme width; front about 33% extreme width of carapace, with median narrow triangular rostrum bordered on either side by broad inner orbital regions. Orbits ovate, moderately oblique; dorsal margin of each orbit beaded and bearing 2 closed fissures.

Anterolateral margins sinuous, terminating at anterolateral angle with short, acicular spine directed anteriorly. Posterolateral margins only slightly convergent to posterolateral angle, then strongly convergent to posterior corners, and narrow posterior margin.

Most prominent transverse raised ridges on dorsal surface of carapace originating at anterolateral tooth, and extending medially marking position of cervical groove. Another prominent transverse groove parallel to cervical ridge marking position of branchial furrow. Protogastric regions with raised ridges in h-shaped pattern on either side of median carina; these attach at their base to transverse Y-shaped ridges. Branchial regions with irregular ridges in irregular pattern of loops.

Affinities.—(See discussion under *Carinaranina,* new genus, for affinities of *Eumorphocorystes* sensu Binkhorst, and *Eu-*

morphocorystes sensu Rathbun. Species referred by Rathbun to *Eumorphocorystes* are herein included in *Carinaranina.*)

Material examined.—4 specimens, Carnegie Museum, Pittsburgh, Pennsylvania, U.S.A.; 11 specimens, Institut Royal des Sciences Naturelles de Belgique (IG 6521, 9.1–9.9; IG 4285, and IG 5185); 5 specimens, Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany.

Remarks.—Cuticular terraces have been the focus of research regarding the burrowing habits of crabs (Savazzi 1981, 1985). However, little attention has been paid to terraces that are irregular in pattern, and that are not transverse. The raised ridges on *Eumorphocorystes sculptus* van Binkhorst, are probably not analogous to the terraces on *Lophoranina* species, because they do not demonstrate an anchoring capability. That is, they are not perpendicular to the borrowing direction of the crab, nor is the anterior side of the terrace raised to prevent withdrawal of the crab from its burrow. On the other hand, the roughened surface may have had some gripping capability, and it is possible that the beading along the margins carried spines, although none has been observed to date on any specimens.

Pelseneer (1886:14) suggested that *Notopocorystes Mülleri* [sic] and *Eumorphocorystes sculptus* might be congeneric and quite similar to *Raninella* species; thus, he placed both species within *Raninella.* He believed that the slight sculpting along the postfrontal region of *N. muelleri* was analogous to the raised ridges on the dorsal surface of *E. sculptus.* However, there are several major differences between the species that are sufficient to require placement within separate genera. *Pseudoraninella muelleri,* reassigned by Lörenthey (*in* Lörenthey & Beurlen 1929), is extremely vaulted transversely, while *E. sculptus* is nearly flat. This is an important distinction that often reflects the positioning of the gills. The fronto-orbital margins of *Eumorphocorystes* are beaded, but without spines; the margins of *Pseudoraninella* species bear orbital spines.

Occurrence.—Late Cretaceous (Maastrichtian) Maastricht Formation, Belgium.

Subfamily Palaeocorystinae Lörenthey (*in* Lörenthey & Beurlen, 1929)

Palaeocorystinae Lörenthey (*in* Lörenthey & Beurlen, 1929):299.

Diagnosis.—Carapace with distinct cervical and branchiocardiac grooves; two or more anterolateral spines; longitudinal carina present, often centrally nodose; rostrum bifid; carapace anterior of cervical groove often tuberculate or lingulate.

Description.—Elongated, somewhat flat to moderately inflated crabs with small projecting bifid rostrum, straight orbitofrontal margin, large oval orbits with 2 fissures above and 1 below. Distinct longitudinal carina may or may not be present. Cervical furrow directed anteriorly from margin, then posteriorly, forming 3 forwardly concave arcs; epibranchial lobes delimited by short furrows; branchiocardiac furrows weak to absent. Upper surface may bear sharp tubercles, or be bare, or have strap-like ornament, or transverse lobed line posterior to depressed frontal area. Pterygostomial regions strongly ridged. [modified from Wright & Collins 1972:73]

Remarks.—Wright & Collins (1972:73) interpreted *Notopocorystes, Eucorystes,* and *Cretacoranina* as subgenera of *Notopocorystes* because of the many features they have in common. Any distinctions that separated the three were considered by Wright & Collins to be of subgeneric importance. For example, they considered that widening of the front and size of the orbits was not an important enough distinction to warrant separation at the level of genus. Features of the fronto-orbital margin are interpreted by this author to be of greater significance than numbers of tubercles. Additionally, the carapace of *Notopocorystes* has a deep cervical groove and many robust tubercles. *Eucorystes* retains the cervical groove, but there is already a loss of tubercles and a unique pattern of raised ridges. *Cretacoranina* has a much fainter cervical groove and is much smoother on the dorsal surface than either Notopocorystes or Eucorystes. Raninids demonstrate a general trend, then, from the tuberculate dorsal surface of *Notopocorystes* with a well defined cervical groove, to the smooth dorsal surface of Recent raninids which, with few exceptions, bear no cervical groove. Wright & Collins (1972:73) also pointed out that these three taxa could be treated equally well as three distinct genera, and this arrangement has been followed in the cladistic analysis.

Wright & Collins (1972:75) used subspecies to distinguish successive populations recovered from many Albian horizons in England. They stated that "Although the differences between them are greater than those sometimes used to distinguish species . . .", but that they preferred to treat them as subspecies. Indeed, other workers have used several of the same characteristics to describe species within one or more of these genera (Secretan 1964:155). Using the same characters to describe species-level taxa one time, and subspecies-level taxa another, contributes to a certain amount of confusion when considering all the species assigned to all three genera. I prefer to structure the descriptions of genera and species within the Raninidae so that there is a sense of uniformity throughout. At the same time, it is important to recognize the remarkable collection of specimens that demonstrates the evolution of several species.

The Palaeocorystinae, comprised of three genera, ranged from the lower Albian to the Cenomanian, and are recognized from Europe, Japan, North America, New Zealand, and Madagascar. The Palaeocorystinae are interpreted to represent the rootstock of the Raninidae.

Key to genera of Palaeocorystinae

1. Dorsal surface decorated with tubercles or vermiform ridges (=strap ornament). Carapace moderately to strongly vaulted. Cervical furrow deep, complete; branchiocardiac furrow complete, but feeble; anterolateral margins straight to slightly convex 2

1′. Dorsal surface finely granulate or smooth. Carapace only weakly vaulted, if at all. Cervical and branchiocardiac furrows shallow, incomplete, often reduced to medial portions only; anterolateral margins distinctly convex . . . . *Cretacoranina* Martin, 1941

2. Distinct, sharp tubercles on anterior dorsal surface of carapace with no vermiform ridges; median carina present, tuberculate or smooth . . . . *Notopocorystes* McCoy, 1849

2′. Anterior dorsal carapace with distinct system of vermiform, steep-sided, flat-topped ridges (=strap ornament) and no tubercles; long ridges parallel to longitudinal axis of carapace may, or may not, be present posteriorly . . . . *Eucorystes* Bell, 1863

Genus *Notopocorystes* McCoy, 1849
Fig. 4(1–2)

Notopocorystes McCoy, 1849:169.
Palaeocorystes Bell, 1863:11, pl. II, figs. 8–13.

Type species.—Subsequent designation by Withers (1928), *Corystes stokesii* Mantell, 1844:533. Gender: Masculine.

Diagnosis.—Distinct sharp tubercles on anterior portion of upper surface of carapace and smooth or dentate median carina or row of tubercles (Wright & Collins 1972: 73). Carapace elongate oval in outline; vaulted transversely, less so longitudinally. Dorsal surface of carapace with distinct, longitudinal, median keel for almost entire length of carapace, often bearing row of tubercles; surface of carapace finely punctate; regions marked by grooves and tubercles or ridges. Fronto-orbital margin broad, greater than 40% extreme width of carapace; supraorbital ridges bearing 2 distinct fissures; rostrum bifid. Cervical furrow distinct; epibranchial region often delimited by furrow. Posterolateral margins straight.

Fig. 4. *Notopocorystes serotinus* Wright & Collins, 1972, KSU 4940 (a plastotype of B22902): 1, dorsal view; 2, ventral view. Scale bar equals 1 cm.

Remarks.—Species in this genus are easily distinguished from other Cretaceous raninids by several characters. *Notopocorystes* species generally are quite tuberculate and almost always bear a tuberculate median keel for their entire length. *Eucorystes* species, on the other hand, do not bear tubercles; rather, they are adorned with steep-sided vermiform ridges, referred to as "strap ornament", especially anterior to the cervical furrow. *Cretacoranina* species generally have a much smoother dorsal surface, and are much less vaulted than *Notopocorystes* species. Additionally, *Cretacoranina* species often have a somewhat concave aspect to the posterolateral margins, not observed on species of either of the other two genera.

See Table 3 for species assigned to this genus.

Genus *Cretacoranina* Mertin, 1941
Fig. 5(1–2)

Cretacoranina Mertin, 1941:237, pl. 8, fig. 9; as subgenus.

Type species.—By original designation, *Raninella schloenbachi* Schlüter, 1879. Gender: Feminine.

Diagnosis.—Carapace oval to oblong; surface finely granulate or smooth; distinct, longitudinal, median keel for almost entire length of carapace not tuberculate. Front slightly produced, rostrum bifid; postfrontal area sometimes depressed. Supraorbital margin bearing 2 distinct fissures. Anterolateral margins toothed.

Remarks.—Characters that distinguish *Cretacoranina* from other Palaeocorystinae include the smooth, nontuberculate dorsal carapace and the often-depressed postfrontal area. Taxa referred to this genus (see Table 4) retain the well-impressed cervical and branchial furrows, although often the furrows are reduced to the median portions of the dorsal carapace. Species of the genus are distinguished upon the basis of the shape of the anterolateral margin and the

Table 3.—Distribution and geologic ages of recognized species of *Notopocorystes*.

Taxon	Age	Locality
Notopocorystes stokesii (Mantell, 1844)	Albian	England
N. praecox Wright & Collins, 1972	Albian	England
N. serotinus Wright & Collins, 1972	Albian	England
N. normani (Bell, 1863)	Cenomanian	England; Germany
N. bituberuculatus (Secretan, 1964)	Albian	Madagascar
N. japonicus (Jimbô, 1894)	late Turonian or early Coniacian	Japan
N. xizangemsos Wang, 1981	Albian	China

Fig. 5. *Cretacoranina testacea* (Rathbun, 1926): paratype USNM 327238: 1, dorsal view of anterior; 2, ventral view showing buccal frame. Scale bar equals 1 cm.

number of anterolateral spines, the presence or absence of a depressed frontal area, and the smoothness of the dorsal carapace. The dorsal median keel is faint to absent on some species.

Genus *Eucorystes* Bell, 1863
Fig. 6(1–2)

Eucorystes Bell, 1863:17, pl. II, figs. 14–17.

Type species.—Subsequent designation by Bell (1863), *Notopocorystes carteri* McCoy, 1854. Gender: Masculine.

Diagnosis.—Carapace rectangular in outline; only slightly vaulted transversely, nearly flat longitudinally. Dorsal surface of carapace with longitudinal median keel for almost entire length of carapace; surface of carapace possessing many granulate, flattened ridges; anteriormost ridges linear and arrayed longitudinally and symmetrically on either side of longitudinal axis of carapace; surface of carapace between ridges finely punctate. Fronto-orbital margin representing extreme width of carapace; supraorbital ridges bearing 2 distinct fissures; rostrum small, bifid or trifid. Cervical furrow distinct; epibranchial region often delimited by furrow. Posterolateral margins straight; converging only slightly posteriorly.

Remarks.—Bell (1863) distinguished this genus based primarily upon the shape of the carapace as more square than *Notopocorystes* species, the shape and greater size of the orbits of *Eucorystes* species, and the "strap" ornament found on the anterior

Table 4.—Distributions and geologic ages of recognized species of *Cretacoranina* Mertin, 1941.

Taxon	Age	Locality
Cretacoranina schloenbachi (Schlüter, 1879)	Coniacian	England; Germany
C. australis Secretan, 1964	late Santonian–early Campanian	Madagascar
C. broderipii (Mantell, 1844)	Albian–Cenomanian	England; France
C. denisae Secretan, 1964	Campanian	Madagascar
C. dichrous Stenzel, 1944	Turonian	Texas
C. exiquus Glaessner, 1980	Cretaceous	Bathhurst Is., Australia
C. fritschi Glaessner, 1930	Turonian	Germany
C. harveyi (Woodward, 1896)	Cenomanian	Vancouver Is., B. C.
C. ornatus Wright & Collins, 1972	Cenomanian	England
C. paututensis Collins & Rasmussen, 1992	late Santonian–early Campanian	Greenland
C. syriacus Withers, 1928	Cenomanian	Syria
C. cf. *syriacus* Withers, 1928	Cenomanian	England
C. testacea (Rathbun, 1926)	Late Cretaceous	Delaware; New Jersey

portions of the carapace. Bell (1863:18) suggested that characteristics of the fronto-orbital region were extremely important at the level of genus. *Eucorystes* species (see Table 5) can be separated on the basis of the shape of the anterolateral borders, the sharpness of anterolateral and orbital spines, the relative width of the fronto-orbital margin, the amount of vaulting, the character of the grooves, and the character of the 'strap' ornamentation.

Subfamily Raninoidinae De Haan, 1841

Raninoidea De Haan, 1841:136–137.

Diagnosis (emending Raninoidinae).—Carapace elongate oval; fronto-orbital margin equal to or more than ½ extreme width of carapace; 2 orbital fissures; medial orbital tooth always present, though not always produced beyond supraorbital rim; never more than 1 anterolateral spine. Sternal shield between third pereiopods at base of sternite 5 relatively wide, sternite 6 relatively broad. Chelipeds with propodus flattened and somewhat elongate, long fixed finger; anterolateral spine, when present, often hypertrophied.

Remarks.—The cladistic analysis (see Phylogenetic Analysis and Fig. 22) suggests that this subfamily consists of two clades. One clade includes *Raninoides, Laeviranina,* and *Carinaranina,* new genus; another includes *Quasilaeviranina,* new genus, *Notopoides,* and *Notosceles.* Characters which unite these two clades and distinguish the Raninoidinae from other raninids include their elongate, ovate outline, the shape of the chelipeds, the shape of sternites, the presence of only a single pair of anterolateral spines (although these are sometimes reduced to absent), and the general conformation of the toothed fronto-orbital region. The *Quasilaeviranina* group is distinguished by the more rounded appearance of the outline of the carapace, and by a fronto-orbital margin that tends to converge anteriorly and often bears closed rather than open orbital fissures. The two groups are so closely related to one another that they should remain united as a single subfamily.

Genus *Carinaranina,* new genus

Type species.—*Eumorphocorystes naselensis* (Rathbun, 1926), by present designation. Gender: Masculine.

Diagnosis.—Carapace elongate, greatest width posteriad to antero-lateral spines; outline of carapace often egg-shaped; fronto-orbital region narrow, orbits marked by fissures; rostrum produced. Anterolateral spines often hypertrophied. Branchial regions usually depressed. Surface of carapace coarsely punctate, often with dorsal

Fig. 6. *Eucorystes carteri* (McCoy, 1854): dorsal view of plastotype 1, KSU 4967; 2, CU 319f. Scale bar equals 1 cm.

ridge extending entire length of carapace, including rostrum.

Remarks.—Rathbun (1926) described a new species of crab from Washington that she referred to *Eumorphocorystes* Binkhorst (1857) because of the egg-shaped body, the dorsal ridge, and the narrow orbital fissures. Apparently, from her comments (Rathbun 1926:100), this decision was based entirely upon written description of the genus by Binkhorst (1857). Rathbun (1932) later referred two more species to *Eumorphocorystes, E. schencki* and *E.* (?) *leucosiae.* Since that time, others (Lörenthey, *in* Lörenthey & Beurlen 1929:297; Glaessner 1969:R2–498) have questioned these assignments; however, none of the species have been reassigned to other genera. Some workers have doubted the accuracy of the lithographic illustration of the type with regard to the rostrum (Pelseneer 1886:174, Lörenthey, *in* Lörenthey & Beurlen 1929:297; Glaessner 1969:R–495), pointing out that the rostrum should have been depicted as quite narrow, carrying a median ridge with furrows on either side, and about 4 mm long for a carapace 36 mm in length (translated from Pelseneer 1886: 174). Indeed, a photograph of a specimen identified as belonging to *Eumorphocorystes sculptus,* but not the holotype, shows the rostrum as described by Pelseneer (1886) (see Fig. 3).

It is necessary, then, to place the species of *Eumorphocorystes* sensu Rathbun (1926, 1932) in a newly erected genus reflecting their close relationships. It is clear that the species Rathbun described are not related at the generic level with the monotypic genus *Eumorphocorystes* sensu Binkhorst (1857). None of the *Eumorphocorystes* species sensu Rathbun bear the strap ornamentation of *Eumorphocorystes sculptus* Binkhorst, but, instead, are covered with evenly spaced, relatively coarse punctae (Fig. 7). Even more fundamental is the fact that the orbits of *Eumorphocorystes* species sensu Rathbun face forward, while those of *E. sculptus* are directed somewhat obliquely away from the longitudinal axis of the animal. The extreme width of the carapace on *Eumorphocorystes* species sensu Rathbun is posterior to the anterolateral spines, rather than at the anterolateral spines as with *E. sculptus.* In-

Table 5.—Distributions and geologic ages of recognized species of *Eucorystes* Bell.

Taxon	Age	Locality
Eucorystes carteri (McCoy, 1854)	Albian	England
E. eichhorni Bishop, 1983	Campanian	Montana
E. intermedius Nagao, 1931	Cenomanian	Japan
E. oxtedensis Wright & Collins, 1972	Albian	England

deed, the only unifying characters are the median ridge and characters which reflect the fact that both groups of organisms belong to the Raninidae. Each of the species of *Eumorphocorystes* sensu Rathbun clearly reflects certain unifying characteristics. In each, the carapace is coarsely punctate and the greatest width is posterior to the anterolateral spines. Each has a relatively narrow fronto-orbital margin, and has a median ridge extending the entire length of the dorsal carapace, including at least part of the rostrum. The three species described by Rathbun, *E. naselensis, E. schencki,* and *E.* (?) *leucosiae,* are herein assigned to *Carinaranina,* new genus.

There are five recognized species included in this genus and described below. In addition, *Carinaranina* was recognized from the ?Aldwell Formation (Squires et al. 1992) at Pulali Point, Washington. Another undescribed species of this genus is recognized from the Oligocene-aged Quimper Sandstone, Port Townsand, Washington.

Etymology.—From Latin *carina* = keel (of a ship), in reference to the dorsal median ridge + *Ranina,* type genus of the family, from Latin *rana* = frog, hence the name "frog crabs" for members of this family. Gender: Feminine.

Carinaranina naselensis (Rathbun, 1926), new combination
Fig. 7(1 & 4)

Eumorphocorystes naselensis Rathbun, 1926:100, pl. 24, figs. 9–10; Lörenthey (*in* Lörenthey & Beurlen), 1929:297; Jeletzky, 1973:339, figs. 3A–D, 4 A–C; Tucker & Feldmann, 1990:412, fig. 4.1–4.2.

Description [emending Rathbun (1926) and Tucker & Feldmann (1990)].—Carapace broadly ovate in outline, widest behind anterolateral teeth; greatest width about 60% total length; carapace convex longitudinally, very convex transversely; lateral margins turned slightly under, taper posteriorly to anterolateral teeth, becoming straight.

Width of fronto-orbital region slightly less than ½ greatest width; fronto-orbital region widest posteriorly, tapering slightly anteriorly; orbits directed forward. Dorsal margin of each orbit marked by 2 U-shaped open fissures, wider than deep, directed posteriorly; approximately parallel to longitudinal axis of animal; outer tooth of orbit longest; 2 inner teeth progressively shorter, second tooth bifid. Frontal margin of carapace produced to form rostrum, not extending beyond orbits, not downturned. Rostrum long, triangular, margins slightly convex, inflated; rostrum keeled medially; keel subtle, extending posteriorly into well-defined medial ridge that extends entire length of carapace; keel bounded laterally by shallow sulci.

Anterolateral margins of carapace convex in outline, turned under at lateral angle, becoming straight and tapering posteriad lateral angle; 1 pair of long, stout lateral spines; spines directed outward and very slightly forward; posterolateral margin convex, converging posteriorly to blunt posterolateral corner; posterior margin slightly concave.

Midline of carapace strongly keeled for entire axial region; urn-shaped cardiac region gently and broadly swollen, tapering, merging into keeled axial region posteriorly; 2 deeply etched branchiocardiac grooves as arcuate impressions; remainder of cardiac groove subtle; 2 arcuate muscle scars, di-

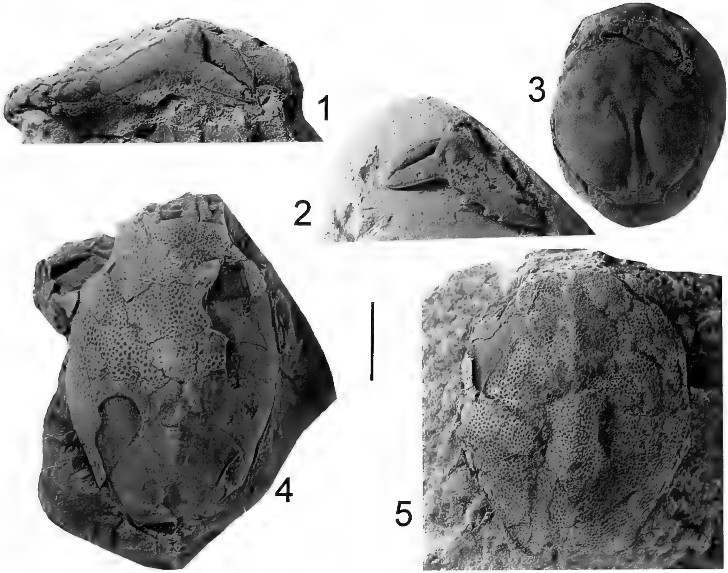

Fig. 7. *Carinaranina naselensis* (Rathbun, 1926), GSC 32066: 1, right major cheliped; 4, GSC32067, dorsal view. *C. leucosiae* (Rathbun, 1932), USNM 371902: 2, dorsal view; 3, left major cheliped. *C. schencki* (Rathbun, 1932), USNM 336007: 5, dorsal view. Scale bars equal 1 cm.

rected toward axis of carapace, lying just anteriad cardiac grooves; pair of gastric pits either side of midline at anterior termini of muscle scars; metabranchial region slightly less inflated than remaining branchial region; dorsal carapace covered by large punctae or pits.

Sternum narrow, elongate; sternites 1–3 narrow anteriorly, broadening at midlength to form rounded, triangular termination separated from sternite 4 by narrower, parallel-sided part; sternite 4 with narrow anterior processes directed anterolaterally, forming widest part of sternum, narrowing at midpoint, wider posteriorly; axis of sternum slightly concave anteriorly, becoming deeply depressed posterior to sternite 4.

Abdominal somites uniformly narrow, somites 3–5 bear median, anteriorly directed spines; telson longer than wide, tapering posteriorly, axial region raised.

Appendages unknown.

Material studied.—USNM 431254, USNM 431255, USNM 431256, USNM 431257, and CAS 29180 (each number represents a single specimen).

Occurrence.—*Carinaranina naselensis* was recovered from "Washington: shale bluffs along Nasel River near mouth of Salmon Creek, Nasel; middle Oligocene" (Rathbun, 1926:100).

Carinaranina leucosiae (Rathbun, 1932), new combination
Fig. 7(2–3)

Eumorphocorystes (?) *leucosiae* Rathbun, 1932:242, fig. 7, fig. 8.

Remarks.—Rathbun (1932:242) expressed reservations about assigning this species to *Eumorphocorystes,* stating that it bore close resemblance to species belonging to the Leucosidae. Although the branchial regions are much more inflated than is typical for species of the *Carinaranina,* new genus, the median carina and the configuration of the claws, which are typically raninid-like and not as in the Leucosidae, suggest that this species can be retained in the *Carinaranina.*

Material examined.—Holotype USNM 371902, paratype USNM 336004.

Occurrence.—Carinaranina schencki (Rathbun, 1932:242) and *C.? leucosiae* (Rathbun, 1932:242) were collected from the Upper Eocene Keasey Formation, "*Cardium weaveri*" zone, Polk County, which was thought at the time to be Oligocene in age. However, Snavely (1987: 310) placed the Keasey Formation in the latest Eocene.

Carinaranina marionae, new species

Fig. 8(1–4)

Diagnosis.—Carapace rather slender for genus; outer, lateral margins of orbits diverge anteriorly. Rostrum not extending beyond orbital spines. Anterolateral margin short, concave; anterolateral spines about 25% total length. Fronto-orbital margin not quite 66% extreme width. Posterior margin concave. Surface coarsely punctate; median ridge covering entire length of carapace, including rostrum.

Description.—Carapace obovate in outline, anterior ⅔ widest, greatest width 66–70% total length; entire surface punctate, punctae more coarse anteriorly; carapace vaulted longitudinally, more so transversely. Width of fronto-orbital region about 60% extreme width; fronto-orbital region widest anteriorly, tapering slightly posteriorly; orbits directed forward. Dorsal margin of each orbit marked by 2 fissures; inner fissure open U-shape, deeper than wide, directed posteriorly, approximately parallel to longitudinal axis of animal; outer fissure open, shallow, asymmetric V-shape, wider than deep, directed posteriorly toward longitudinal axis of animal; outer tooth of orbit longest; 2 inner teeth progressively shorter. Frontal margin of carapace produced to form rostrum, not extending beyond orbits; not downturned. Rostrum long, triangular, margins straight; rostrum keeled medially; keel subtle, extending from posterior ½ of rostrum into well-defined medial ridge that extends entire length of carapace.

Anterolateral margins concave in outline; 1 pair of elongate, slender lateral spines; spines directed outward and very slightly forward; posterolateral margin convex, converging posteriorly to posterolateral corner; posterior margin concave. Midline of carapace strongly keeled for entire axial region; urn-shaped cardiac region gently and broadly swollen, merging into keeled axial region posteriorly; 2 shallow branchiocardiac grooves as arcuate impressions; remainder of cardiac groove not obvious; cardiac region bearing pair of nodes on either side of distinct boss on midline of carapace on a transverse line posteriad termini of cardiac grooves; metabranchial region less inflated than remaining branchial region; dorsal carapace covered by large punctae or pits.

Abdomen, pterygostomial region, sternum, buccal cavity unknown.

Merus of major appendage compressed, bearing transverse ridges. Upper margin of propodus bears four distinct spines, the second proximal spine reduced in size relative to remaining spines. Remaining appendages unknown.

Measurements.—(See Table 6, and Fig. 9).

Types.—Holotype, T 408 (RB32–302), and paratypes, T433 (RB32–114), T530 (RB33–173), T417 (RB32–301), T411 (RB34–3), T407 (RB30–1), and T531 (RB32–113).

Type locality.—The type locality is the shoreline encompassing RB 30, 31, 32, and 34 (RB refers to the localities noted by

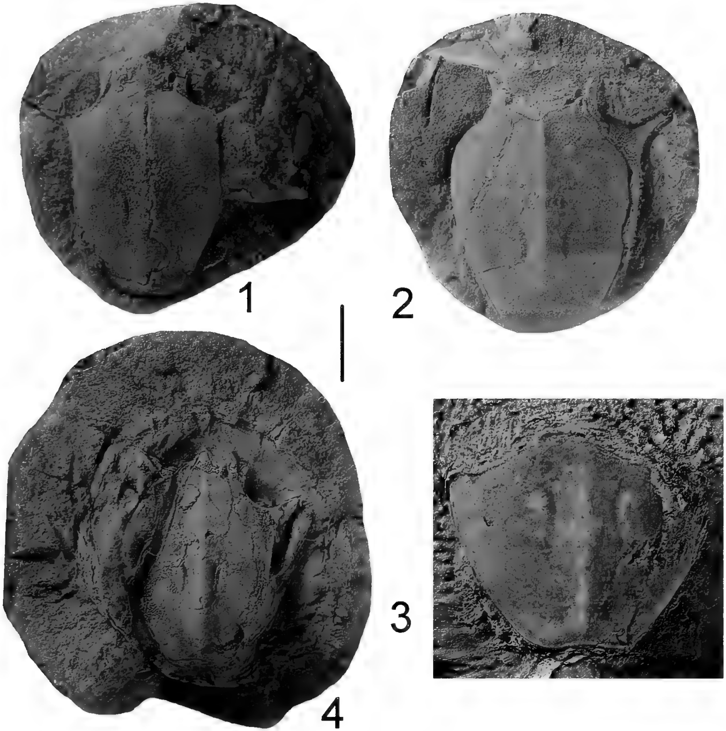

Fig. 8. *Carinaranina marionae,* new species: 1, holotype USNM 494628, dorsal view; 2, paratype USNM 494629, dorsal view, preservation showing two phases of concretion formation; 3, paratype USNM 494631, dorsal view; 4, paratype USNM 494630, dorsal view of posterior, by comparison shows variation in size. Scale bars equal 1 cm.

Table 6.—Representative measurements (mm) of *Carinaranina marionae* new species. L = length, W = width (for definition of measurements see Fig. 9).

Specimen number	L1	L2	L3	L4	W1	W2	W3	W4	W5	W6
USNM 494628*	31.6	7.5	23.8	21.0	24.8	11.6	5.9	4.0	4.9	10.8
USNM 494629	27.9	5.1	20.1	16.7	25.2	13.8	—	3.4	4.3	8.4
USNM 494630	—	—	—	—	—	—	—	—	—	13.2
USNM 494631	—	7.3?	20.2	—	24.2	13.3	—	—	—	—
USNM 494632	—	7.9	—	—	20.4	—	—	—	—	—

* Holotype.

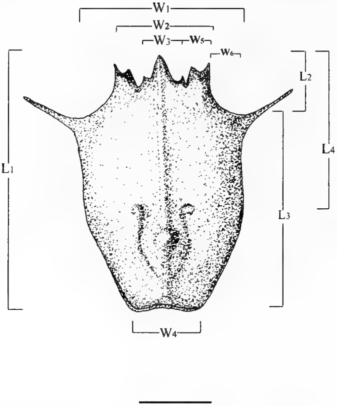

Fig. 9. *Carinaranina marionae,* new species; line drawing of dorsal view of carapace, showing measurements given in Table 6. L = length, and W = width. Scale bar equals 1 cm.

Ross Berglund who collected most of the specimens), from Warmhouse beach east to Kydaka Point, along the Strait of Juan de Fuca, Cape Flattery Quadrangle, 15 min series, Clallam, Washington (Fig. 10).

Etymology.—The specific name honors Marion Berglund who has spent many hours devoted to helping her husband Ross Berglund collect fossil crabs in Washington and Oregon. Without Marion's assistance, sharp eyes, encouragement, and constant companionship, Ross's collecting likely would have been at least slightly less inspired. Gender: Feminine.

Material.—The five specimens referable to this taxon were preserved within concretions. All were preserved as partially exfoliated molds of the interior, with some integument preserved by replacement. One specimen, USNM 494628, is stained red-brown by an iron oxide, others have manganese dioxide dendrites on the surface.

Another specimen, USNM 494629 has a very obvious inner rind around the crab, and a much thicker outer layer. This multiple layering probably implies reworking of some of the concretions. Indeed, many of the concretions have an inner rind with a weathered outer surface.

The range in size (see Fig. 8) suggests some of the smaller specimens may be juveniles. Alternatively, this range in size may be the result of sexual dimorphism. It is not possible, based upon the number of specimens and degree of preservation, to distinguish with certainty which is the case. The range seems to be gradual rather than bimodal, which would suggest that the interpretation of a range in age is more likely than sexual dimorphism.

Stratigraphic and geographic ranges.—Specimens belonging to this taxon were recovered from the Eocene Hoko River Formation at localities RB30, RB32, RB33, and RB34 (Fig. 10).

Remarks.—Representatives of this taxon exhibit several characters compatible with placement within the Raninidae. The essential character is an elongate carapace that does not cover the proximal abdominal terga, and flattened chelipeds. The combination of characters including the greatest width of carapace posterior to the anterolateral spines, narrow fronto-orbital region, orbits marked by fissures, rostrum produced, anterolateral spines often quite long and well-developed, dorsal ridge extending entire length of carapace, and coarsely punctate dorsal surface of the carapace clearly demonstrates this taxon's relationship to the other species within *Carinaranina,* new genus.

Carinaranina marionae is smaller than its congeners; the dorsal ridge is more obvious than on *C. schencki* or *C. leucosiae,* but is similar to that of *C. naselensis.* The outer margins of the orbits of *C. marionae* diverge in an anterior direction, whereas *C. naselensis* have outer orbital margins that are parallel to the longitudinal axis of the animal. The orbital margins on *C. schencki* and *C. leucosiae* were not preserved. The anterolateral spines are similar in shape and attitude to those of *C. naselensis,* but are placed slightly more forward on *C. marion-*

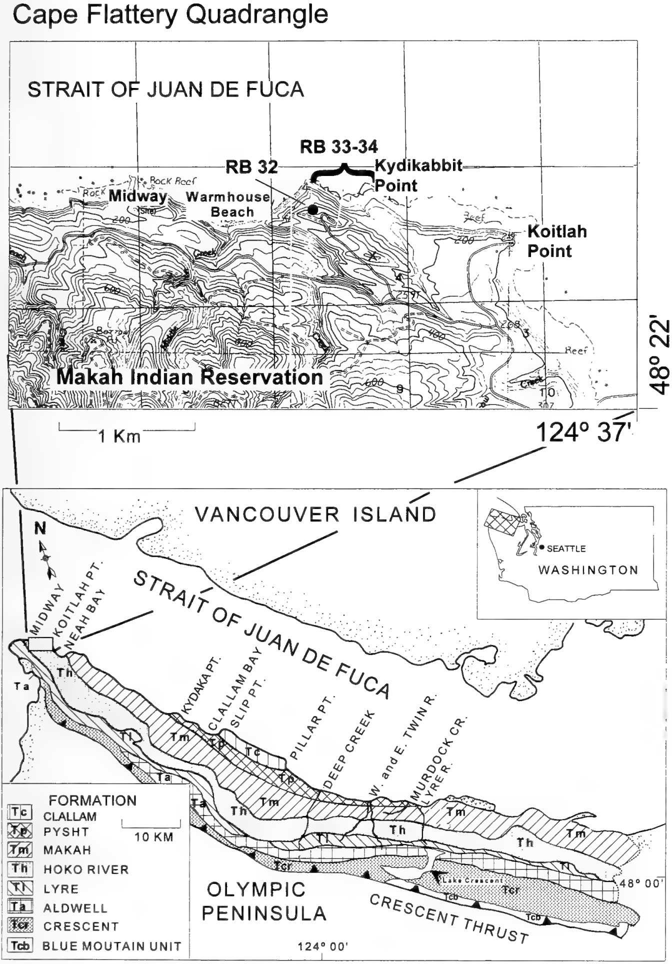

Fig. 10. Geology of the Twin River Group on the Olympic Peninsula, Washington (revised after Snavely 1983:8–9) with inset illustrating approximate position of Hoko River Formation localities RB 32–34.

ae. The anterolateral spines of *C. schencki* and *C. leucosiae* are unknown. This combination of unique characters clearly distinguishes this taxon from its congeners.

Even though *C. schencki* and *C. leucosiae* are known from the latest Eocene age rocks of the Keaseay Formation, it is quite likely that *Carinaranina marionae,* new species represents one of the earliest occurrences for the genus. This is implied as the result of earlier formation of the crab-bearing concretions with subsequent reworking and downslope movement interpreted for the Hoko River Formation (Feldmann et al. 1991).

Carinaranina willapensis (Rathbun, 1926), new combination

Fig. 11(1–11)

Ranidina willapensis Rathbun, 1926:99, pl. 21, figs. 4–5.

Diagnosis.—Carapace elongate, greatest width at midlength; fronto-orbital region narrow, outer extraorbital margins concave, diverging anteriorly; orbits marked by fissures; rostrum produced. Anterolateral spines often quite long and well developed. Posterolateral margin slightly sigmoidal, converging rapidly toward posterior. Posterior margin concave. Surface of carapace coarsely punctate; subtle medial ridge on anterior half of dorsal carapace.

Description emending R. willapensis.—Carapace obovate in outline, widest at or just slightly anteriad mid-length; greatest width about 66% total length; carapace only slightly convex longitudinally, much more so transversely; anterolateral flanks turned under; entire surface coarsely and evenly punctate.

Width of fronto-orbital region about 60% extreme width; fronto-orbital region widest anteriorly, tapering posteriorly; orbits directed slightly away from longitudinal axis of carapace. Ventral margin of each orbit concave, bearing single, open, U-shaped fissure near proximal edge; dorsal margin of each orbit marked by 2 deeply grooved, open fissures, distalmost fissure V-shaped, about twice as deep as wide, directed away from longitudinal axis of animal; interior fissure U-shaped, wider than lateral fissure, approximately parallel to lateral margin of orbit. Extra-orbital tooth wide, bifid, outer margin produced into long spine, inner portion of tooth blunt, anterior margin serrated; second tooth a triangle, extending forward about ¾ as far as extra-orbital spine; inner tooth a short triangle directs anteriorly away from longitudinal axis. Frontal margin of carapace produced to form rostrum that extends just beyond extra-orbital tooth, very slightly downturned; rostrum long, narrow triangle, with straight, beaded margins. Anterolateral margin of carapace slightly concave in outline, bearing 1 pair of very elongate, slender hepatic spines directed forward and outward; posterolateral margin weakly sigmoid, tapering to posterolateral corner, with narrow, beaded marginal rim. Posterior margin narrower than fronto-orbital margin, concave, with narrow, beaded rim.

Midline of carapace smooth, subtly carinate on anterior ½; cardiac region poorly defined, just slightly elevated, marked by 2 subtle arcuate cardiac grooves; cephalic groove slightly indicated; other regions undefined.

Buccal frame longer than wide; pterygostomian regions with sharp ridge originating at about mid-point of buccal cavity and diverging posteriorly. Sternum, narrow, elongate, and smooth, fused through sternites 1–6; sternites 1–3 separated from sternite 4 by narrow extension with margins diverging posteriorly; slender alate processes at anterior sternite 4, directed slightly anteriorly, quite broad; margins of sternite 4 concave, but not converging posteriorly; processes between sternites 4 and 5 wider, but not broader than sternites 3–4; sternite 6 narrower than 5; processes between 6 and 7 narrower than 4–5.

Abdomen unknown.

Chelipeds unknown. Manus of major cheliped compressed, surface granulate. Other appendages unknown.

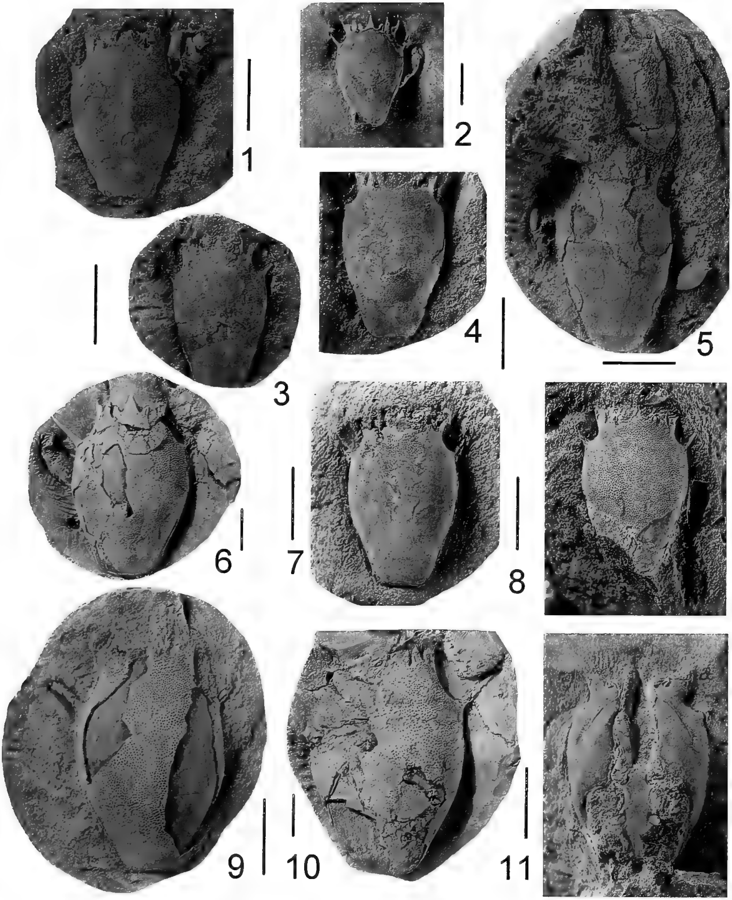

Fig. 11. *Carinaranina willapensis,* new combination: dorsal views of 1, USNM 494637; 2, USNM 494635; 3, USNM 494639; 4, USNM 494642; 5, USNM 494640; 6, USNM 494641; 7, USNM 494636; 8, USNM 494634; 9, USNM 494638; 10, USNM 494633; 11, ventral view of USNM 494643. Scale bars equal 1 cm.

Measurements.—(See Table 7, Fig. 12).

Localities.—Hoko River Formation localities include the shoreline encompassing RB 32–33, from Warmhouse beach east to Kydaka Point, along the Strait of Juan de Fuca, Cape Flattery Quadrangle, Clallam, Washington.

Material.—12 specimens: all but 1 pre-

Table 7.—Representative measurements (mm) of *Carinaranina willapensis,* new combination. L = length, W = width, ? = uncertain measurement (for definitions of measurements see Fig. 12).

Specimen number	L1	L2	L3	L4	W1	W2	W3	W4	W5	W6
USNM 494633	?47.9	12.6	37.1	24.1	?20.4	—	—	6.9	4.6	13.6
USNM 494634	23.1	4.9	18.3	8.3	14.4	11.4	4.8	4.0	1.3	?6.9
USNM 494635	23.3	5.1	18.2	12.3	14.4	12.1	5.1	4.5	1.7	6.4
USNM 494636	24.3	5.3	18.7	10.0	14.8	12.0	4.7	4.2	1.2	5.6
USNM 494637	?22.9	5.2	?18.6	11.7	13.9	11.8	5.2	4.9	1.0	7.3
USNM 494638	?31.1	8.7	23.2	12.1	19.9	13.1	—	—	—	7.8
USNM 494639	22.0	4.3	16.8	10.2	12.8	10.9	4.7	4.2	1.3	?6.1
USNM 494640	25.5	6.1	19.1	10.6	15.6	13.5	5.6	4.7	1.4	6.9
USNM 494641	38.4	10.1	28.7	21.4	25.2	19.0	7.1	6.1	3.3	10.7
USNM 494642	?22.4	4.3	18.2	8.4	13.9	11.3	—	4.0	1.1	6.0
USNM 494643	—	5.8	—	—	17.5	14.0	—	—	—	—

served in concretions as partially exfoliated molds of the interior of the dorsal carapace with replacement of the preserved integument; 1 (USNM 494643) preserved as a mold of the interior of the venter with the sternum well preserved; 2 of the concretions (USNM 494637 and USNM 494642) show concentric layering as seen on *C. marionae,* new species.

Location and stratigraphic position.—The specimens in this study were collected primarily from localities RB32 and RB33. Rocks from these localities are late Eocene in age, based upon benthic foraminiferans recovered from the matrix (Rau 1964:G6; Snavely et al. 1978:A115; Snavely 1987: 310). Many of the specimens were preserved in concretions which were collected as float that was weathered out of the matrix by wave action along a wave-cut platform on the southern shore of the Strait of Juan de Fuca. Some specimens were collected as float from the upper cliffs above Warmhouse Beach. As suggested above, some of the concretions were reworked and possibly were formed sometime prior to the downslope movement. The same genus also was recognized from the ?Aldwell Formation (Squires & Demetrion 1992; Tucker, unpublished data) at Pulali Point, Washington. In addition, another undescribed species of this genus is recognized from the Oligocene-aged Quimper Sandstone, Port Townsand, Washington.

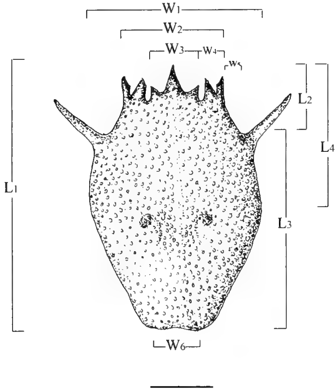

Fig. 12. *Carinaranina willapensis,* new combination: line drawing of dorsal view showing measurements given in Table 7. L = length and W = width. Scale bar equals 1 cm.

Remarks.—Representatives of this taxon exhibit characters compatible with placement within *Carinaranina.* The greatest width of the carapace is posterior to the anterolateral corner, the fronto-orbital margin is narrow relative to the greatest width of the carapace, the rostrum is produced, the orbits bear two fissures, the anterior spines are quite long, and the surface of the carapace is punctate.

Carinaranina willapensis is not as egg-shaped as *C. nasselensis, C. schencki,* or *C. leucosiae*. *Carinaranina willapensis* most closely resembles *C. marionae*. Both have orbital margins with two fissures; however, the fissures are deeper and more closed on *C. willapensis*. The extreme width of the carapace of *C. willapensis* is more anterior than that of *C. marionae*. In addition, the outer orbital tooth of *C. willapensis* is broader and bifid, unlike the more acicular, narrower outer tooth of *C. marionae*. The anterolateral spines are quite similar in size for both taxa, but the spines of *C. willapensis* are directed more toward the anterior. This taxon, however, bears a dorsal ridge that is much less pronounced than any of its congeners. Although this last character is an important one for establishing a relationship with *Carinaranina* species, the unique shape of the sternum of *C. willapensis* supersedes it. The sterna of *Carinaranina naselensis* (Rathbun 1926), as described by Tucker & Feldmann (1990:413), have a very similar parallel-sided posterior extension between sternites 3 and 4, and alar processes on the anterior portion of sternite 4. This unusual sternal configuration is sufficiently unique that the two taxa are deemed to be congeneric, notwithstanding the inconspicuous dorsal ridge of *C. willapensis*. Sterna from the remaining members of *Carinaranina* species are unknown.

Carinaranina schencki (Rathbun 1932), new combination
Fig. 7(5)

Eumorphocorystes schencki Rathbun, 1932: 242, figs. 5–6.

Remarks.—The surface of the dorsal carapace is coarsely punctate, and there is a distinct dorsal median carina typical for the genus. The position and configuration of the anterolateral spine also is typical for the genus. This taxon is most like *C. naselensis,* but is relatively wider and more egg-shaped.

Material examined.—Holotype USNM 371921; paratype USNM 336007.

Occurrence.—Upper Eocene Keasey Formation, "*Cardium weaveri*" zone, Polk County, Oregon.

Genus *Laeviranina* Lörenthey (*in* Lörenthey & Beurlen 1929)

Laeviranina Lörenthey (*in* Lörenthey & Beurlen 1929):105, pl. 4, figs. 10–12.

Type species.—*Ranina budapestinensis* Lörenthey, 1898:23, by original designation. Gender: Feminine.

Diagnosis.—Carapace elongate oval, lateral margins convex; fronto-orbital margin directed anteriorly, bearing 2 fissures on upper border and medial orbital tooth. Anterolateral spines near fronto-orbital region. Postfrontal ridge present.

Remarks.—There has been much disagreement about the placement of species referred to the genera *Raninoides* H. Milne Edwards (1837), *Laeviranina* Lörenthey (*in* Lörenthey & Beurlen 1929), and *Notosceles* Bourne (1922). The following review illustrates the confusion about the systematic position of species referred to these three genera. Glaessner & Withers (1931:489) recognized the problems in distinguishing among these genera; ultimately, they (1931: 490) regarded *Laeviranina* and *Raninoides* as distinct genera, and distinguished *Laeviranina* species as having relatively narrower fronto-orbital margins, relative to the extreme width of the carapace, than did *Raninoides* species. In addition, the distance between the extraorbital spine and the anterolateral spine was observed to be shorter in *Laeviranina* species, and more importantly, *Laeviranina* species bore a postfrontal ridge. Although Glaessner & Withers differentiated between these two genera, they did so with reservations, "There is no clearly marked division between the forms included in *Laeviranina* and *Raninoides,* but the Eocene forms have a common character, namely, the greater comparative width of the carapace" (Glaessner & Withers 1931:491).

Förster & Mundlos (1982:156) not only agreed with the conclusions of Glaessner & Withers (1931), but they thought *Raninoides* species and *Laeviranina* species should be united within a single genus, with *Raninoides* the senior subjective synonym. Förster & Mundlos (1982:156) based their conclusions on comparisons of *Laeviranina* species and their specimens with *Raninoides serratifrons* Henderson (1893). Bourne (1922:75) had proposed that *R. serratifrons* should be placed within a newly erected genus, *Notosceles.* Serène & Umali (1972:35) and Goeke (1985:219) concurred with Bourne's proposal by placing *R. serratifrons* with *Notosceles,* and they suggested that separation of *Raninoides* species and *Notosceles* species remained uncertain.

Feldmann & Maxwell (1990:785) recognized several characters, based upon the orbital fissures and the postfrontal ridge, which could be used to differentiate between *Raninoides* and *Laeviranina.* They indicated that the orbital fissures had a tendency to be open and distinct, and the postfrontal ridge was reduced or absent in *Raninoides* species. On the other hand, the orbital fissures of *Laeviranina* species appeared to be smaller and more closed, and the postfrontal ridge more pronounced. Examination of all species referred to each group suggests otherwise. There are at least two species referred to *Raninoides, R. crosnieri* and *R. personatus,* which have closed orbital fissures. Also, there are many species referred to *Laeviranina* that have open orbital fissures, including the type *L. budapestiniensis.* Feldmann (1991:20) further suggested that two points of distinction might be made with regard to the sterna of *Laeviranina* and *Raninoides.* He indicated that the anterior alation of sternite 4 of the sternum of *L. perarmata* appeared to project laterally farther than the posterior termination of the same sternite, whereas the anterior and posterior terminations of sternite 4 on many species of *Raninoides* were more equal. Additionally, Feldmann (1991:20) suggested that the cleft exhibited along the midline of sternite 5 of the sternum of *Laeviranina* species was narrow and well defined, and typically terminated anteriorly at the level of the chelipeds; whereas a similar cleft on *Raninoides* species was less pronounced and did not extend as far anteriorly. Collins & Rasmussen (1992:33) agreed with these distinctions. However, examination of many specimens of Recent *Raninoides* species, as well as sterna from specimens confidently referred to *Laeviranina* (see Table 9), suggests that these characteristics are mixed within each genus. Furthermore, inspection of Recent *Raninoides* species seems to eliminate the possibility of sexual dimorphism for both the width of the sternum and the extent of the medial cleft due to the variability among both sexes. Sterna from *Laeviranina* species present another problem typical of fossil taxa; that is, often both the sternum and the dorsal carapace are not present for the same specimen, so that one is not always confident of the true identity of the specimen.

Upon further inspection of examples of all three genera, the following observations are offered. Distinguishing *Notosceles* species from *Laeviranina* species and *Raninoides* species is, in most cases, rather straightforward. *Notosceles* species have a serrated or trifid rostrum a granulated postfrontal region, a converging fronto-orbital margin, a first abdominal somite which is equal in width to the posterior margin of the cephalothorax, a narrow obliquely-directed anterior process on the sternite 4, and a very restricted sternum between the third pereiopods.

In contrast, distinguishing between *Laeviranina* species and *Raninoides* species is more difficult. There appears to be a mixture within each genus with regard to the nature of the sternum, especially the sternal cleft; thus, although not enough is known about the sterna of *Laeviranina* species to draw firm conclusions, this seems to be a character best suited for discrimination among species within each group. It seems, so far, that this is somewhat true for the conformation of the orbits. Finally, although not many specimens of *Laeviranina* bear preserved abdominal somites, observation of those that do suggests that the anterior border of the first somite is more narrow than the posterior margin of the carapace, as is true with *Raninoides* species (Feldmann & Duncan 1992:458, Glaessner & Withers 1931:487–488).

Upon careful inspection of a combination of borrowed material, and published photographs and interpretive drawings, the nature of the postfrontal region seems to offer an excellent way to distinguish between *Raninoides* and *Laeviranina,* as well as the new genus herein, *Quasilaeviranina,* with *Laeviranina* sensu stricto and *Quasilaeviranina* bearing a postfrontal escarpment or ridge, and *Raninoides* having a smooth postfrontal region. The position of the anterolateral spines also appears to indicate a separation among the three groups. A new genus is necessary to distinguish those species previously referred to *Laeviranina* that possess a combination of characters that set them apart from *Raninoides* or *Laeviranina.* As more material representing the sterna of *Quasilaeviranina* species and *Laeviranina* species becomes available, it is possible that other discriminating characters for all three genera might become more obvious. At this point, observations suggest that species referred to *Raninoides* and *Laeviranina* sensu stricto more strongly resemble each other than species referred to either *Quasilaeviranina* or *Notosceles* (see key below).

Key to *Raninoides, Notosceles, Quasilaeviranina,* new genus, and *Laeviranina*

[This key is to be used as an aid in identification of the three most problematic genera of seven assigned to this subfamily (see Fig. 22). The key is based upon personal observations and characters recognized by Serène & Umali, 1972:35].

1. Rostrum trifid or serrated; carapace granulate at postfrontal region; width of first abdominal somite equal to width of posterior margin; anterior border of sternite 4 of sternum narrow, somewhat narrowly alate, directed obliquely forward; sternum between third pereiopods quite narrow; sternal processes between pereiopods 1 and 2 with blunt termination; no spine on ischium of first pereiopods .... *Notosceles* Bourne, 1922

1′. Rostrum not trifid, but triangular, blunt or acutely pointed at termination; carapace either smooth or bearing postfrontal ridge; width of first abdominal somite narrower than posterior margin of carapace, or unknown; anterior borders of fourth sternite convex forward, not oblique or narrowly alate sternum between third pereiopods often wide where known; sternal lateral processes, where known, between pereiopods 1 and 2 not blunt; spine sometimes present on ischium of first pereiopods 2

2. Carapace without postfrontal ridge; orbital teeth often long, usually delimited by open, deep orbital fissures; anterior border of sternite 4 of sternum convex forward, but perpendicular to longitudinal axis of cephalothorax; sternum between third pereiopods usually quite wide; sternal process between pereiopods 1 and 2 broad, with acute termination; spine present on ischium of first pereiopods .... *Raninoides* H. Milne Edwards, 1837

2′. Carapace with postfrontal ridge; orbital teeth often short, often delimited by shallow, closed fissures; anterior border of sternite 4 of sternum perpendicular to longitudinal axis of cephalothorax, often straight, sometimes moderately convex; sternum between third pereiopods moderately narrow; sternal processes between pereiopods 1 and 2 generally blunt, not well known; occurrence of spine on ischium of first pereiopods unknown 3

3. Carapace ovate with convex lateral margins, sometimes rounded in outline; anterolateral spines reduced, positioned at

posterior of the fronto-orbital region, or absent; orbital fissures narrowed or entirely closed; orbital spines weak with medial orbital tooth truncated, not extending beyond orbital margin; fronto-orbital region convergent anteriorly ..... *Quasilaeviranina,* new genus

3′. Carapace elongate oval with somewhat straight lateral margins, sometimes rectangular in outline; anterolateral spines quite well developed, set just posteriad to fronto-orbital region; orbital fissures open or closed; orbital spines robust; external margins of orbits straight or divergent .... *Laeviranina* sensu stricto

Laeviranina goedertorum, new species

Fig. 13.1–13.7

Types.—Holotype, USNM 494657, and 21 paratypes (see Table 8).

Diagnosis.—Carapace elongate hexagonal, widest at anterior ⅓, covered with fine setal pits; orbit interrupted by 2 well-developed U-shaped fissures; rostrum extending very slightly beyond extraorbital teeth; postfrontal escarpment obvious; posterior margin fairly wide.

Description.—Moderately sized raninid, carapace elongate hexagonal in outline, bearing sinuous postfrontal escarpment; vaulted transversely, only slightly so longitudinally. Fronto-orbital region broad, about 62% maximum width; maximum width at about anterior one-third. Rostrum triangular, bounded on each side by short, broad, acicular innerorbital tooth directed away from longitudinal axis of carapace. Rostrum about as long as broad, width of base about ¼ total width of front; midline only slightly depressed. Orbits not quite as deep as wide, 2 pairs deeply impressed, open supraorbital fissures; inner fissures about ½ as wide as deep, directed very slightly toward midline of carapace; outer fissures not quite as deep, parallel to inner fissures. Orbital teeth somewhat shorter than rostrum inner teeth directed anteriorly, bifid, with outer projections shorter than inner; extraorbital teeth directed anteriorly just slightly farther than inner teeth, bifid, with inner projections shorter than outer, external tooth long and slender; extraorbital teeth forming lateral margins of front, converging only slightly toward anterior. Anterolateral margins short, slightly concave; bounded by short, acicular anterolateral spine directed more forward than out. Lateral margins comprised of 2 straight segments; anterior segments short, diverging posteriorly to extreme width; posterior segments much longer, converging from extreme width to posterolateral corners. Lateral margin bearing furrow and narrow, beaded rim, extending from point of maximum width, continuous with finely beaded posterior margin; flanks turned under. Posterolateral corners smoothly and tightly curved. Posterior margin relatively broad, about 50% extreme width, convex across entire posterior width, with slight medial concavity.

Carapace surface smooth, except for very fine setal pits, subtle cardiac grooves, and an unornamented postfrontal escarpment arising at level between postorbital region and anterolateral spines, traversing entire width of carapace.

Width of first abdominal somite about 70% width of posterior margin. Venter unknown.

Merus of cheliped obovate in cross section; transverse shallow furrows evenly distributed on upper surface. Carpus bearing a single spine on distal outer margin; tubercle on anterior upper surface. Chelipeds with single spine on distal upper margin of hand, lower margin toothed, number of teeth unknown. Hand compressed; fixed finger quite bent, compressed, spines unknown. Dactylus quite slender.

Remarks.—*Laeviranina* embraces fifteen species, all fossil (see Table 9). *Laeviranina goedertorum,* new species shares several characters with its congeners that serve to confirm their relationships: the carapace tends to be smooth, with the exception of very fine setal pits; the orbits are interrupted by two open fissures; the postfrontal re-

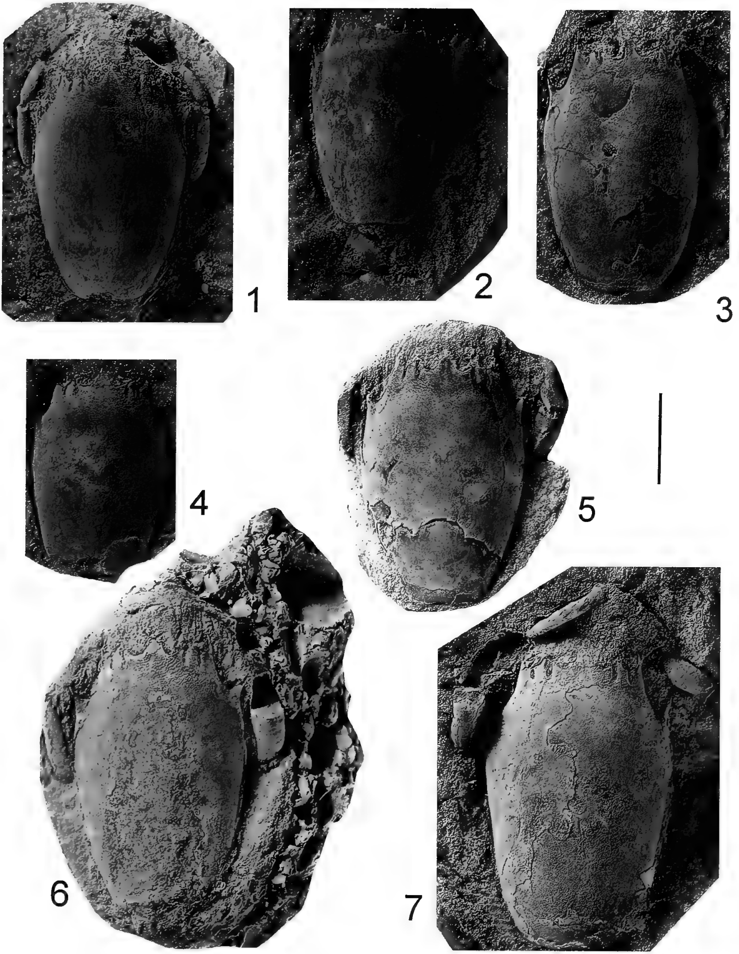

Fig. 13. *Laeviranina goedertorum,* new species, dorsal views: 1, USNM 494663; 2, USNM 494649; 3, USNM 494647; 4, USNM 494651; 5, holotype USNM 494657; 6, USNM 494656; 7, USNM 494662. Scale bar equals 1 cm.

Table 8.—Representative measurements (mm) of *Laeviranina goedertorum,* new species. L = length, W = width, ? = uncertain measurement (for definitions of measurements see Fig. 14).

Specimen number	L1	L2	W1	W2	W3
USNM 494646	31.9	4.6	20.9	17.1	9.3
USNM 494647	30.8	4.2	20.5	16.1	10.3
USNM 494648	28.6	—	—	—	—
USNM 494649	31.7	3.7	21.6	15.6	9.1
USNM 494650	32.3	4.0	20.7	17.6	8.3
USNM 494651	—	3.5	16.9	14.7	0.0
USNM 494652	33.1	4.7	21.5	17.3	8.4
USNM 494653	24.3	2.8	15.3	13.1	6.7
USNM 494654	—	4.4	19.4	16.2	8.9
USNM 494655	30.0	4.8	19.5	16.7	—
USNM 494656	35.8	5.5	22.4	18.5	9.4
USNM 494657*	34.0	5.5	23.4	18.5	12.4
USNM 494658	31.9	4.0	21.0	16.5	9.3
USNM 494659	31.7	3.8	19.2	15.9	7.6
USNM 494660	23.8	3.4	14.6	12.2	7.1
USNM 494661	?27.0	5.0	—	—	8.1
USNM 494662	36.3	5.7	23.5	18.6	12.9
USNM 494663	28.8	4.3	19.7	16.6	7.4
USNM 494664	—	4.4	19.9	17.4	—
USNM 494665	23.9	3.4	16.1	14.7	9.2
USNM 494666	34.9	4.6	23.3	19.4	10.1

* Holotype.

gion is set off by an escarpment or ridge; and the anterolateral teeth are set quite far forward, with the extreme width of the carapace posterior to these. The presence of these characters serves to distinguish species of *Laeviranina* from species of other raninid genera.

Laeviranina goedertorum appears most like *L. gottschei* in the shape of the outline of the carapace; however, the orbital fissures of *L. goedertorum* are more open, the postfrontal escarpment more pronounced, the cephalothorax relatively shorter, and the lateral margins slightly more convex. The tip of the rostrum of *L. vaderensis* extends somewhat beyond the extraorbital spines; the tip of the rostrum and the extraorbital spines of *L. goedertorum* are about equidistant. The posterior margin of *L. lewisanus* is more narrow relative to the maximum width of the carapace.

Measurements.—(See Table 8, Fig. 14).

Etymology.—The specific name honors James Goedert, and his wife Gail, of Gig Harbor, Washington and Section of Vertebrate Paleontology, Natural History Museum of Los Angeles County. Jim and Gail have spent countless hours in the field collecting decapods, as well as vertebrate material for their own endeavors.

Laeviranina lewisana (Rathbun, 1926)

Figs. 15.1–15.4, 17.3

Raninoides lewisanus Rathbun, 1926:94, pl. 22, fig. 4; Glaessner, 1929:372; Förster & Mundlos, 1982:158.

Laeviranina lewisana.—Glaessner & Withers, 1931:490, 491.—Vìa Boada, 1965: 263.—Vìa Boada, 1969:125.

Diagnosis.—Postfrontal escarpment subtle and concave forward axially, less subtle abaxially; carapace marked by granules on margins anterior to anterolateral teeth. Rostrum relatively long, about equal in length to orbital spines. Posterior margin narrow, almost straight.

Description emending L. lewisana.—Carapace ovate, egg-shaped, widest posterior to anterolateral teeth; greatest width about 57% total length; carapace slightly convex longitudinally, quite vaulted transversely. Width of fronto-orbital margin about 72% extreme width of carapace; orbital region widest posteriorly, tapering slightly anteriorly; orbits directed anteriorly. Dorsal margin of each orbit marked by 2 U-shaped fissures; exterior fissure almost as wide as deep, inner fissure deeper than wide. Outer tooth of orbit bifurcate with exterior spine produced almost to tip of rostrum, separated from inner spine by broad, shallow concave margin, inner spine short, blunt. Medial orbital tooth bifurcate, with inner spine longest, produced approximately equal to extraorbital tooth. Inner orbital spine acute, separated from base of rostrum by U-shaped margin, narrower and deeper than outer tooth; spine directed more forward than outward. Rostrum with base about ⅔ length, not downturned; extending somewhat beyond orbital teeth.

Table 9.—Distributions and geologic ages of recognized species of *Laeviranina* (Lörenthey *in* Lörenthey & Beurlen, 1929).

Taxon	Age	Locality
Laeviranina budapestiniensis (Lörenthey, 1897)	late Eocene	Hungary
L. araucana (Philippi, 1887a, b)	early Eocene	Chile
L. borealis Collins & Rasmussen, 1992	middle Paleocene	Greenland
L. bournei (Rathbun, 1928)	Paleocene	Alabama
L. fabianii (Lörenthey *in* Lörenthey & Beurlen, 1929)	middle to late Eocene	N. Germany Hungary
L. goedertorum new species	late Eocene	Washington
L. glabra (Woodward, 1871)	early Eocene	England
L. gottschei (Böhm, 1927)	early Eocene	England
L. lewisanus (Rathbun, 1926)	late Eocene	Washington
L. nodai (Karasawa, 1992)	middle Eocene	Japan
L. notopoides (Bittner, 1883)	early Eocene	England
L. perarmata Glaessner, 1960	middle Eocene	New Zealand
L. pulchra Beschin et al., 1988	middle Eocene	Italy
L. sinuosus Collins & Morris, 1978	early Eocene	Pakistan
L. vaderensis (Rathbun, 1926)	middle to late Eocene	Washington, Alaska

Postfrontal ridge subtle, but distinct; originating just anteriad anterolateral spines and extending across entire carapace, slightly concave at midpoint. Anterolateral spines directed outward and forward, forming V-shaped angle with carapace. Anterolateral margin gently convex in outline, merging into gently convex posterolateral margins; lateral margins terminating posteriorly in blunt corner that joins convex posterior margin.

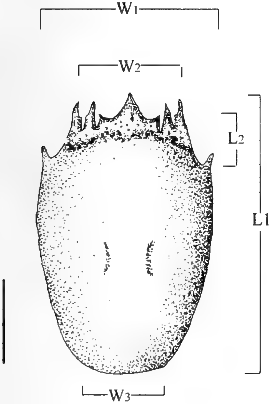

Fig. 14. *Laeviranina goedertorum,* new species: dorsal view showing measurements given in Table 8. L = length and W = width. Scale bar equals 1 cm.

Surface of carapace finely punctate, more coarsely so at postfrontal ridge and on orbital teeth. Adductor epimeralis scars marking lateral positions of cardiac region, about ⅔ toward posterior.

Sternum narrow, elongate; sternites 1–3 narrow anteriorly, broadening at midlength to form rounded, triangular termination, separated from sternite 4 by slight lateral emargination; base of sternite 4 more narrow than anterior; sternite 5 expanding laterally to broadened alate processes which extend slightly beyond anterior width of sternite 4, then converging toward posterior and juncture with sternite 6. Juncture of sternites 5 and 6 marked by deep pit. Axial cleft on sternites 5 and 6.

First abdominal somite not quite as wide as posterior margin; somites progressively more narrow. Somites 1–4 visible dorsally, raised medially on somites 2 and 3, 4 less so, 1 not at all.

Appendages unknown.

Remarks.—Laeviranina lewisana is most like *L. vaderensis,* but is distinguished by a

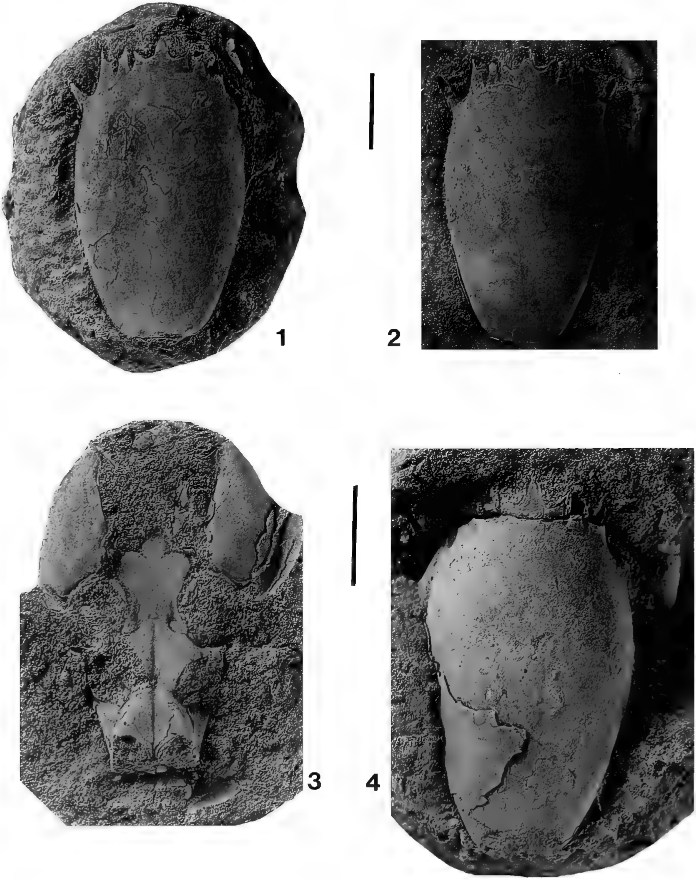

Fig. 15. *Laeviranina lewisana* (Rathbun, 1926), dorsal views: 1, USNM 494676; 2, USNM 494670; 4, USNM 494675; 3, ventral view. Scale bars equal 1 cm.

less produced front, by the greater width of the fronto-orbital margin, by a slightly wider posterior margin, and by the more convex lateral margins, giving it a more egg-shaped appearance.

Material examined.—10 specimens, preserved in concretions primarily as partially exfoliated molds of the interior of the dorsal surface of the carapace.

Measurements.—(See Table 10, Fig. 16).

Table 10.—Representative measurements (mm) of *Laeviranina lewisana* (Rathbun, 1926). L = length, W = width (for definitions of measurements see Fig. 16).

Specimen number	L1	L2	L3	W1	W2	W3
USNM 494668	35.3	11.0	5.2	21.1	14.6	7.8
USNM 494669	36.4	10.7	4.5	20.8	12.6	8.2
USNM 494670	35.8	12.4	3.7	20.8	13.7	8.4
USNM 494671	—	11.1	4.4	19.2	12.9	—
USNM 494672	—	9.7	4.6	18.3	12.4	—
USNM 494673	35.6	9.5	5.1	18.8	13.8	—
USNM 494674	35.8	12.0	5.5	20.3	14.4	8.5
USNM 494675	35.3	11.9	3.5	20.3	13.3	8.6
USNM 494676	34.2	12.2	4.1	19.2	11.9	7.6
USNM 494644	33.0	12.6	3.3	20.6	13.4	8.7

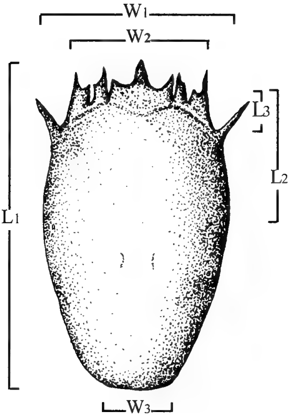

Fig. 16. *Laeviranina lewisana* (Rathbun, 1926): dorsal view showing measurements given in Table 10. L = length and W = width. Scale bar equals 1 cm.

Occurrence.—Until now, *L. lewisana* was recognized only from Lewis County, Washington. This study extends the geographic range northward to include the Hoko River Formation of the Olympic Peninsula, Washington, U.S.A.

Laeviranina vaderensis (Rathbun, 1926)

Fig. 17.1–17.2, 17.4–17.5

Raninoides vaderensis Rathbun, 1926:93. pl. 22, fig. 5.—Glaessner, 1929:372.—Tucker & Feldmann, 1990:412, figs. 3.1–2.—Karasawa, 1992:1252.

Laeviranina vaderensis.—Glaessner & Withers, 1931:490, 491.—Vìa Boada, 1965:263.—Vìa Boada, 1969:125.

Diagnosis.—Postfrontal escarpment quite subtle axially, less so abaxially. Rostrum produced well beyond orbital margin. Carapace widest near midpoint Posterior margin narrow.

Description emending R. vaderensis.—Carapace oblong oval in outline, widest posterior to anterolateral spines; greatest width about 56% total length; carapace slightly convex longitudinally, more so transversely.

Width of fronto-orbital margin about 70% extreme width; fronto-orbital margin widest at midlength, tapering slightly posteriorly; orbits directed forward, dorsal margin of each orbit marked by two narrow, U-shaped, open fissures, inner deeper than exterior, both deeper than wide, directed posteriorly and toward longitudinal axis of carapace. Extraorbital tooth bifurcate, outer margin of tooth convex abaxially, tip directed toward rostrum; inner portion of extraorbital tooth short and blunt. Medial orbital tooth bifurcate, not as long or wide as extraorbital, inner spine longest. Inner orbital tooth directed more outward than forward, connected to base of rostrum by broad, shallow margin. Front produced to form rostrum a little longer than width of base, extending well beyond orbital rim.

Postfrontal ridge subtle, more obvious laterally, forming steep arc directed anteriorly. Anterolateral spines close to front, tip arched toward axis, of medium length; spines form U-shaped angle with anterolateral margin. Posterolateral margins slightly concave, beaded rim for entire margin. Posterior margin straight or just slightly convex. Carapace punctate, except posterior branchial region; feeble, widely separated attractor epimeralis scars delimit cardiac region.

Remarks.—The postfrontal ridge of *L.*

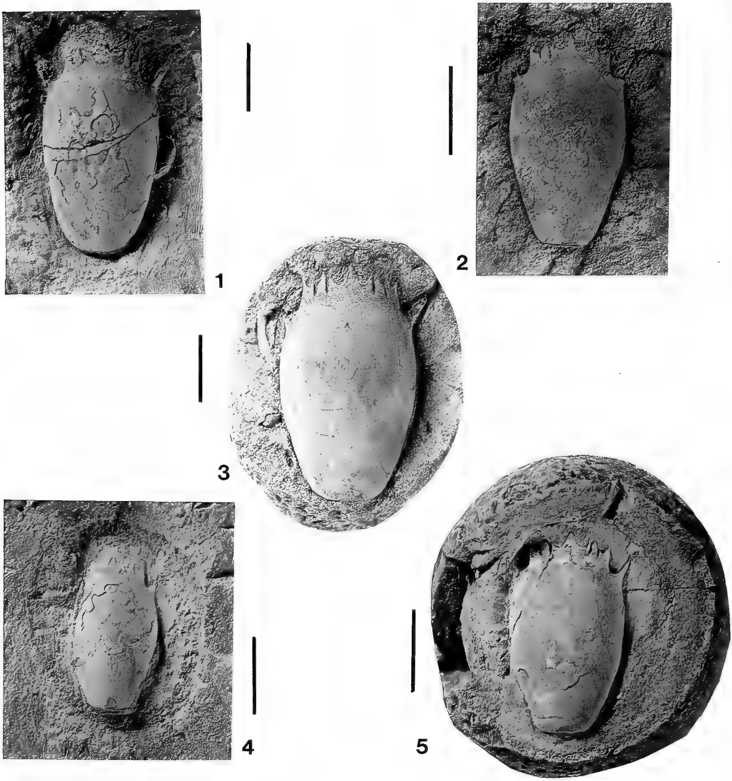

Fig. 17. *Laeviranina vaderensis* (Rathbun, 1926), dorsal views: 1, USNM 494679; 2, USNM 494678; 4, USNM 494680; 5, USNM 494677; *Laeviranina lewisana* (Rathbun, 1926): 3, USNM 494644, for comparison. Scale bars equal 1 cm.

vaderensis and the anterior placement of the anterolateral spines, clearly places this species within *Laeviranina*. *Laeviranina vaderensis* is most like *L. lewisana*; however, the two species are distinguished by several characters. *Laeviranina vaderensis* has a less distinct and extensive postfrontal ridge that is steeply and tightly arched, while that of *L. lewisana* is less arched and has a median concavity; the front of *L. vaderensis* is more produced; the posterolateral margins are straighter, so that the carapace is less egg-shaped in outline; the posterior is narrower; and the anterolateral spines form a U-shaped connection with the anterolateral margin, rather than the V-shaped angle observed on *L. lewisana*.

Laeviranina vaderensis is easily distinguished from other raninids found along the northwest coast of North America. *Rani-*

Table 11.—Representative measurements (mm) of *Laeviranina vaderensis* (Rathbun, 1926). L = length, W = width (for definitions of measurements see Fig. 18).

Specimen number	L1	L2	L3	W1	W2	W3
USNM 494677	24.8	3.5	10.5	14.0	9.8	6.2
USNM 494678	22.7	3.5	9.2	12.8	8.7	5.7
USNM 494679	28.1	4.1	10.9	15.5	10.8	7.5
USNM 494680	20.9	2.8	7.2	—	—	4.9

noides fulgidus has much longer orbital spines and a narrower carapace and *Carinaranina* species are more egg-shaped, bear much larger punctae that cover most of the carapace and a median ridge.

Material examined.—10 specimens: 2 (USNM 494677 and USNM 494680) show concentric rings in the matrix surrounding the specimen as result of reworking of the concretions. The holotype is deposited in the Burke Memorial Washington State Museum, University of Washington (not seen). 4 additional specimens (USNM 6649414, USNM 431250, USNM 431251, and USNM 431253) were studied.

Measurements.—(See Table 11, Fig. 18).

Occurrence.—*Laeviranina vaderensis* is known from the middle Eocene Orca Group of Valdez, Alaska; the upper Eocene Tejon Formation in Lewis County, Washington; the middle Eocene of Oregon, and the upper Eocene Hoko River Formation of Washington.

Genus *Quasilaeviranina*, new genus

Type species.—*Ranina simplicissima* Bittner, 1883, by present designation.

Diagnosis.—Carapace elongate oval in outline, greatest width posteriad anterolateral spines; convex transversely, less so longitudinally; surface often covered with very fine setal pits; cardiac grooves sometimes present; postfrontal region bearing raised transverse escarpment between anterolateral spines. Fronto-orbital margin weakly dentate with shallow, closed orbital fissures. Anterolateral spines directly posterior to fronto-orbital region.

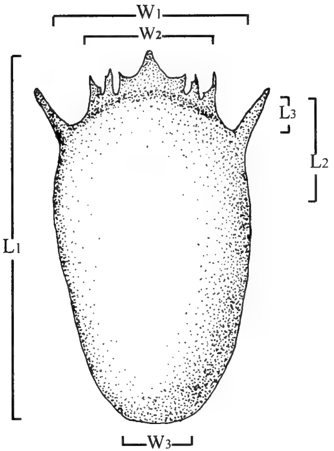

Fig. 18. *Laeviranina vaderensis* (Rathbun, 1926): dorsal view showing measurements as given in Table 11. L = length and W = width. Scale bar equals 1 cm.

Etymology.—From Latin *quasi* = appearing like, in reference to *Laeviranina*. Gender: Feminine.

Remarks.—All 6 species referred to this genus are treated below. *Laeviranina* sensu stricto is distinguished by the wider fronto-orbital margin, open orbital fissures, the more rectangular outline of the cephalothorax, and the slight migration of the anterolateral spines to a more posterior position. *Quasilaeviranina* is distinguished by the convergent fronto-orbital region, the closed orbital fissures, the reduced size of the medial orbital tooth, the more anterior position of the anterolateral spines as well as their diminutive size, and by the broadened appearance of the dorsal carapace resulting from the more convex lateral margins.

The oldest species assigned to the genus, *Q. ovalis* (Fig. 19), used in the cladistic analyses, was recovered from Paleocene age rocks in Alabama. Based upon the cladistic analysis (see Phylogenetic Analysis

Fig. 19. *Quasilaeviranina ovalis* (Rathbun, 1935), USNM 371689 (2 of 32 syntypes): 1, dorsal view; 2, ventral view showing swollen area on sternite 4. Scale bar equals 1 cm.

and Fig. 22), *Quasilaeviranina* is most closely related to *Notosceles* and *Notopoides.*

Quasilaeviranina simplicissima (Bittner, 1883), new combination

Ranina simplicissima Bittner, 1883:305, pl. 1, fig. 4.

Laeviranina simplicissima.—Lörenthey (*in* Lörenthey & Beurlen), 1929:106, pl. 4, fig. 11.

Laeviranina cf. *simplicissima.*—Busulini et al., 1983:59, pl. 1, fig. 3.—Beschin et al., 1988:173, fig. 5-1, pl. 4, figs. 4–5.—Beschin et al., 1994:173, pl. 3, fig. 2.

Remarks.—*Quasilaeviranina simplicissima* has a fronto-orbital region that is convergent anteriorly and displays shallow, closed orbital fissures and truncated medial orbital teeth. The diminutive anterolateral spines are placed just posterior to the postorbital teeth and are joined by a distinct postfrontal escarpment. Although the cephalothorax is somewhat elongated, the lateral margins are convex. The taxon is differentiated from its congeners by granulation along the escarpment and by the more narrow carapace.

Material examined.—Line drawings and photographs, especially those of Beschin et al. (1988).

Occurrence.—*Quasilaeviranina simplicissima* is recognized from the middle Eocene of Italy.

Quasilaeviranina arzignanensis (Beschin, Busulini, de Angeli, & Tessier, 1988), new combination

Notosceles arzignanensis Beschin et al., 1988:193–196, pl. 10, figs. 2–3, fig. 11.

Remarks.—*Quasilaeviranina arzignanensis* has all the characters which distinguish *Quasilaeviranina* species from *Notosceles* species (see key). Furthermore, the sternum, which is well preserved for *Q. arzignanensis,* is much more typical of *Quasilaeviranina* species than of *Notosceles* species. On Recent *Notosceles* species, the anterior of sternite 4 is quite alate and directed anteriorly, and is distinctly narrower than the alation between the first and second pereiopods. This taxon has a sternum that is more robust at the anterior of sternite 4 and is about equal in width at the anterior of sternite 4 and the alation between the first and second pereiopods, characters more typical of *Quasilaeviranina* species. Therefore, it seems best to include this species with *Quasilaeviranina.*

Material examined.—Figures and plates from Beschin et al. (1988, fig. 11, and pl. 10, figs. 2–3).

Occurrence.—*Quasilaeviranina arzignanensis* is known from the middle Eocene of Italy.

Quasilaeviranina keyesi (Feldmann & Maxwell, 1990), new combination

Laeviranina keyesi Feldmann & Maxwell, 1990:784–786, figs. 3–4.

Remarks.—The closed orbital fissures, reduced and truncated medial orbital tooth, convergent fronto-orbital region, and anteriorly positioned, diminutive anterolateral spines clearly indicate that this taxon should be moved to *Quasilaeviranina.*

Material examined.—Holotype, NZGS AR 958, and 2 paratypes, NZGS AR 962 and AR 1931, deposited in the New Zealand Geological Survey, Lower Hutt, New Zealand.

Occurrence.—*Quasilaeviranina keyesi* is known from the Eocene of South Island, New Zealand.

Quasilaeviranina ombonii (Fabiani, 1910), new combination

Ranina ombonii Fabiani, 1910:2, pl. 2, Fig. 1.
Ranina (*Laeviranina*) *ombonii.*—Lörenthey (*in* Lörenthey & Beurlen), 1929:105, 106, 107.
Laeviranina ombonii.—Beschin et al., 1988:169, pl. 3, figs. 4–6, Text fig. 5.3.

Remarks.—Examination of illustrations and drawings by Beschin et al. (1988) confirms that this species should be placed within *Quasilaeviranina.* The fronto-orbital margin is convergent, the anterolateral spines are quite diminutive, the medial orbital tooth is reduced and truncated, and the lateral margins are convex. Interestingly, Glaessner & Withers (1931:490—footnote) recognized that both *Q. ombonii* and *Q. simplissima* differed from descriptions of many of the species referred to *Laeviranina,* primarily because of the diminutive size of the anterolateral spines. *Quasilaeviranina ombonii* is differentiated from its European congeners by possessing anterolateral spines that are placed a little farther forward and by its more convex lateral margins.

Material examined.—None.

Occurrence.—*Quasilaeviranina ombonii* is known from the Eocene of Italy.

Quasilaeviranina ovalis (Rathbun, 1935)
Fig. 19.1–19.2

Raninoides ovalis Rathbun, 1935:5, 11, 81, 143, pl. 18, figs. 1–8.
Laeviranina ovalis.—Glaessner, 1960:16.

Remarks.—The postfrontal ridge and the overall configuration of the carapace confirm the placement of this taxon with *Quasilaeviranina.* The diminutive anterolateral spines are placed well forward and the fronto-orbital region is convergent. The orbits bear two closed, shallow fissures, which is typical for the genus. Several specimens have a venter with a unique swollen region at the midpoint of sternite 4; otherwise, the general character of the sternum is typical for the genus.

Material examined.—Syntypes, 32 carapaces, USNM 371689 and USNM 371692

Occurrence.—*Quasilaeviranina ovalis* is known from the Eocene of Alabama.

Quasilaeviranina pororariensis (Glaessner, 1980)

Ranilia pororariensis Glaessner, 1980, by monotypy:177, figs. 6, 6A.
Laeviranina pororariensis.—Feldmann & Maxwell, 1990:786, figs. 5.1–2, 6.

Remarks.—At first glance, the outline of the carapace of *Quasilaeviranina pororariensis* does not appear to agree with the outline typical for the genus; that is, it appears to be much wider across the front than is typical. Glaessner (1980:177), however, described the single specimen as slightly distorted by preservational flattening of the carapace. This certainly could account for the observed differences. Feldmann & Maxwell (1990:786) pointed out that the morphology of the claws precluded an assignment of the species to *Ranilia*. Placement within *Quasilaeviranina* appears to be reasonable based upon the configuration of the fronto-orbital region, the diminutive anterolateral spines, and the postfrontal ridge.

Material examined.—None.

Occurrence.—A single specimen of *Quasilaeviranina pororariensis*, the holotype, was recognized from the Eocene of New Zealand and is maintained at the Canterbury Museum, Christchurch, South Island, New Zealand.

Phylogenetic Analysis

Previous work on raninid classification and phylogeny.—As put forth earlier in this work, much confusion remains about the phylogenetic position of the Raninidae among the Decapoda, although their position as specialized members of the Brachyura is no longer in dispute. Spears et al. (1992) used a molecular approach to test hypotheses about the phylogeny of selected brachyuran crabs. Results from their study suggest that the Raninidae form a distinct lineage, at the lower limit of the Brachyura, which diverged early from an unknown ancestral lineage.

Not much work has been done on the phylogenetic relationships within the Raninidae. Most discussions have revolved around how to subdivide the family into related groups. Lörenthey (*in* Lörenthey & Beurlen 1929), in a review of the primarily fossil Raninidae, recognized three subfamilies based upon the front margin of the carapace: the Palaeocorystinae (*Palaeocorystes, Eucorystes, Eumorphocorystes, Raninella, Notopocorystes,* and *Hemioon*), the Ranininae (*Ranina, Laeviranina, Lophoranina, Hela,* and *Notoporanina*) and the Raninoidinae (*Pseudoraninella, Raninoides, Notopella, Ranidina, Raninellopsis, Tribolocephalus,* and *Lyreidus*). Serène & Umali (1972:25), who considered only extant genera, recognized two subfamilies defined by the type and relative position of male pleopods and the resting position of the eye peduncles: the Notopodinae (*Cosmonotus, Notopus,* and *Ranilia*) and the Ranininae sensu Serène & Umali (*Ranina, Lyreidus, Notopoides, Raninoides, Notosceles, Symethis,* and *Cyrtorhina*). Work by Hartnoll (1979), following earlier works by Gordon (1963, 1966) which centered on the structure of the spermathecal pits of female raninids, indicated some uncertainty about the validity of the two subfamilies recognized by Serène & Umali.

Goeke (1981) accepted the divisions of Serène & Umali (1972) and distinguished a third subfamily, the Symethinae, for a single genus, *Symethis*. Goeke (1981:978) established the uniqueness of the Symethinae based upon possession of seven gills instead of eight, and the unornamented terminus of the first male pleopod. In addition, three more characteristics set the Symethinae apart: the form of the chelipeds which is unique among all Raninidae, the greatly reduced eye peduncles, and the very narrow, but extremely produced fronto-orbital region. The present study supports the significance of these characters, and in the interest of maintaining the Raninidae as a monophyletic group, *Symethis* is removed from the Raninidae.

Based upon the sternum and the paired spermathecae, Guinot (1993:1325) organized the Raninidae into six subfamilies: Ranininae (*Ranina*), Notopodinae (*Notopus, Ranilia, Cosmonotus, Umalia*), Symethinae (*Symethis*), Raninoidinae (*Raninoides, Notosceles, Notopoides*), Lyreidinae (*Lyreidus, Lysirude*), and Cyrtorhininae (*Cyrtorhina*). Serène & Umali (1972:49) had suggested that *Cyrtorhina* and *Symethis* were closely related. Monod (1956:49), on the other hand, indicated that *Cyrtorhina* and *Ranina* might be closely related, based upon the 1st male pleopods; Goeke (1980: 976) agreed with Monod, recognizing the similarity of the spermathecae. Guinot (1993:1325) suggested that *Symethis* and *Cyrtorhina* should each form a separate monotypic subfamily. She further suggested that *Symethis* was sufficiently unique to be elevated to the rank of family and that the Cyrtorhininae could then be removed from the Raninidae and placed as a monotypic subfamily under the Symethidae. This study supports the observations made by Goeke (1980) and Guinot (1993); thus, the Symethidae, under the Raninoidea, is erected to receive *Symethis*. However, the present study does not agree with the removal of Cyrtorhininae from the Raninidae as suggested by Guinot (1993:1329).

Fraaye (1995) described a new genus, *Pseudorogueus,* based upon a single specimen from the lower Eocene of Catalunya, Spanish Pyrenees. Fraaye (1995) distinguished *Pseudorogueus* based upon its unique anterolateral spines, which bear extra smaller spines along the forward borders. This gives Pseudorogueus a superficial resemblance to *Rogueus.* A cladistic analysis, which included *Pseudorogueus,* was run. This test confirmed that the specimen described by Fraaye (1995) is more closely related to the Raninoidinae clade, not the Lyreidinae which includes *Rogueus.* Indeed, when *Pseudorogueus* was inserted into the data matrix, a new analysis resulted with *Pseudorogueus* and *Raninoides* unresolved. Therefore, *Pseudorogueus rangiferus* should be moved to *Raninoides.* The multibranched anterolateral spines observed on both *Pseudorogueus* and *Rogueus* are not unlike those observed on adult members of *Ranina*; therefore, this character probably is homoplasic (reversal) within the Raninidae and should not be used to name a new genus. Furthermore, the fronto-orbital region is most like species of *Raninoides* and there is no obvious postfrontal escarpment as is found in species of *Laeviranina,* a genus very similar to, and often confused with, *Raninoides.* Because *Pseudorogueus rangiferus* is removed to *Raninoides, Pseudorogueus* was not included in the phylogenetic analyses described below.

Methods.—Fossils present a special problem in phylogenetic analysis. Wiley (1981) suggested three distinct problems associated with classifications incorporating fossils and Recent organisms: fossil organisms are intrinsically incomplete; whenever a fossil taxon is classified with Recent taxa, there is a very real risk that the fossil may indeed be the ancestral "stem group" for one of the Recent taxa; and it becomes increasingly difficult to incorporate fossil groups into a Linnaean classification without the addition of more and more categories with fewer and fewer specimens. Though these problems cannot be ignored, there are methods to deal with the problems and still provide valid phylogenetic conclusions that permit stable rank designations. Furthermore, fossils offer the most direct historical evidence available to researchers and allow speculation about character transformations and evolutionary scenarios.

The objective of this study was to reconstruct the phylogeny of the Raninidae, and to include within the phylogenetic analysis all genera of the family, both fossil and living. Fossil taxa, heretofore unassigned to the various subfamilies designated by Guinot (1993), were placed within the appropriate subfamily based upon the results of the phylogenetic analyses. The construction of a hypothetical phylogeny for the entire family, using cladistic analysis as a tool, was compared to the prevailing taxonomic subfamilial classification of living genera (Guinot 1993) as a means of congruence testing of the present analysis. As a result of fossil placements, descriptions of each of the subfamilies were emended to reflect important characteristics of their fossil members, as well as the characters already in use by neontologists.

The analysis herein tested trees that contain higher taxa, namely genera. Recognizing that species may be ancestral to other species or to higher taxa, but that higher taxa may not be ancestral to other higher taxa, the characters of the genera analyzed in this study are those represented by the oldest known species for each genus. The reasoning behind this method was that the first occurrence of the species should come closest to representing the speciation event (cladogenesis) for the initiation of a new genus (see Wiley 1981:96). In the case of very poorly preserved fossil representatives, the next oldest taxon for which there was improved fossil material, was used. In the case of Recent taxa with no fossil record, characters of the type species were used.

This study used PAUP 3.1.1 (Phylogenetic Analysis Using Parsimony) for analysis of the data matrix (Swofford & Begle 1993). The PAUP program, run on a Macintosh computer, analyzed the data matrix (Appendix I) and inferred a hypothetical phylogeny using the principle of parsimony. Various choices were made to control the heuristic search. These selections were made based upon the least amount of constraint or a priori assumptions. All characters were treated equally and no characters were weighted, as weighting would have required a priori decision. Character states were unordered (Fitch parsimony); that is, each character with more than two states was permitted to transform directly from one state to any other state and transitions between any pair of character states were weighted equally for tree length (Quicke 1993:24). For any taxon with missing values, a character state was assigned by PAUP that would be most parsimonious given its location on the tree; however, only those characters that had non-missing values could actually affect the position of any taxon on the tree (Swofford & Begle 1993). The steepest descent option was set to on so that all trees from each round were examined; that is, no trees were discarded the moment a shorter tree was discovered. This allowed the maximum number of trees to be explored.

PAUP also provides several choices for optimizing character reconstructions. For characters of the unordered type, character tracings may turn out to be ambiguous as to the interpretation of homoplasies. The ambiguities can be resolved partially based upon acceleration or delay of transformations (Swofford & Maddison 1987). Of these, the ACCTRAN (=accelerated transformation optimization) tracing method, using the Ferris algorithm (Maddison & Maddison 1992:108), reveals those most-parsimonious assignments that accelerate character changes toward the root; thus, character state changes are placed as close to the root as possible so that homoplasies tend to be explained in terms of distal reversals to plesiomorphic states. Using this procedure forces reversals by maximizing early gains and tends to reduce the number of parallelisms allowed. If, in spite of a bias against them, a pattern of parallelisms continues to appear, one can then argue for adaptation for that trait (see Swofford & Begle 1993).

Multistate taxa, unusual in the present study, were treated as polymorphism. Using multiple states as polymorphism forces PAUP to assume that a terminal taxon is a heterogeneous group, which a supraspecific taxon is by its very nature. Although the oldest recognized species was used for characters traits in this study, there were a few occasions where the expression of two states by different species was deemed important for a true representation of the genus. For example, the oldest known species of *Lophoranina,* from the Cretaceous of Mexico, bears distinguishable cervical and branchial grooves not present in later species of the genus.

Finally, an outgroup was selected to polarize the character states. As previously discussed, the Raninidae do not have a reliable sister group. In fact, the immediate ancestor of the Raninidae remains enigmatic; therefore, the outgroup used for the original analysis was a "Hypothetical Ancestor." This outgroup method of attaching a "Hypothetical Ancestor" (Swofford & Be-

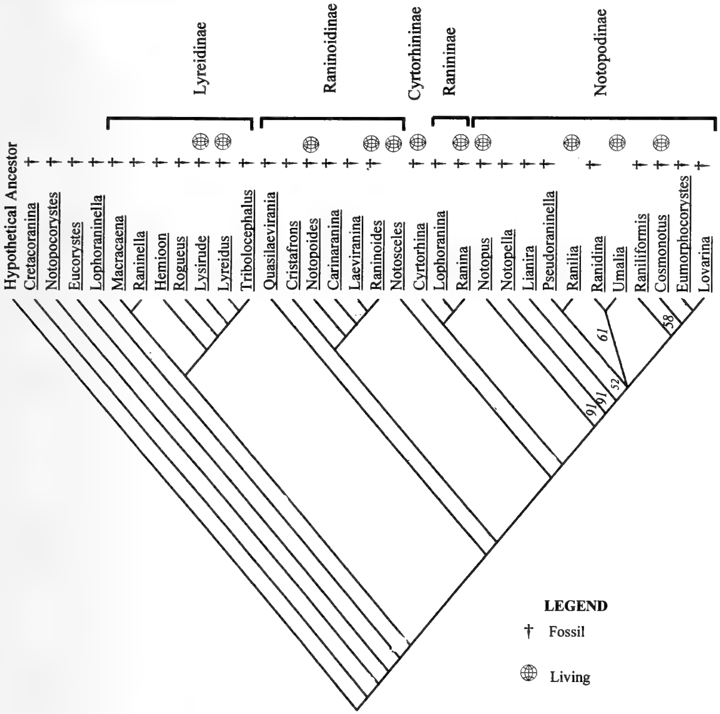

Fig. 20. Majority-rule consensus tree at 50%, where the consensus retains all groups found in over half of the rival trees. Tree illustrates consensus indices (100% where not otherwise indicated) indicating the percentage of the 33 shortest trees in which the figured arrangement of genera occurs.

gle 1993) was employed in order to polarize the characters, and only after first computing an unrooted tree for ingroup taxa.

Because of the large data matrix, the present study used the heuristic method to search for the most parsimonious tree, and when more than one tree resulted from an analysis, the resulting trees were computed for a Majority-rule consensus tree at 50%, where the consensus retained all groups found in over half of the rival trees (Swofford & Begle 1993). Trees generated as a consensus were constructed from a set of trees, rather than from the data directly. Although such trees thus are useful in systematic evaluation, they are not considered a true cladogram or a true phylogeny. The consensus tree was used here as a guide to the phylogeny of the Raninidae, rather than as a true cladogram.

The final "Majority-rule consensus" tree was compared to the taxonomic arrangement by Guinot (1993) to see if there was agreement at the higher taxonomic level of

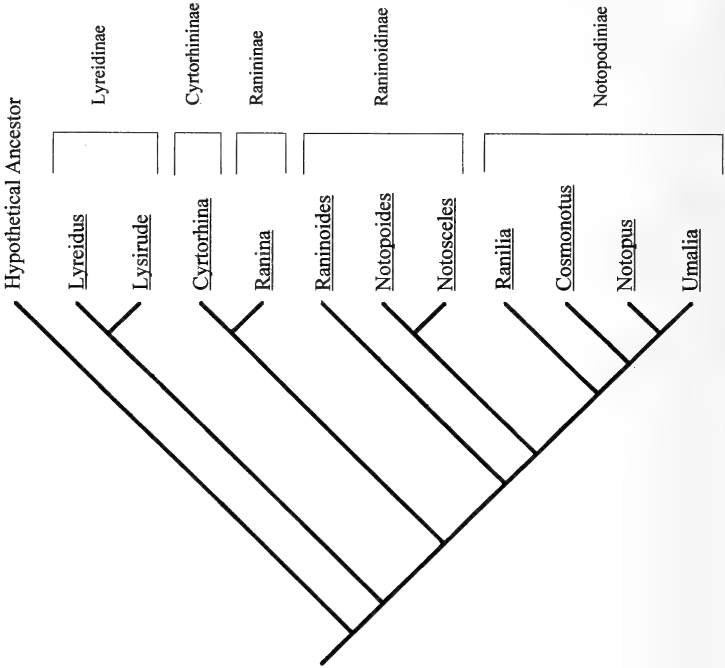

Fig. 21. One of three equally most-parsimonious alternative phylogenies for Recent genera of Raninidae.

subfamily; that is, to explore the possibility that the same genera were grouped together on the consensus tree as were grouped by Guinot (1993) using traditional means and a different data set. The "Majority-rule consensus" of these 33 trees is illustrated in Fig. 20. The subfamilies designated by Guinot (1993) are indicated on this tree. *Lophoraninella* and *Notosceles* appear out of place on the tree (Fig. 20) based upon accepted systematics of those taxa. *Lophoraninella* tended to shift to different positions on the tree with the any change in characters or taxa in the data matrix. This is likely the result of insufficient data for that taxon. *Notosceles* was placed at the base of the Ranininae (Fig. 20); however, upon analysis of only living genera, *Raninoides, Notopoides* and *Notosceles* formed a clade (Fig. 21).

Excluding the taxa discussed above, there is reasonable congruence between the present cladistic analysis and Guinot's arrangement of subfamilies within the Raninidae. After making some adjustments to the tree (Fig. 20) to reflect presently accepted systematics, the new tree was tested to see how many steps the changes added to the most parsimonious tree. These changes added only 5 steps, which is insig-

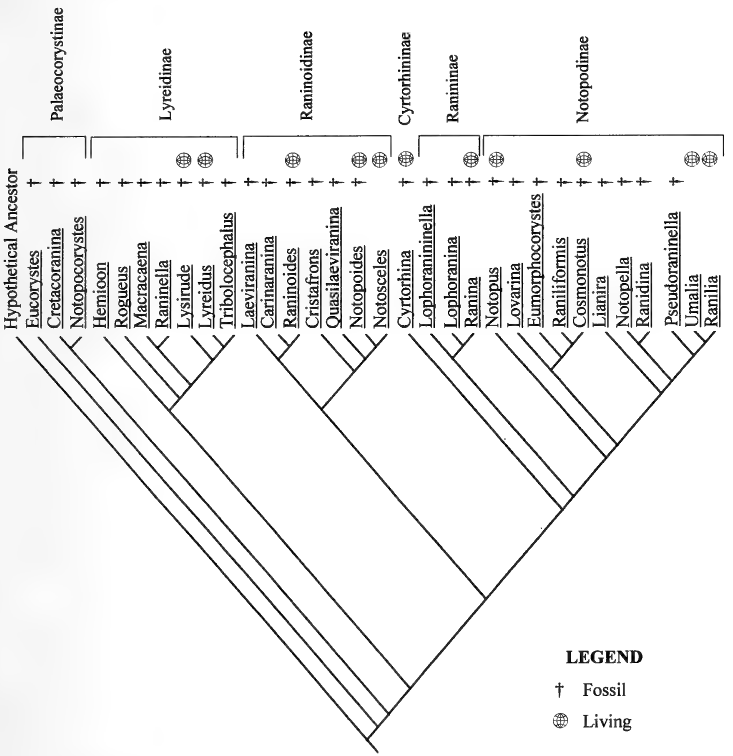

Fig. 22. "Constraint" tree built by testing each clade separately using the outgroup method and physically moving some genera. Testing the "constraint" tree resulted in adding 12 steps to the total length.

nificant. Therefore, a final tree was constructed (Fig. 22) placing these taxa in their currently accepted systematic positions.

Ranina and *Cyrtorhina* formed a clade on the Recent consensus tree. Interestingly, as discussed previously, Monod (1956:49) considered *Cyrtorhina* to be very close to *Ranina,* but indicated that the two genera were differentiated by the shape of the dactyli of pereiopods 3 to 4, the supraorbital and anterolateral teeth, and by the palm and fingers of the chelipeds. Serène & Umali (1972:49) considered *Cyrtorhina* closer to *Symethis,* but stated that the male pleopods resembled those of *Raninoides.* Observations in this study indicated that the sternal configurations of *Cyrtorhina* and *Raninoides* were very different. Furthermore, sternites 2 and 3 on *Cyrtorhina* are broad in front and taper posteriorly, while the same elements on the sterna of *Ranina* widen posteriorly. Although analysis of the Recent genera did not support *Cyrtorhina* and *Ranina* each forming a monotypic subfamily, for reasons just stated they have been retained as subfamilial groups.

Conclusions

The systematic review of the Raninidae places 32 genera, embracing 190 species, into six subfamilies: the Ranininae, Cyrtorhininae, Lyreidinae, Raninoidinae, Notopodinae, and the re-established Paleocorystinae. The monogeneric subfamily Symethinae was elevated to the rank of family, under the Raninoidea, based upon its unusual morphology, especially the characteristic of seven gills, compared to eight for the rest of the family. *Lyreidus* and *Notopocorystes,* both containing subgenera, were re-evaluated and the subgeneric groups were elevated to the level of genus. Three new genera were erected, *Carinaranina, Quasilaeviranina,* and *Macracaena,* as well as the two new species mentioned, *Laeviranina goedertorum,* and *Carinaranina marionae.*

Cladistic analysis of the recognized genera embraced within the Raninidae indicated that the subfamilial divisions of Guinot (1993) are useful for fossils as well as living taxa. Cladistic analysis also indicated the need for a reestablished subfamily, the Palaeocorystinae, to embrace the oldest genera within the Raninidae, *Notopocorystes, Eucorystes,* and *Cretacoranina.*

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Appendix 1.—Data matrix used for phylogenetic analysis of Raninidae. ? = missing data.

	Characters																																		
Taxa of Raninidae	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Hypothetical Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carinaranina +	1	1	1	1	2	0	2	2	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	?	0	?	1	1	1	1	0	0	0	2	3
Cosmonotus 0 +	1	1	1	2	3	2	3	3	3	2	0	2	1	0	1	2	?	2	1	1	1	1	0	0	0	1	1	0	1	1	1	1	0	1	1
Cretacoranina +	0	0	0	0	0	0	0	2	0	1	0	1	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Cristafrons +	0	0	0	1	0	0	1	2	0	0	1	0	0	2	1	1	1	1	0	0	1	0	0	?	0	?	?	?	?	?	?	?	?	2	3
Cyrtorhina 0 +	1	1	0&2	1	0	0	1	2	0	2	1	0	0	2	0	0	0	0	0	0	1	0	0	0	0	1	0	0	2	1	1	1	0	0	0
Eucorystes +	0	0	0	0	0	3	1	0	0	1	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	?	?	?	?	?	?	?	0	1
Eumorphocorystes +	0	0	1	1	2	1	2	1	0	1	0	1	1	0	1	2	1	1	1	1	1	1	1	?	0	?	?	?	?	?	?	?	?	2	2
Hemioon +	1	1	1	0	0	0	1	1	0	0	1	0	0	0	2	0	1	0	1	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1
Laeviranina +	1	1	0	1	1	0	2	2	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0&1	?	0	?	1	0	1	0	0	0	0	2	1
Lianira +	1	1	1	1	2	0	2	2	0	1	1	0	0	2	0	1	0	2	0	2	1	1	1	0	0	1	1	0	1	0	1	?	0	1	3
Lophoranina +	0&1	0&1	0	0	0	1	0	2	0	1	1	1	0	2	0	1	1	0	0	0	0	0	0	?	0	?	1	0	1	0	1	1	0	0	3
Lophoraninella +	0	1	2	0	2	1	1	2	0	1	1	1	0	0	0	0	1	1	1	1	1	0	0	0	0	?	?	?	?	?	?	?	?	0	0
Lovarina +	1	1	1	1	1	1	2	2	0	1	1	0	1	0	0	2	0	2	0	1	1	1	1	?	0	?	?	?	?	?	?	?	?	2	1
Lyreidus 0 +	1	1	1	1	1	0	3	0	0	2	1	0	0	0	1	0	1	2	1	2	1	0	0	0	1	0	1	0	1	0	0	0	1	2	0
Lysirude 0 +	1	1	1	1	0	0	1	1	0	0	1	0	0	1	0	0	1	2	1	2	1	0	0	0	1	0	1	0	1	0	0	0	1	2	0
Macracaena +	1	1	1	1	1	0	1	1	0	0	0	0	0	2	0	0	1	0	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	2	2
Notopella +	1	1	1	1	2	0	2	2	0	0	1	0	0	0	1	0	0	2	0	2	1	0	1	?	0	?	?	?	?	?	?	?	?	0	3
Notopocorystes +	0	0	0	0	0	0	0	2	0	1	0	1	0	0	0	0	1	1	1	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Notopoides 0 +	1	1	0	1	2	0	3	3	3	2	1	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1	1	0	1	1	1	0	0	1	0
Notopus 0 +	1	1	0	1	2	0	2	2	0	1	0	0	0	1	1	0	0	2	0	2	0	1	0	0	0	1	1	0	1	1	1	1	0	0	1
Notosceles 0	1	1	2	1	2	0	2	2	0	1	1	1	0	0	1	0	1	0	0	0	1	0	0	1	0	1	1	0	1	1	1	0	0	2	1
Pseudoraninella +	1	1	2	1	2	0	2	2	0	?	1	?	0	2	2	0	0	0	1	2	2	1	1	?	0	?	?	?	?	?	?	?	?	1	3
Quasilaeviranina +	1	1	0	1	1	0	2	2	0&3	1&2	1	0	0	0	1	0&1	1	1	1	1	1	0	0	?	0	?	1	0	1	0	0	0	0	2	3
Ranidina +	1	1	1	1	2	0	2	2	0	1	0	0	0	0	1	0	?	2	1	2	2	0	1	?	0	?	?	?	?	?	?	?	?	1	3
Ranilia 0 +	1	1	2	1	1	0	2	2	0	1	1	1	0	0	1	0	0	0	1	1	2	1	1	0	0	1	1	0	1	1	1	1	0	0	3
Raniliformis +	1	1	1	1	0	2	2	2	0	0	1	?	1	0	1	2	0	2	1	1	1	0	1	?	0	?	?	?	?	?	?	?	?	1	1
Ranina 0 +	1	1	1	0	0	0	1	2	1	0	1	1	0	2	0	0	1	0	0	0	1	0	?	?	0	?	1	0	1	0	1	1	0	0	3
Raninella +	1	1	0	1	0	0	1	1	0	1	0	0	0	2	1	0	1	0	1	1	0	0	0	?	0	1	?	?	?	?	?	?	?	1	2
Raninoides 0 +	1	1	1	1	1	0	2	2	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0&1	0	0	1	1	0	1	0	0	0	0	2	1
Rogueus +	1	1	1	0	0	0	2	2	1	0	1	0	0	0	0	0	1	0	1	2	1	0	0	?	0	?	1	0	1	0	1	?	1	2	1
Tribolocephalus +	1	1	1	1	1	0	3	3	3	2	0	0	0	0	0	0	1	?	1	2	1	0	0	?	1	?	?	?	?	?	?	?	?	2	3
Umalia 0	0	0	2	1	2	3	2	2	0	1	0	0	0	0	1	0	0	2	1	2	1	0	0	1	0	1	1	0	1	1	1	1	0	1	3

Appendix II

Character 1—Obvious cervical groove
1–0: Present
1–1: Absent

Character 2—Obvious branchiocardiac groove
2–0: Present
2–1: Absent

Character 3—Postfrontal region
3–0: Ridged—a postfrontal terrace or raised area
3–1: Undifferentiated or flat
3–2: Rough or granulated

Character 4—Rostrum
4–0: Bifid or trilobate rostrum
4–1: Single, triangular rostrum
4–2: No rostrum

Character 5—Axis of rostrum
5–0: Sulcate
5–1: Flat
5–2: Ridged
5–3: No rostrum

Character 6—Carapace surface type
6–0: Smooth or finely punctate
6–1: Terraced
6–2: Scabrous
6–3: Granulate

Character 7—The number of anterolateral spines
7–0: Three or more
7–1: Two
7–2: One
7–3: None or extremely reduced

Character 8—Position of the anterolateral spine, or the longest spine in the case where there is more than a single spine. Position measured as distance of spine from the orbital margin relative to distance between orbital and posterior margins.
8–0: Between ½ and ⅓ the total length of the carapace as measured from the orbital ridge to the posterior margin
8–1: Between ⅓ and ¼
8–2: Between ¼ and the front
8–3: No anterolateral spine

Character 9—Character of major anterolateral spine
9–0: Simple, single spine
9–1: Complex spine with one or more subspines
9–2: No spine

Character 10—Anterolateral spine length—length judged relative to rostrum and extraorbital spine length; longer than either was considered long and shorter was considered short
10–0: Long
10–1: Short
10–2: Very reduced or none

Character 11—Longitudinal carina
11–0: Present, at least in part
11–1: Absent

Character 12—Sides of the rostrum almost parallel. This character is used to define both very narrow, single rostral projections and wider, often bifid rostral projections
12–0: Not parallel
12–1: Parallel
12–2: No rostrum

Character 13—Relative length of the extraorbital spines
13–0: Shorter than or equal to the length of the rostrum
13–1: Longer than rostrum
13–2: Not produced beyond orbital margin

Character 14—Shape of the outer margin of the extraorbital spines
14–0: Straight
14–1: Concave
14–2: Convex

Character 15—Orientation of the outer margin of the extraorbital spine
15–0: Directed forward
15–1: Converging toward long axis of carapace
15–2: Diverging from long axis of carapace

Character 16—Character of the extraorbital spines
16–0: Single spine
16–1: Bifid or multiple spines
16–2: No spines protruding beyond orbital margin

Character 17—Characteristics of the inner orbital tooth
17–0: Produced beyond supraorbital ridge
17–1: Even with supraorbital ridge

Character 18—Median orbital tooth—a tooth or spine between the extraorbital tooth and the inner orbital tooth
18–0: Produced beyond orbital ridge
18–1: Not produced beyond orbital ridge
18–2: No tooth

Character 19—Inner orbital fissure—the fissure separating the inner orbital tooth from the next tooth, whether the median tooth or the extraorbital tooth
19–0: Open
19–1: Closed

Character 20—Outer orbital fissures
20–0: Open
20–1: Closed or
20–2: No obvious fissure, sometimes as the result of the spines or teeth protruding from the edge of the supraorbital margin and sometimes because there is no intervening midorbital tooth

Character 21—Character of the supraorbital fissures
21–0: Deep, obvious fissures
21–1: Shallow fissures—almost obscure
21–2: No obvious fissures

Character 22—The orientation of the orbits—expressed as anteriorly directed, horizontal orbits or orbits that are directed obliquely downward
22–0: Horizontal
22–1: Obliquely downward

Character 23—Cardiac furrows—arcuate grooves along lateral edges of cardiac region

23–0: Present
23–1: Absent

Character 24—The width of the posterior margin relative to the width of the first abdominal somite

24–0: Posterior margin greater than width of abdomen
24–1: Width of posterior margin equal to or less than width of abdomen

Character 25—Relative width of posterior margin—as compared to the fronto-orbital margin

25–0: Width of posterior margin less than fronto-orbital margin
25–1: Width of posterior margin greater than fronto-orbital region

Character 26—Spine present on abdominal somite three or four

26–0: Present
26–1: Absent

Character 27—Relative size of fused thoracic sternites one to three

27–0: Sternites 1 to 3 reduced in size, quite small
27–1: Sternites 1 to 3 not reduced in size

Character 28—The juncture of fused sternites 1 to 3 with sternite 4

28–0: Direct fusion with no elongation between elements 3 and 4
28–1: An elongated, parallel-sided "neck" between elements 3 and 4

Character 29—The width of the anterior of sternite 4 relative to the width of the posterior of sternite 4

29–0: Posterior greater than anterior
29–1: Anterior greater than, or equal to, the posterior
29–2: Extremely narrow and linear

Character 30—Anterior shape of sternite 4

30–0: Not alate
30–1: Alate or narrowed

Character 31—Width of the posterior of sternite 5

31–0: Somewhat reduced
31–1: Very reduced

Character 32—Visibility of sternite 6

32–0: Visible
32–1: Not visible

Character 33—Abdominal hooking mechanism ("pterygoid processes" sensu Bourne, 1922:69)

33–0: Absent
33–1: Present

Character 34—Ratio of width to length

34–0: Ratio greater than 80%
34–1: Ratio 70 to 79%
34–3: Ratio less than 70%

Character 35—Position of greatest width

35–0: Anterior half
35–1: Between half and one-third
35–2: Between anterior one-third and one-fourth
35–3: Anterior one-fourth to front

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Notes on distribution and taxonomy of five poorly known species of pinnotherid crabs from the eastern Pacific (Crustacea: Brachyura: Pinnotheridae)

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Abstract.—The Pinnotherid crabs *Glassella costaricana* (Wicksten, 1982) [from Costa Rica], *Pinnixa richardsoni* (Glassell, 1936) [from Panama] and *P. scamit* Martin & Zmarzly, 1994 [from California, U.S.A.] are reported for the first time from the Mexican Pacific. They were collected at Acapulco, Guerrero, Juchitán de Zaragoza, Oaxaca, and Todos Santos Bay, Baja California, respectively. The southern distribution of *P. barnharti* Rathbun, 1918 is found to be restricted to Punta Banda estuary, Todos Santos Bay, Baja California, Mexico. A second male of *Pinnaxodes gigas* Green, 1992, is reported from the upper Gulf of California; its range is extended from Estero Tastiota, Sonora to Bajo Macho, northeast Consag Rock. Based on the new material taxonomic remarks on the species are provided.

The distribution of five poorly known species of symbiotic crabs of the family Pinnotheridae is updated based on new material collected on the west coast of Mexico. *Glassella costaricana* (Wicksten 1982), *Pinnixa richardsoni* Glassell 1936, and *Pinnixa scamit* Martin & Zmarzly, 1994, are recorded for the first time in Mexican waters. The new records extend the distribution of those reported by Zmarzly (1992), Martin & Zmarzly (1994) and Hendrickx (1995). The southern distribution of *Pinnixa barnharti* is found to be restricted to Punta Banda estuary, Todos Santos Bay, Baja California, and the distribution of *Pinnaxodes gigas* is extended from Tastiota estuary, Sonora, to Bajo Macho, NE of Consag Rock, in the upper Gulf of California. For each species, taxonomic remarks based on the new material are provided.

The new material has been compared with specimens deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Natural History Museum of Los Angeles County, Los Angeles, California (formerly Allan Hancock Foundation, University of Southern California, Los Angeles, California) (LACM); Colección de Equinodermos (CE) and Colección de Macroinvertebrados Bentónicos (EMU), Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México. The new material is deposited in the Colección de Invertebrados, Facultad de Ciencias, Universidad Autónoma de Baja California (UABC). Abbreviations used are: Gulf of California (GC); Baja California (BC); Baja California Sur (BCS); Sonora (SON); walking legs (WL); third maxilliped (MXP3).

Systematic Account

Glassella costaricana (Wicksten, 1982)
Fig. 1A

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

Glassella costaricana: Campos & Wicksten, 1997:69–73, figs. 1, 2A–D.

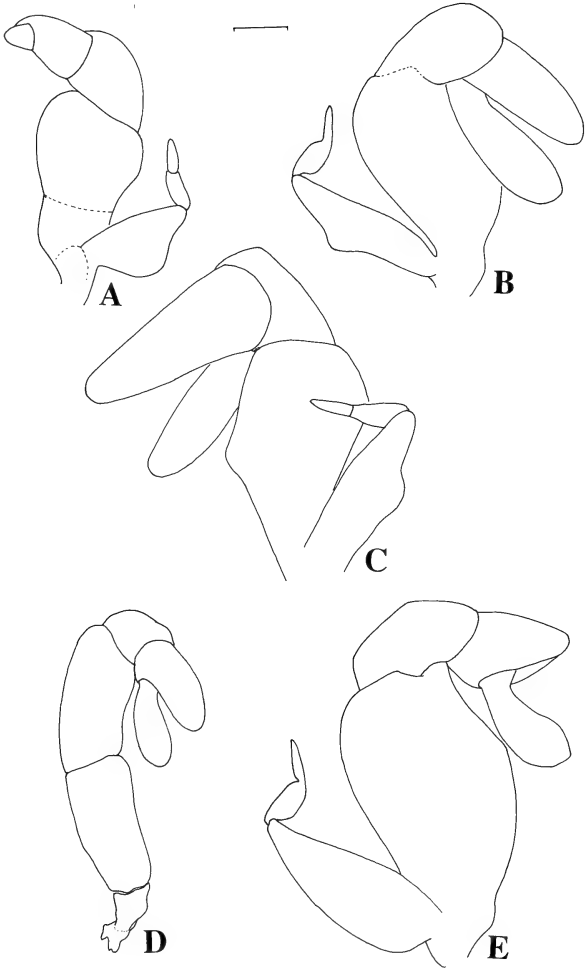

Fig. 1. Third maxilliped. A, *Pinnixa scamit* Martin & Zmarzly, 1994; B, *Pinnixa barnharti* Rathbun, 1918; C, *Scleroplax granulata* Rathbun, 1893; D, *Alarconia seaholmi* Glassell, 1936: E, *Holothuriophilus* sp. (A, from Martin & Zmarzly 1994; D, from Glassell 1936). Not to scale.

Previous distribution.—Playa de Coco, Guanacaste province, Costa Rica (about 10°5′N, 85°45′W); low intertidal zone, sand and rocks (type locality).

Material examined.—1 female holotype (LACM 2252-17); 1 female, Manzanillo Beach, Acapulco, Guerrero, Mexico, 4 Aug 1988 (UABC). Host unknown.

Remarks.—The singular shape of MXP3 allows separation of *G. costaricana* from American species with a *Pinnixa*-like morphology. These species have a wider than long carapace, firm or hard, and the third pair of walking legs are the longest. The MXP3 in *Glassella costaricana* has a pyriform ischium-merus. Moreover, the palp of this appendage has a carpus larger than the conical propodus and a small, digitiform dactylus inserted subdistally on the inner face of the propodus (Fig. 1A). *Pinnixa* spp., *Scleroplax granulata* Rathbun, 1893 and *Alarconia seaholmi* Glassell, 1938, in contrast, have a subtrapezoidal or subrectangular ischium-merus (in the latter species these articles are well-separated). Furthermore, the palp has a carpus shorter than the spatulated propodus and, a large and spatulate dactylus inserted on the proximal ventral margin of the propodus (Fig. 1B–D).

Pinnaxodes gigas Green, 1992
Figs. 2A–B, 3A–B

Pinnaxodes gigas Green, 1992:775–779, figs. 1, 2A–B, 3A–F; Hendrickx, 1995: 141 (listed).

Previous distribution.—Morro Colorado (Tastiota estuary), SON, Mexico.

Material examined.—1 male, Bajo Macho, northeast of Consag Rock, upper Gulf of California, Mexico, May 1995 (UABC); shrimp trawl.

Remarks.—Green (1992) pointed out that *P. gigas* resembles the Atlantic species *P. floridensis* Wells & Wells, 1961. Males of these species are also morphologically similar to males of the Pacific species *Opisthopus transversus* Rathbun, 1918. These species share a suborbicular carapace, a MXP3 with a spoon-shaped dactylus proximally inserted on the spatulate propodus, and a narrow and triangular abdomen (Figs. 2A–F; 3A, C, E). However, morphological differences between the former two species and *O. transversus* do exist, including shape of the front, meri of WL, and telson. *Pinnaxodes gigas* and *P. floridensis* have the front entire (Fig. 2A, C), meri of WL distally swollen (Fig. 3B, D) and telson basally expanded (Fig. 3A, C). *Opisthopus transversus,* in contrast, has the front emarginated (Fig. 2A), meri of WL uniformly wide (Fig. 3F), and telson not basally expanded (Fig. 3E).

Regarding the taxonomic status of the monotypic genus *Opisthopus* Rathbun, 1893, Rathbun (1918) noted that perhaps this genus should be united with *Pinnaxodes* Heller, 1865. The shared features here recorded among *O. transversus, P. gigas* and *P. floridensis,* seem to support this unification. However, we prefer to maintain *Opisthopus* separated from *Pinnaxodes* until an ongoing systematic revision of the pinnotheird crabs symbiotic with sea cucumbers is completed by the senior author.

Hopkins & Scatland (1964) reported that *O. transversus* develops a bright-red mottling on the carapace when harbored in the cloaca of holothurids. This is due to the crab eating mud rich in carotenoids from the cloaca of its host. Wells & Wells (1961) and Green (1992) reported the same red spots on *P. floridensis* and *P. gigas.* The dry male recorded here, features red-orange spots on the carapace as well. The hypothesis is that *P. gigas* is a symbiont of holothurids, capable of leaving its host temporarily perhaps in search of a solitary female harbored in the cloaca of another host.

Pinnixa barnharti Rathbun, 1918
Fig. 1B

Pinnixa barnharti Rathbun, 1918: 130, 144, 149, 150. pl. 32, fig. 1; Schmitt, McCain, & Davidson, 1973:103; Garth & Abbott,

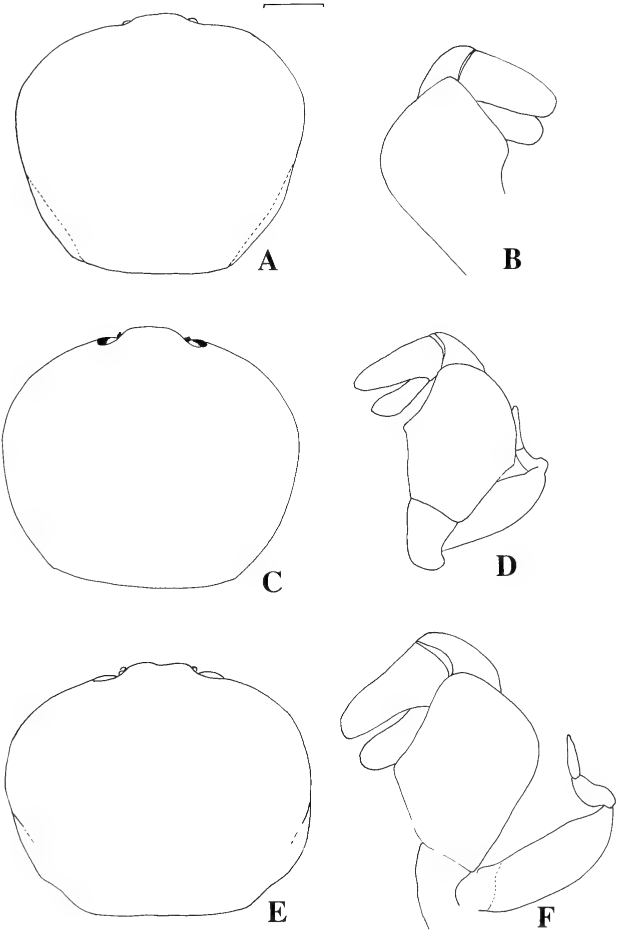

Fig. 2. *Pinnaxodes gigas* Green, 1992: A, carapace; B, third maxilliped. *P. floridensis* Wells & Wells, 1961: C, carapace; D, third maxilliped. *Opisthopus transversus* Rathbun, 1893; E, caparace; F, third maxilliped. Scale (mm), A = 3.4; B = 0.87; C = 1.45; D = 0.4; E = 1.27, F = 0.36.

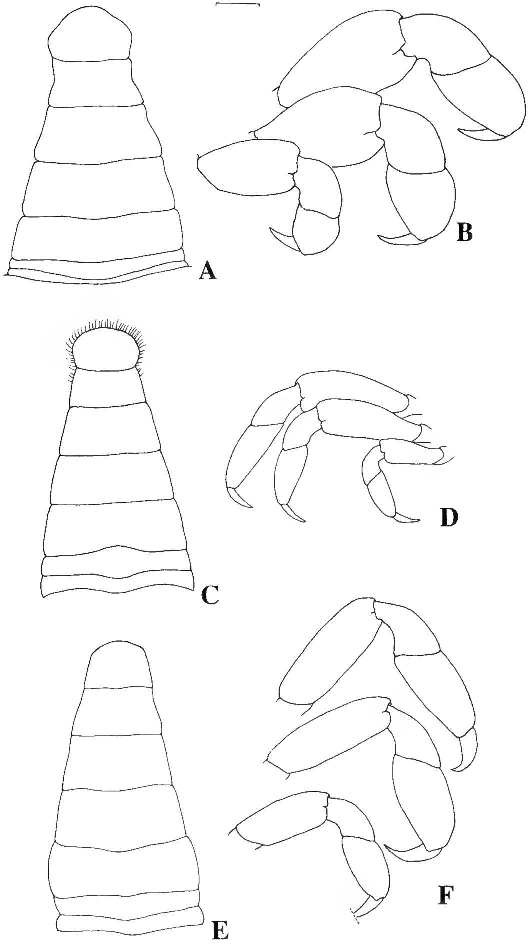

Fig. 3. *Pinnaxodes gigas* Green, 1992: A, abdomen; B, walking legs 2–4. *P. floridensis* Wells & Wells, 1961: C, abdomen; D, walking legs 2–4. *Opisthopus transversus* Rathbun, 1893: E, abdomen; F, walking legs 2–4. Scale (mm), A = 1.46; B = 2.17; C = 1.18; D = 1.52; E = 0.73; F = 1.27.

1980:614; Ricketts, Calvin & Hedgpeth, 1985:338; Bonfil, Carvacho & Campos, 1992:47–48; Zmarzly, 1992:679–682, figs. 2, 3; Hendrickx, 1995:141 (listed).

Previous distribution.—From Puget Sound, Washington, U.S.A., to Punta Banda estuary, Todos Santos Bay, Ensenada, BC, Mexico; Ixtapa Island, Zihuatanejo, Guerrero, Mexico (Zmarzly 1992).

Material examined.—2 females, Punta Banda estuary, Todos Santos Bay, Ensenada, BC, Mexico, 24 Jun 1935, LACM 35-189-1; 1 male, same locality, 24 Feb 1995; infesting the holothurid *Caudina arenicola* (Stimpson, 1857), UABC.

Remarks.—Caso (1965) reported *Pinnixa barnharti* to Ixtapa island, Zihuatanejo, Guerrero, Mexico in *Paraholothuria riojai* Caso, 1964. One of us (EC) studied the crab specimen on which Caso based her report (CE uncat), and it actually is a species of the genus *Holothuriophilus* Nauck, 1880. Manning (1993) discussed the taxonomy of this genus. Typical members of the *Pinnixa*-complex differ from *Holothuriophilus* by the enlargement of the third pair of walking legs. In *P. barnharti,* that leg is not notoriously enlarged. *Pinnixa barnharti* and members of the genus *Holothuriophilus* share a carapace broader anteriorly, chelipeds large and robust, and walking legs short and wide. They differ in their MXP3 morphology. In *P. barnharti* the exopod has an external lobe, and the endopod has a carpus shorter than the spatulated propodus (Fig. 1B). In *Holothuriophilus* the exopod lacks an external lobe, and the endopod has a carpus larger than the conical propodus (Fig. 1E).

The southern distribution of *P. barnharti* Rathbun, 1918 is found to be restricted to Punta Banda estuary, Todos Santos Bay, BC, Mexico. This crab seems to occur only in the cloaca of the holothurid *Caudina arenicola* (Stimpson).

Pinnixa richardsoni Glassell, 1936
Fig. 4A–B

Pinnixa richardsoni Glassell, 1936:301–302, pl. 21, fig. 3; Wicksten, 1982:356–357, Fig. 2; Hendrickx, 1995:141 (listed).

Previous distribution.—Balboa, Canal Zone, Panama (type locality).

Material examined.—4 males, 2 females, Laguna Superior, inlet front to Santa Maria Xadani, Juchitan de Zaragoza, Oaxaca, 17 Nov 1994; mud bottom, 1.6 m.

Remarks.—The morphology of our specimens agrees with the original description of *P. richardsoni* provided by Glassell (1936). He noted that the male in this species has the abdominal somites 3–5 fused. Wicksten's (1982) statement that abdominal somites 1–3 are fused in this species is incorrect. According to Glassell (1936), *P. richardsoni* is very closely allied to *P. valerii* Rathbun, 1931. This is widely supported by the very similar shape of MXP3 and abdomen in these species (Fig. 4A–D). Wicksten pointed out that *P. valerii* can be separated from *P. richardsoni* by the presence of six free abdominal somites and telson in the former. One of us (EC) examined two male specimens of *P. valerii* (UABC) and although a demarcation line is faintly indicated, somites 3–5 are clearly fused and the arthrodial membrane is absent (Fig. 4D). Michel Hendrickx, on our request, examined the male specimen of *P. valerii* (EMU 646) from El Verde, Sinaloa, Mexico on which Wicksten (1982) based her report. Hendrickx observed that *Pinnixa richardsoni* also has a demarcation line among the fused abdominal somites 3–5 (Fig. 4B). However, morphological differences between these species do exist, including shape and robustness of WL and shape of sixth abdominal somite. Wicksten (1982), who studied the holotype of both species, pointed out that the legs of *P. richardsoni* are stouter than those of *P. valerii.* She noted that the former species has the merus of WL3 1.9 times as long as wide; in *P. valerii* it is 2.7 times as long as wide. Regarding the sixth abdominal somite, *P. richardsoni* has the distal margin concave; in *P. valerii* it is straight (Fig. 4B, D).

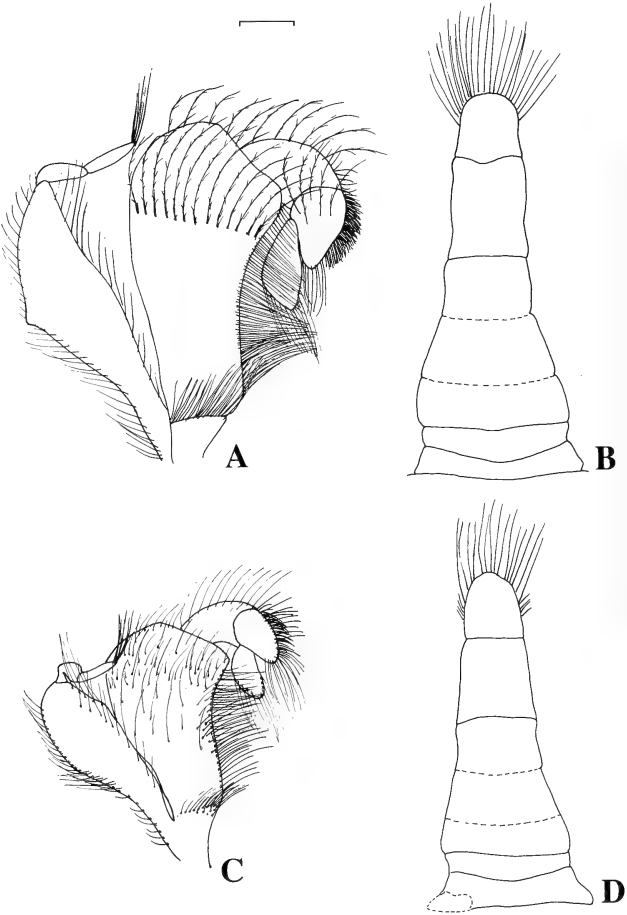

Fig. 4. *Pinnixa richardsoni* Glassell, 1936: A, third maxilliped; B, abdomen. *P. valerii:* C, third maxilliped; D, abdomen. Scale (mm): A = 0.3; B = 1.26; C = 0.36; D = 0.83.

Pinnixa scamit Martin & Zmarzly, 1994
Fig. 5A–C

Pinnixa scamit Martin & Zmarzly, 1994: 354–359, Figs. 1, 2.

Previous known distribution.—Western Santa Barbara Channel, just seaward of,

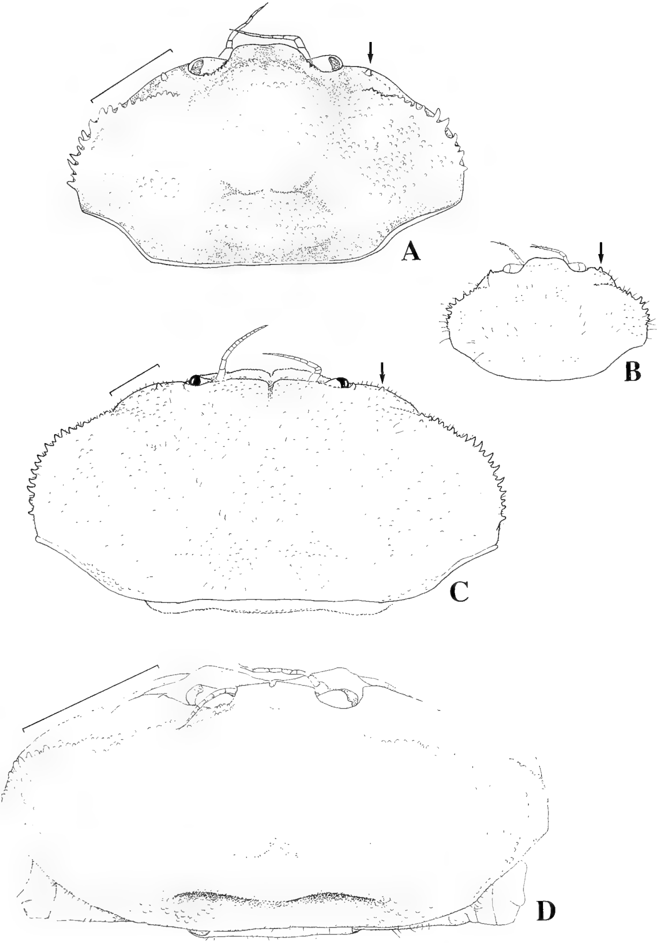

Fig. 5. *Pinnixa scamit* Martin & Zmarzly, 1994: anterodorsal view of carapace, A, male; B, juvenile (sex indetermined). *P. occidentalis* Rathbun, 1893: C, female; D, male juvenile, anterodorsal view of carapace. Arrows indicate the subhepatic tooth. Scale = 1 mm (B–C from Martin & Zmarzly 1994; D, from Zmarzly 1992).

and SSW of, Pt. Arguello, California, 34°29.04′N, 120°44.01′W.

Material examined.—2 males, 2 females, all lacking pereiopods, Todos Santos Bay, Ensenada, BC, Mexico (UABC); dredge, slime-clay bottom, 27–48 m.

Remarks.—Bonfil et al. (1992) and Zmarzly (1992) recorded eight species of the genus *Pinnixa* for the west coast of BC. *Pinnixa scamit* Martin & Zmarzly, 1994, a species morphologically close to *P. occidentalis* Rathbun, 1893, is the ninth newly recorded *Pinnixa* species in Mexico. Although our male (previously unknown) and female specimens lack WL, we assigned them to *P. scamit* by the presence of several morphological features: a well developed, granular, cardiac ridge on the carapace; larger, acute, slightly curved teeth along the anterolateral margin of the carapace; and a well-developed subhepatic tooth (Fig. 2A–C). Males and females of *Pinnixa occidentalis* have: an acute, sometimes bilobate cardiac ridge; anterolateral margin with a granulated ridge; and no trace of a subhepatic tooth (Fig. 2D).

Although the host of *Pinnixa scamit* remains unknown, specimens of polychaete worms belonging to 20–28 families co-occurred in the dredges. Members of Spionidae, Cirratulidae and Paraionidae were the most abundant. They remain as potential hosts for this crab (Table 1).

Table 1.—Common polychaete worms dredged with the crab *Pinnixa scamit* at Todos Santos Bay, Ensenada, Baja California, Mexico.

Family	Species*
Cirratulidae	*Cauperiella alata* Southern
	Monicellina tesselata Hartman
Paraonidae	*Aricidea wassi* Pettibone
	Cirrophours sp.
	Allia ramoso Annenkova
Spionidae	*Laonice cirrata* Sars
	Paraprionospio pinnata Ehlers
	Spiophanes bombyx Claparede

* Deposited in the Invertebrate Collection (Marine Ecology Department) of Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, Bc, México.

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A new species of the genus *Chirostylus* Ortmann, 1892 (Crustacea: Decapoda: Anomura: Chirostylidae) from the Ogasawara Islands, southern Japan

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Abstract.—A new anomuran crustacean, *Chirostylus rostratus,* is described and illustrated based on a male specimen collected from the Ogasawara Islands. A well-developed rostral spine displayed by the species requires redefinition of the genus *Chirostylus.* Re-examination of Ogawa & Matsuzaki's (1993) material reveals that *C. ortmanni* should not be synonymized with *C. dolichopus.*

The genus *Chirostylus* Ortmann, 1892, includes four species: *C. dolichopus* Ortmann, 1892 (the type species of the genus), *C. ortmanni* Miyake & Baba, 1968, *C. micheleae* Tirmizi & Khan, 1979, and *C. novaecaledoniae* Baba, 1991; all are recorded only from the Indo-West Pacific (Baba 1991:466). Ogawa & Matsuzaki (1993:65) synonymized *C. ortmanni* with *C. dolichopus,* but as herein discussed this is hardly accepted.

Recently, an unusual specimen of *Chirostylus* was collected from the Ogasawara (Bonin) Islands, the southern oceanic islands of Japan. The specimen does not fit any known species of the genus in having a well-developed rostral spine, the character resembling that of species of the genus *Gastroptychus* Caullery, 1896. We herein describe and illustrate the Ogasawara specimen as a new species of *Chirostylus,* and the genus is redefined to include this species.

The holotype is deposited in the National Science Museum, Tokyo (NSMT). The post-orbital carapace length (CL) is measured from the dorsal posterior margin of the orbit to the median posterior end of the carapace.

Chirostylus rostratus, new species
Figs. 1, 2

Type specimen.—Holotype: male (CL 7.3 mm); west of Minamijima Island, Ogasawara Islands; 180 m; 14 Sep 1996; coll. S. Yokoyama; NSMT-Cr 12028.

Description.—Carapace (Fig. 1A, B) excluding rostrum, 1.11 times longer than greatest width. Rostrum 0.18 length of post-orbital carapace; basal portion broad; rostral spine longer than epigastric spines, directed anterodorsally. Anterolateral spines prominent, preceded by smaller spine at lateral limit of orbit. Pair of epigastric spines situated behind eyes, directed anterodorsally. Gastric region moderately inflated, unarmed. Cardiac region somewhat flat, without spine. Cervical grooves weakly developed. Branchial regions ridged posteriorly along row of 4 spines nearly parallel to lateral margin, first and second spines slender, last spine smallest. Lateral margins of carapace diverging posteriorly to point approximately ⅓ from posterior end, converging behind it with strong concavity. Posterior margin strongly concave.

Pterygostomian flaps (Fig. 1B) with row of irregularly arranged, small spines parallel to lateral margin of carapace, accompanied by a few spinules ventral to this row on posterior half, anteriorly ending in small, sharply pointed spine; small depression situated at anterior ⅓.

Third thoracic sternite (Fig. 1C, D)

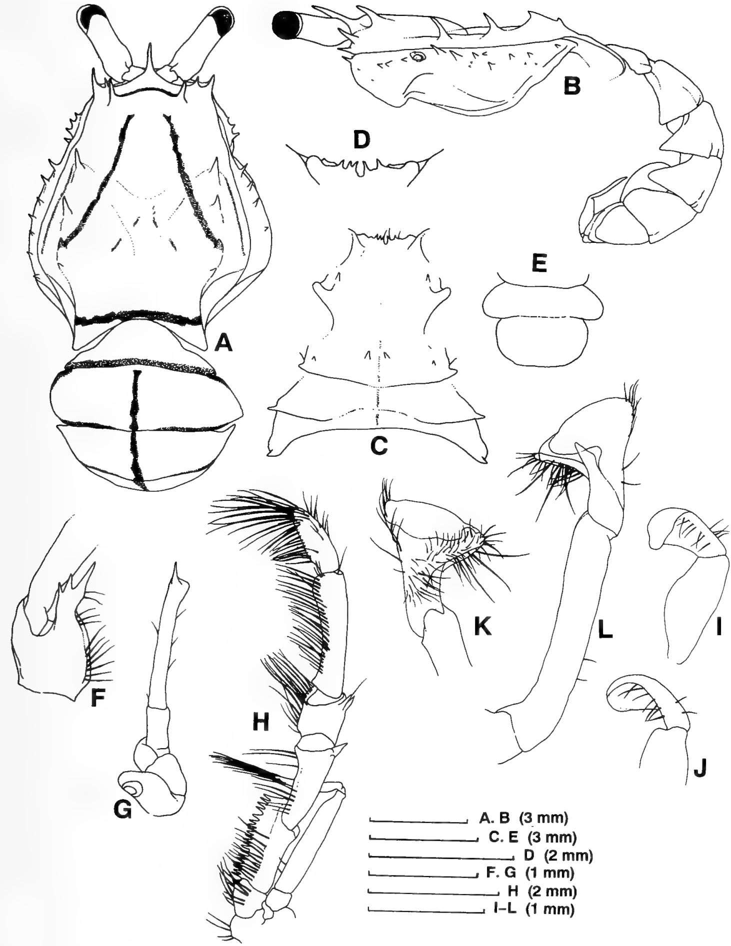

Fig. 1. *Chirostylus rostratus,* new species. Holotype, male (CL 7.3 mm, NSMT-Cr 12028). A, carapace and abdomen, dorsal; B, same, left lateral; C, thoracic sternum, ventral; D, third thoracic sternite, ventral; E, telson, dorsal; F, left antennular peduncle, ventral; G, left antennal peduncle, ventral; H, left third maxilliped, ventral; I, left first pleopod, dorsal; J, same, ventral; K, left second pleopod, dorsal; L, same, ventral.

somewhat depressed from level of following sternite; anterior margin nearly transverse, with 5 small spines, U-shaped median notch flanked by 2 submedian spines. Fourth thoracic sternite with distinct spine on each proximal lateral margin. Fifth thoracic sternite with 2 pairs of spines on posterior transverse line, each pair situated at median and lateral regions. Following sternites unarmed.

Abdomen (Fig. 1A, B) glabrous and unarmed; pleura of second to fourth somites triangular with rounded (second and fourth somites) or pointed (third somite) apex, those of fifth and sixth somites ending in rounded margin. Telson (Fig. 1E) divided into 2 lobes by indistinct transverse fissure; anterior lobe with strongly convex lateral margins, 1.31 times as broad as posterior; posterior lobe 1.65 times longer than anterior, semi-elliptical.

Eyestalks (Fig. 1A, B) elongate, 0.35 length of postorbital carapace, subcylindrical, slightly broadened proximally; cornea slightly dilated, approximately ⅓ length of remaining ocular peduncle.

Antennular basal segment (Fig. 1F) with 3 spines on distolateral projection, distalmost largest; distal 2 segments unarmed.

Antennal peduncles (Fig. 1G) 5-segmented, lacking scale; ultimate segment 3.32 times as long as penultimate, with ventromesial terminal spine; proximal 4 segments unarmed.

Third maxillipeds (Fig. 1H) having basis with small but broad spine at distomesial end, ischium with crista dentata of 20 acute teeth, merus with strong distolateral spine, carpus with 2 distolateral spines.

Chelipeds (Fig. 2A–C) similar to each other but right slightly longer than left, subcylindrical, slender, 11.2 times as long as postorbital carapace, bearing sparse coarse setae except for setose fingers. Merus, carpus, and palm provided with 6 longitudinal rows of spines (2 dorsal, 2 ventral, 1 mesial, and 1 lateral) and irregularly arranged smaller spines. Merus and palm 1.76 and 1.16 times longer than carpus, respectively. Fingers 0.43 as long as palm; opposable margins with small, rounded or subtriangular tubercles on gaping median ⅓; proximal ⅓ margins with distinctly larger, subtriangular teeth (2 on movable finger, and 1 on immovable finger); distal ⅓ margins with small, low protuberances bearing slender, corneous spinules; distal ends with 2 corneous, larger spines.

Ambulatory legs (Fig. 2D–I) slender, spinose, subcylindrical, somewhat depressed lateromesially, slightly overreaching end of cheliped carpus; meri successively diminishing in size posteriorly but carpi and propodi each subequal in three legs. Coxa of third leg visible entirely in dorsal view, closely fitting strong concavity of lateral margin of carapace. Ischium short, with several small spines. Merus 0.89 (first leg), 0.82 (second leg), and 0.79 (third leg) as long as carpus and propodus combined, with rows of slender spines on extensor and flexor margins and irregularly arranged, smaller spines on lateral surface. Carpus resembling merus in its spiny condition, but spines on extensor margin more closely arranged. Propodus 0.94 length of carpus, slightly narrower than carpus in lateral view, with 2 rows of fixed spines along extensor margin; flexor margin with movable, slender spines: 21 on first leg, 21 or 22 on second leg, and 19–22 on third leg, including distal 2 pairs (terminal pair much larger). Dactyl 0.13 length of propodus, moderately curving, with flexor margin bearing 7 (first and second legs) or 8 (third leg) spines (including terminal) gradually decreasing in size toward base of segment, penultimate spine slightly longer than ultimate.

Male with 5 pairs of pleopods on first to fifth abdominal somites; those of first and second somites modified as gonopods, those on third to fifth somites each reduced to very small, elongate bud. First pleopod (Fig. 1I, J) moderately elongate; protopod inflated dorsolaterally, naked; endopod directed dorsolaterally, curving dorsally in distal half, bearing several short setae on

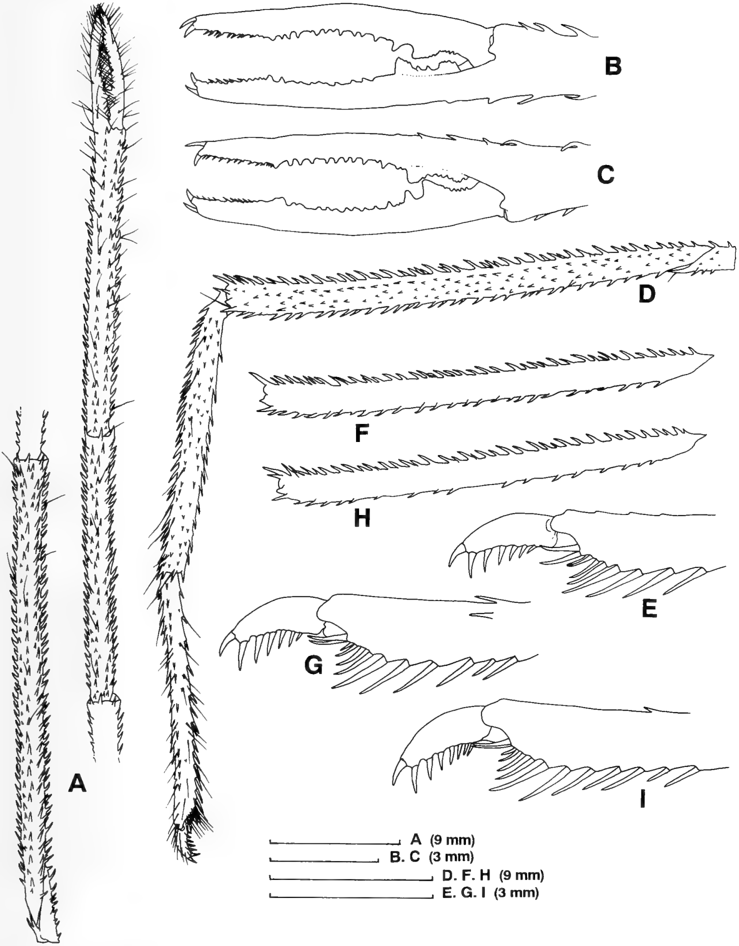

Fig. 2. *Chirostylus rostratus,* new species. Holotype, male (CL 7.3 mm, NSMT-Cr 12028). Appendages from left side except for C, right side. A, cheliped, dorsal; B, C, same, distal part of chela, dorsal, setae omitted; D, first ambulatory leg, lateral; E, same, distal part of propodus and dactyl, lateral, setae omitted; F, second ambulatory leg, merus, lateral; G, same, distal part of propodus and dactyl, lateral; H, third ambulatory leg, merus, lateral; I, same, distal part of propodus and dactyl, lateral.

proximal ⅔ of mesial region. Second pleopod (Fig. 1K, L) considerably larger than first, elongate; protopod slender, bearing 2 short setae on proximal part of lateral region; endopod strongly expanded distally, dorsally curved in distal portion, giving subtriangular rounded appearance in dorsal or ventral view; dorsal surface covered with setae of irregular-sizes; ventral surface with keel-like structure terminating in slender process.

Color.—Body and pereopods whitish pink, with reddish lines and bands on carapace and abdomen as figured. Carapace with distinct line in large triangle and narrow lines between epigastric spines and along branchial spines. Abdominal somites each with transverse band along dorsoposterior margin, bands of second to sixth somites interrupted by median longitudinal line. Pterygostomian flaps with reddish longitudinal lines along anterior, dorsal, and ventral margins. Third thoracic sternite pale reddish along anterior margin. Ocular peduncles whitish pink, with pale reddish distal part on dorsal face, and reddish longitudinal narrow line on ventral face. Chelipeds with reddish longitudinal line on mesial face of coxa to ischium, ischium and merus each with reddish spines on proximal ⅔ of ventrolateral to mesial faces. Ambulatory legs with reddish line on coxa to ischium as in chelipeds, merus with reddish spines on proximal ¼ of mesial face, carpus with broad transverse band of pale red.

Etymology.—The specific name is derived from the Latin, *rostratus* meaning beaked, in reference to the characteristic rostral spine.

Remarks.—*Chirostylus rostratus* is immediately distinguishable from the other known species of the genus by the rostral spine being longer than the epigastric spines. Baba (1988:5) mentioned that the rostral spine of *Chirostylus* species should not be regarded as the true rostrum and is structurally identical with spines appearing irregularly elsewhere on the carapace. Therefore, the presence or absence of a distinct spiniform rostrum has been believed to be the sole character discriminating between *Chirostylus* and *Gastroptychus.* The rostral spine of *Chirostylus rostratus,* however, seems not to be a small slender structure on the rounded rostrum but to form a spiniform rostral area. To accommodate the new species in *Chirostylus,* the genus can be redefined by a combination of the following characters: the carapace is so strongly concave on the posterior lateral margins that the coxa of the third ambulatory leg closely fits the concavity and is visible entirely in dorsal view; and the ocular peduncles are elongate and far overreaching the rostral spine.

Ogawa & Matsuzaki (1993:65) concluded that *C. ortmanni* should be synonymized with *C. dolichopus,* because of variation of spines on the carapace, pterygostomian flaps, third thoracic sternite, and basal segment of the antennular peduncles. However, they did not discuss the relative sizes of the ultimate and penulitimate spines on the flexor margin of the ambulatory dactyls, which is a distinguishing character between the two species originally indicated by Miyake & Baba (1968:386). Re-examination of Ogawa & Matsuzaki's material now in the collection of the National Science Museum, Tokyo (NSMT-Cr 11672 to 11686) discloses that the sizes of the two spines are approximately equal in most of the specimens. Even if the ultimate spine is somewhat smaller than the penultimate on one side, these spines are subequal on the other side of the same specimen. The material also lacks a spine near the anterior extremity of the branchial region as in the account and figure of *C. ortmanni* by Miyake & Baba (1968:386, fig. 3a). We are inclined to believe that the material disscussed by Ogawa & Matsuzaki (1993) is referable to *C. ortmanni.* The re-examination of their material also reveals that the third thoracic sternite bears four or five spines on the anterior margin except for a juvenile specimen from the Ryukyu Islands (CL 1.9 mm, NSMT-Cr 11686, 2 spines), and the fourth thoracic sternite has a bluntly or acutely pointed tubercle, which is sometimes indistinct, on each lateral side.

Chirostylus rostratus resembles *C. novaecaledoniae* in the following: the carapace has a row of dorsal spines along each of the branchial lateral margins; and the fourth thoracic sternite is provided with a distinct lateral spine. However, the former species is distinguishable from the latter by the unarmed posterior gastric and anterior cardiac regions (usually one spine on each the two regions in *C. novaecaledoniae*); the chelipeds and ambulatory legs are covered with numerous spines (less spinose in *C. novaecaledoniae*); and the dactyls of the ambulatory legs have the penultimate spine slightly longer than the ultimate (these spines are subequal in *C. novaecaledoniae*). The very spinose pereopods also seem to link *C. rostratus* to *C. micheleae*. *Chirostylus micheleae,* however, is rather distant from the remainder of the species of the genus, including *C. rostratus,* in the very spinose body, the carapace in particular, and the presence of a dorsomedian projection on the fourth abdominal somite.

The triangular line pattern on the dorsal surface of the carapace as displayed by *C. dolichopus, C. ortmanni,* and *C. novaecaledoniae* is also found in *C. rostratus,* but its coloration is different. *Chirostylus rostratus* possesses a reddish line pattern on the whitish pink ground color, while the other three species have a white or light colored line pattern on the light carrot-orange or reddish purple ground color (Miyake 1960: pl. 48, fig. 8, 1982: pl. 48, fig. 1; Miyake & Baba 1968:385; Baba 1991: 465, fig. 8a, b).

Key to species of the genus *Chirostylus*

1. Carapace covered with numerous spines on dorsal surface. Fourth abdominal somite with distinct median projection on dorsal surface . . . . *C. micheleae*
   Carapace less spinose. Fourth abdominal somite unarmed on dorsal surface. 2
2. Rostral spine longer than epigastric spines. Chelipeds and ambulatory legs very spinose . . . . *C. rostratus*
   Rostral spine shorter than epigastric spines or lacking. Chelipeds and ambulatory legs less or moderately spinose . . 3
3. Carapace with anterior cardiac region bearing spine, branchial regions with row of spines along lateral margins . . . . *C. novaecaledoniae*
   Carapace with anterior cardiac region unarmed, posterior branchial regions unarmed or bearing 1–3 spines near each anterior part of strong lateral concavities 4
4. Spine present near each anterior extremity of branchial regions. Third thoracic sternite with 6 spines on anterior margin. Dactyls of ambulatory legs bearing penultimate spine stronger than ultimate . . . . *C. dolichopus*
   Spine absent near each anterior extremity of branchial regions. Third thoracic sternite with 4 or 5 spines on anterior margin. Dactyls of ambulatory legs bearing penultimate spine subequal with ultimate. . . . . *C. ortmanni*

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We thank Dr. M. Takeda of the National Science Museum, Tokyo, for loaning the comparative material. The Ogasawara specimen was kindly made available from Mr. S. Yokoyama of the Ogasawara Fishermen's Union. We also wish to express our sincere gratitude to Dr. K. Baba of Kumamoto University, Dr. A. B. Williams of the Systematics Laboratory, the National Marine Fisheries Services, Dr. A. L. Rice of the Institute of Oceanographic Sciences Deacon Laboratory, and Dr. R. K. Kropp of Battelle Ocean Sciences, for their valuable comments on the manuscript.

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A new deep-water crab from Belau, Micronesia, with a key to the Pacific species of *Chaceon* (Crustacea: Decapoda: Brachyura: Geryonidae)

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Abstract.—A new species of deep-water geryonid crab is described from Belau in Micronesia. It belongs to the *Chaceon granulatus* species group, but can be distinguished from other members of this group in possessing a relatively flatter carapace and proportionately more elongate male ambulatory legs.

Hastie & Saunders (1992) recently reported the presence of the deep-sea geryonid crab *Chaceon granulatus* (Sakai, 1978) from Belau (= Palau, see Motteler 1986) in Micronesia. The species was also featured in a 1993 stamp depicting the seafood of Palau. *Chaceon granulatus* has also been reported from various parts of central Japan to the northern part of the Ryukyus, Taiwan and possibly East China Sea (Sakai 1978, Miyake 1982, Tung et al. 1988, Ng et al. 1998). A study of these specimens from Belau, however, shows them to represent a distinct species, named here. This crab, while belonging to the *C. granulatus* species group, differs in several diagnostic carapace and ambulatory leg features.

The type specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington (USNM). Other repositories mentioned in the text include: NNM, Nationaal Natuurhistorisch Museum, Leiden; NTOU, National Taiwan Ocean University, Keelung; ORI, Ocean Research Institute, Tokyo; RMNH, TM, Taiwan Museum, Taipei; ZRC, Zoological Reference Collection, Singapore. Measurements are expressed as width by length, in millimeters (mm).

Family Geryonidae Colosi, 1923

Chaceon micronesicus, new species

Figs. 1–3, 6A

Chaceon granulatus.—Hastie & Saunders, 1992:26 [not *Chaceon granulatus* (Sakai, 1978)].

Material examined.—Holotype: male (150.0 by 147.0 mm), Belau, Micronesia, Caroline Islands, North Pacific, coll. L. C. Hastie, 1987 (USNM 221817). Paratype: female (141.0 by 139.0 mm), same data as holotype (USNM 260858).

Description of male holotype.—Carapace semi-quadrate; dorsal surface gently convex transversely and longitudinally; gastric region inflated, granulated, rugose; branchial and posterolateral regions swollen, surfaces distinctly granulated; suborbital, sub-branchial and subhepatic regions smooth; pterygostomial region gently granulose to almost smooth. Front relatively narrow, quadridentate; median teeth acutely triangular, tips slightly anterior of lateral teeth; lateral teeth triangular; distance between median teeth distinctly closer than distance between median and lateral teeth. Supraorbital margin smooth, with small submedian fissure. Infraorbital margin almost smooth or slightly granular, inner edge with sharp, triangular, anteriorly directed tooth. Anterolateral margin convex; first, third and fifth anterolateral teeth largest; first tooth most acute; second tooth very low; fourth tooth hardly or indiscernible. Posterolateral margin gently convex, granulose. Posterior margin of carapace subcristate, sinuous, median margin distinctly concave. Cornea well developed, pigmented. Merus of third maxilliped squarish; external angle low, rounded. Ischium subrectangular, with deep oblique median sulcus. Exopod stout, reaching half to three-quarters length of merus; flagellum long.

Chelipeds subequal in size. Outer surfaces rugose. Merus with sharp subdistal dorsal tooth. Carpus with well developed sharp tooth on distal inner margin. Fingers longer than palm, cutting edges of fingers of larger chela with basal molariform teeth; cutting edges of fingers of smaller chela with well developed teeth and denticles. Legs relatively short; last leg shortest. Dactyli of all legs slender, appearing dorsoventrally compressed, dorsal margin flattened, gently curved downwards, height at midlength subequal to or slightly shorter than width, dorsal margin with deep, distinct median longitudinal groove which may be interrupted at parts; meri relatively stout, laterally compressed, dorsal margin with low, rounded subdistal tooth (sometimes indiscernible), maximum length to width ratio of meri of first to fourth walking legs: male—4.5 and 4.6, 4.7, 4.8 and 4.9, 5.6, respectively; female—4.0 and 4.1, 4.2 and 4.3, 4.3, 4.9, respectively (each specimen is missing two legs).

Surface of anterior thoracic sternum almost smooth; sternites 1 and 2 fused, suture not discernible; sutures between sternites 2 to 6 incomplete, interrupted medially; sutures from sternite 6 onwards complete. Male abdomen triangular, sutures of segments 3–5 distinct, but segments not freely movable; telson broadly triangular, lateral margins gently concave to almost straight. Male first pleopod stout, C-shaped; distal half gently tapering towards subtruncate tip, distal part cylindrical; group of long setae on submedian part of outer margin, distalmost surfaces covered with numerous small, sharp granules. Male second pleopod almost as long as male first pleopod, with elongate distal segment.

Female.—The female paratype differs most distinctly from the male in having the metabranchial regions more strongly rugose and granulose. Whether this is attributable to infraspecific variation cannot be ascertained. In addition, all the ambulatory legs of the female are proportionately shorter than those of the male. Such sexual dimorphism in leg proportions has already been reported for *C. granulatus* and *C. manningi* by Ng et al. (1998).

Color.—The background color of the carapace and appendages of the fresh specimens is beige-brown.

Size.—Hastie & Saunders (1992) reported the following size ranges for the material they examined: males (n = 105), carapace width 124–179 mm; non-ovigerous females (n = 68), carapace width 114–174 mm; ovigerous females (n = 11), carapace width 134–170 mm.

Etymology.—The new species is named after the area where it was found, i.e., Micronesia.

Remarks.—Three species are currently recognized in the *Chaceon granulatus* species group, viz. *C. granulatus* (Sakai, 1978), *C. manningi* Ng, Lee, & Yu, 1994, and *C. karubar* Manning, 1993(a) (see Ng et al. 1998). The present description of *C. micronesicus,* new species, adds a fourth member to this group. These species are all easily recognized by their distinctly granulose carapaces (especially on the metabranchial surfaces) (Fig. 4) and having the ambulatory dactyli dorso-ventrally compressed but with the height at midlength subequal to or greater than the width at midlength. In other *Chaceon* species, the height at midlength of the ambulatory dactyli is distinctly less than the width at midlength (Fig. 5). Of these species, *C. karubar* is distinct being the only species with a well developed

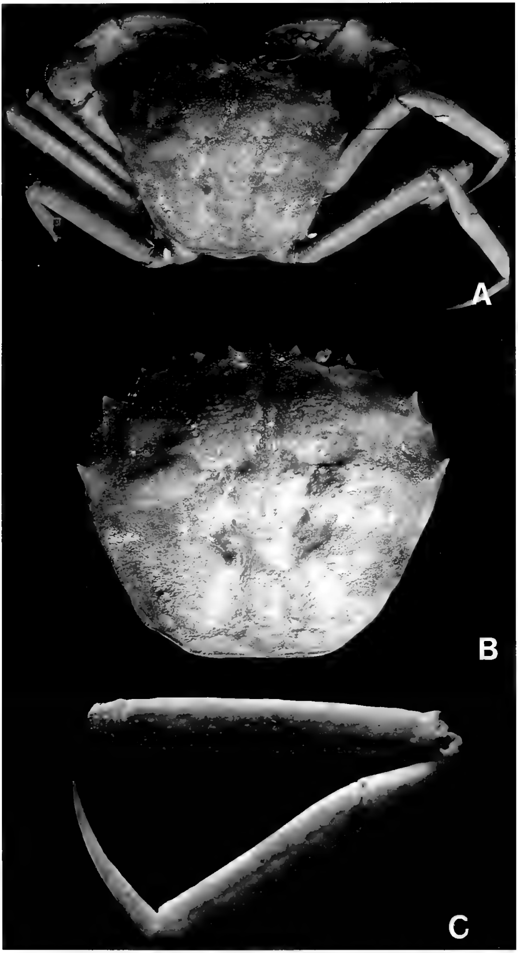

Fig. 1. *Chaceon micronesicus,* new species. Holotype male (150.0 by 147.0 mm) (USNM 221817). A, Overall view; B, Carapace; C, Fourth right ambulatory leg.

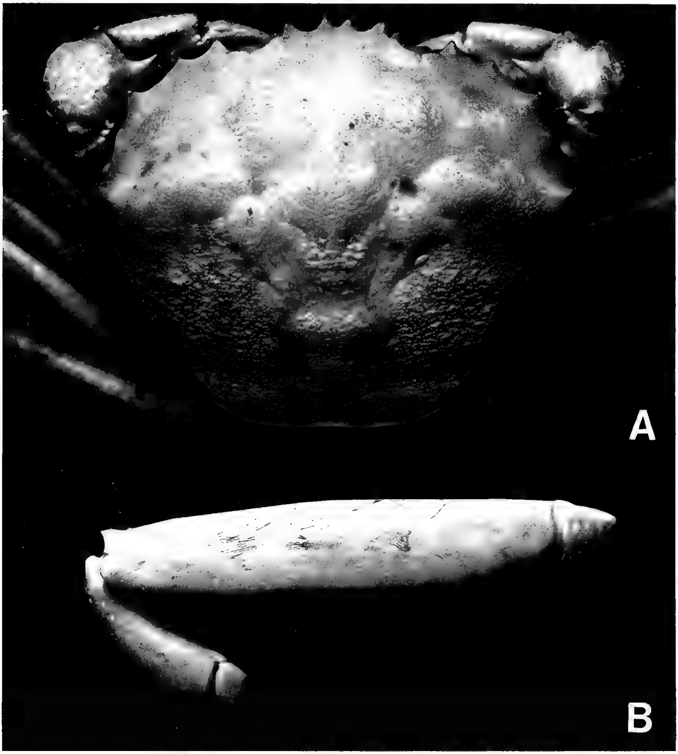

Fig. 2. *Chaceon micronesicus*, new species. Paratype female (141.0 by 139.0 mm) (USNM 260858). A, Carapace; B, Fourth right ambulatory leg.

tooth on the outer surface of the carpus of the cheliped.

Chaceon micronesicus has the flattest and least granulated carapace of all these species, with its posterolateral margins almost straight. These features are most similar to that in *C. bicolor* Manning & Holthuis, 1989, but *C. bicolor*, however, have ambulatory dactyli in which the height at midlength is distinctly less than the width at midlength. In addition, the merus of the fifth ambulatory leg is proportionately shorter and the anterolateral teeth are also more spiniform. The relatively elongate proportions of the last male ambulatory merus allies *C. micronesicus* with *C. manningi*, but the latter species has a distinctly more swollen and granulose carapace (Fig. 5). The four frontal teeth of *C. granulatus*, *C. karubar* and *C. manningi* are all directed distinctly anteriorly, but, in *C. micronesicus*, the lateral teeth are distinctly directed obliquely outwards. The male first pleopod of *C. micronesicus* most closely resembles that of *C. manningi*.

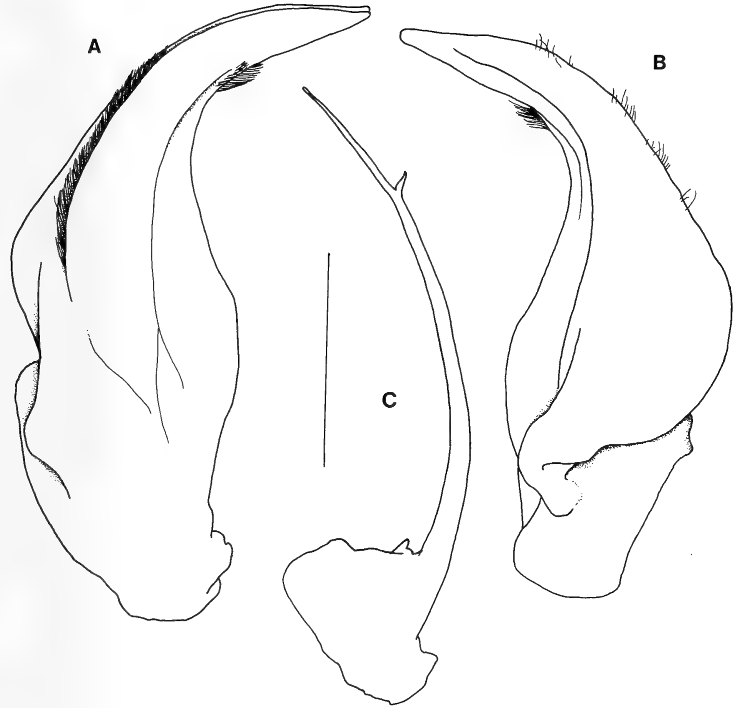

Fig. 3. *Chaceon micronesicus,* new species. Holotype male (150.0 by 147.0 mm) (USNM 221817). A, abdominal face, B, sternal face, left male first pleopod; C, left male second pleopod, sternal face. Scale = 10 mm.

The male first pleopod of *C. micronesicus,* however, is more strongly curved and the distal part is proportionately longer than that of *C. manningi.* Ng et al. (1998) noted that a large male specimen of *C. granulatus* from Taiwan has the distal part of the male first pleopod proportionately longer than typical *C. granulatus* which are smaller, but in *C. micronesicus,* this condition is apparent even for the single small specimen available for study. The abdomens of *C. micronesicus, C. granulatus,* and *C. manningi* are shown in Fig. 6.

The comparative material of *C. granulatus* and *C. manningi* examined for this study is listed below. Of all the syntypes of *C. granulatus* examined now in the Nationaal Natuurhistorisch Museum, Leiden only one specimen measuring 138.8 by 124.3 mm and collected from Sagami Bay in Japan is wet-preserved, in good condition and complete. As such, it is here designated as the lectotype of *C. granulatus* (RMNH D-32228).

The ecology and fishery for this species (as *C. granulatus*) has already been treated at length by Hastie & Saunders (1992).

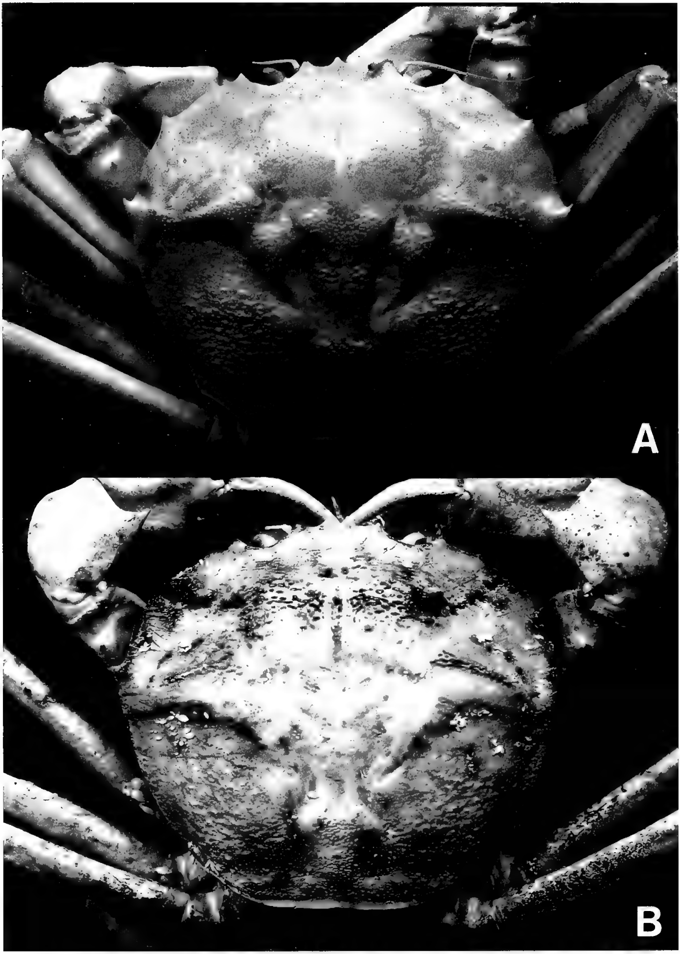

Fig. 4. Carapaces. A, *Chaceon granulatus,* lectotype male (138.8 by 124.3 mm) (RMNH, cat. no. D.32228); B, *C. manningi,* holotype male (185.0 by 159.0 mm) (ZRC, cat. no. 1993.6588).

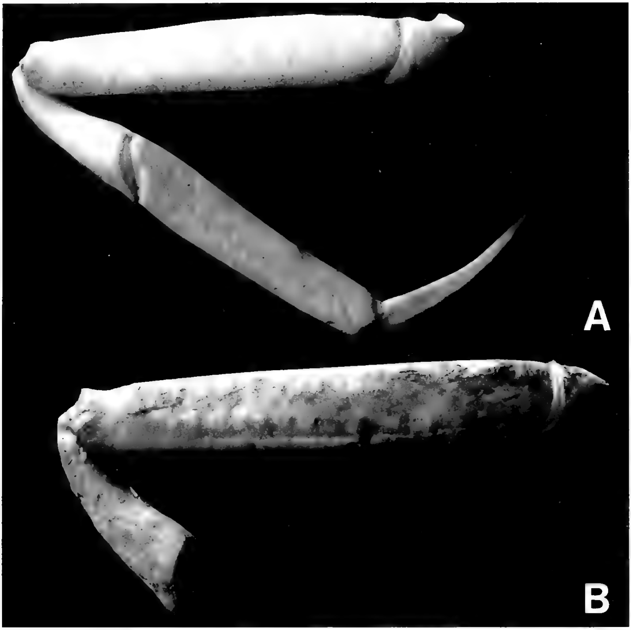

Fig. 5. Left fourth ambulatory legs. A, *Chaceon granulatus,* lectotype male (138.8 by 124.3 mm) (RMNH, cat. no. D.32228); B, *C. manningi,* holotype male (185.0 by 159.0 mm) (ZRC, cat. no. 1993.6588).

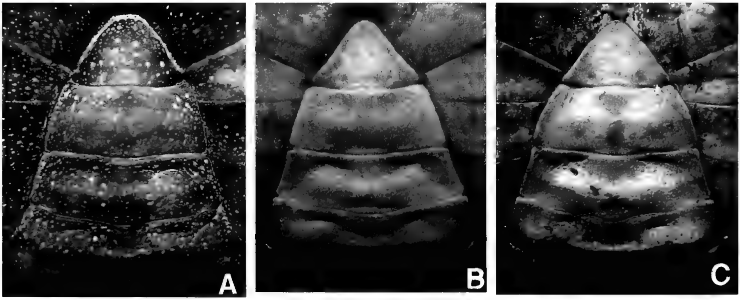

Fig. 6. Male abdomens. A, *Chaceon micronesicus,* new species, holotype male (150.0 by 147.0 mm) (USNM 221817); B, *C. granulatus,* lectotype male (138.8 by 124.3 mm) (RMNH, cat. no. D.32228); C, *C. manningi,* holotype male (185.0 by 159.0 mm) (ZRC, cat. no. 1993.6588).

Comparative material examined.—Chaceon granulatus: Lectotype male (138.8 by 124.3 mm) (NNM, cat. No. D-32228), Hayma, Sagami Bay, Kanagawa-ken, Japan, coll. H. Ikeda, 1977–1978.—2 paralectotype carapaces only (dried) (NNM, cat. no. D-43810, 43811), Kanagawa-ken, Sagami Bay off Hayama, Japan, coll. H. Ikeda, 1978.—1 male (dried) (177.6 by 179.3 mm) (USNM 32006), Japan, from Ward's National Science Establishment.—1 male (164.0 by 144.3 mm) (ORI), station SE-01, KT-93-09, hydrothermal vent, South Ensei Knoll, Japan, coll. Sep 1993.—1 male (190.0 by 182.0 mm), 1 female (180.0 by 173.0 mm) (NTOU), port at Tai-Chi, I-Lan County, northeastern Taiwan, ca. 450 m depth, sandy-muddy bottom, by inshore commercial trawlers, coll. T. Y. Chan, 2 Nov 1995.—1 male (197.0 by 178.0 mm) (ZRC), 1 male (170.0 by 153.0 mm) (NTOU), probably from deep waters in East or South China Sea, Taiwanese commercial offshore trawlers, coll. P. K. L. Ng, Aug 1996.

Chaceon manningi: Holotype male (185.0 by 159.0 mm) (ZRC, cat. no. 1993.6588), paratype male (187.0 by 167.0 mm) (NTOU, cat. no. 1991-618), Tung-Sa Islands, South China Sea, 438–636 metres depth, coll. D. A. Lee, 13 Jun 1991.—1 male (200.0 by 195.0 mm), 2 females (129.0 by 127.0 mm, 142.0 by 139.0 mm) (NTOU), Tung-Sa Islands, South China Sea, coll. D. A. Lee, no date.—3 males (192.0 by 201.0 mm, 206.0 by 201.0 mm, 158.0 by 155.0 mm) (ZRC), 1 male (193 by 170 mm) (TM), probably from deep waters in East or South China Sea, Taiwanese commercial offshore trawlers, coll. P. K. L. Ng, Aug 1996.—1 male (162.0 by 141.0 mm) (ORI), station HY-04, KT-93-09, hydrothermal vent, Hyuga Nada, Japan.

Key to Pacific species of *Chaceon*

1. Dactylus of ambulatory legs dorsoventrally flattened, height at midlength 0.8 times or less than width at midlength .. 2
— Dactylus of ambulatory legs laterally flattened, height at midlength subequal to or greater than width at midlength (0.9 times and above) 6
2. Merus of ambulatory leg with distinct dorsal subdistal spine or tooth 3
— Merus of ambulatory leg unarmed, without distinct dorsal subdistal spine or tooth 5
3. Anterolateral margins of adults with low, lobiform teeth .... *C. bicolor* Manning & Holthuis, 1989
— Anterolateral margin of adults with spiniform teeth 4
4. Dorsal margins of merus and carpus of ambulatory legs smooth; merus of fifth male ambulatory leg 5.9–6.0 times longer than high .... *C. australis* Manning, 1993(b)
— Dorsal margins of merus and carpus of ambulatory legs gently serrated; merus of fifth male ambulatory leg 5.1–5.3 times longer than high ...... *C. yaldwyni* Manning, Dawson, & Webber, 1990
5. Anterolateral teeth distinct, sharp, carapace appearing more hexagonal; merus of male fifth ambulatory leg 4.3–4.4 times longer than high .... *C. imperialis* Manning, 1992
— Anterolateral teeth very low, carapace appearing very rounded; merus of male fifth ambulatory leg 5.1–6.0 times longer than high ..... *C. poupini* Manning, 1992
6. Outer surface of chelipedal carpus with spine or projection; merus of ambulatory legs with distinct dorsal subdistal spine or tooth .... *C. karubar* Manning, 1993(a)
— Outer surface of chelipedal carpus unarmed; merus of ambulatory legs unarmed, without distinct dorsal subdistal spine or tooth 7
7. Merus of male fifth ambulatory leg 4.6–5.1 times longer than high .. *C. granulatus*
— Merus of male fifth ambulatory leg 5.2–5.6 times longer than high 8
8. Metabranchial regions low; posterolateral margins almost straight; not distinctly swollen .... *C. micronesicus*, new species
— Metabranchial regions swollen; posterolateral margins distinctly convex .... *C. manningi*

Acknowledgments

The senior author is grateful to S. H. Tan for his help with the present study and taking the necessary photographs. This study has been partially supported by a research grant to the senior author from the National University of Singapore (RP 950326). This is contribution number 98/3 of the Systematics and Ecology Laboratory, National University of Singapore.

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A new ghost shrimp of the genus *Lepidophthalmus* from the Pacific coast of Colombia (Decapoda: Thalassinidea: Callianassidae)

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Abstract.—*Lepidophthalmus rafai* is described from an intertidal shoreline in the vicinity of Buenaventura, Pacific coast of Colombia, South America. While recent collecting has uncovered populations assignable to described and undescribed species of the genus in intertidal habitats of the tropical eastern Pacific, most of these are forms with a ventrally plated or armed abdomen and a strongly trilobate posterior margin on the telson, features that suggest close relationship to *L. bocourti* (A. Milne Edwards) or *L. eiseni* Holmes. The new species is smaller in size than its congeners and is the most southerly distributed species of the genus known from the eastern Pacific. It lacks conspicuous sclerotized plates on ventral surfaces of the abdomen, a feature that it shares with a pair of antitropically distributed species in the western Atlantic. The two Atlantic forms, and the herein described new Pacific species, may have diverged from common stock partitioned by closing of the Panamanian Isthmus. The occurrence of *L. rafai* in a perturbated, hypoxic estuarine habitat is consistent with tolerances and adaptations documented previously for other species of the genus.

Previous reports of the ghost shrimp genus *Lepidophthalmus* Holmes, 1904, from Colombia have included materials of an endemic species, *L. sinuensis* Lemaitre & Rodrigues, 1991, limited in distribution to a restricted area of the Caribbean coast (Lemaitre & Rodrigues 1991, Felder et al. 1995, Nates et al. 1997), and materials assigned to *L. bocourti* (A. Milne Edwards, 1870) from Malaga Bay and Gorgona island on the Pacific coast (Lemaitre & Ramos 1992, Lemaitre & Alvarez-León 1992). All of these specimens exhibit a characteristic armor of sclerotized plates on ventral surfaces of the anterior abdominal somites (Felder & Manning 1997) and/or have a strongly trilobate posterior margin on the telson.

In the course of our ongoing studies of *Lepidophthalmus* spp. in the eastern Pacific, which includes populations from Mexico to Colombia, we have found that previously unrecognized variation in pattern and sculpture of ventral sclerites and other structures may be of value in distinction of *L. bocourti, L. eiseni* Holmes, 1904, and other regional forms, most of which appear to be closely related to one another. These, including the aforementioned materials of *L. bocourti* from Colombia and other eastern Pacific materials previously reported as either *L. bocourti* or *L. eiseni* will be treated together in a forthcoming revision. However, a single eastern Pacific lot of five specimens from the coast of Colombia lacks both abdominal sclerotization and a strongly trilobate posterior margin on the telson. On the basis of these unique specimens, we herein describe a new species and suggest it to represent the first known eastern Pacific cognate of two similarly unarmed western Atlantic forms, *L. louisianensis* (Schmitt, 1935) and *L. siriboia* Felder & Rodrigues, 1993.

As members of the genus *Lepidophthalmus* are known to exhibit an abbreviated larval life history with limited planktonic dispersal (Felder et al. 1991, Manning & Felder 1991, Nates et al. 1997), it is perhaps not surprising that regionally endemized populations and undescribed species continue to be found in the course of sampling infauna from isolated river mouths and coastal estuaries of the tropical Americas. However, throughout this region, rapidly expanding maricultural, urban and port development activities now threaten to alter distributions of these populations by way of both habitat modification and cross-seeding of regionally endemized forms. Given their at least short term negative impacts on shrimp production (Felder et al. 1995, Nates & Felder 1998), opportunistic species such as *L. sinuensis* that invade and densely colonize penaeid culture ponds in tropical estuaries are considered pest species for which extermination and control measures are being sought. The above issues compel urgency for thorough understanding of diversity, systematic relationships and ranges for this taxocene, both to gain zoogeographic insights from natural distributions and to predict impacts of regional anthropogenic developments.

Material examined is listed by location followed by date, collector, number of specimens by sex, size in parenthesis, and museum number. Size is expressed as postorbital carapace length (CL) or postorbital total length with the abdomen extended (TL) and measured in millimeters (mm). The holotype and paratype females of *L. rafai* have been deposited in the National Museum of Natural History Smithsonian Institution, Washington, D.C. (USNM); the paratype male has been deposited in crustacean collections of the Museo de Historia Natural del Instituto de Ciencias Naturales de la Universidad Nacional de Colombia, Santa Fe de Bogotá (ICN-MNH-Cr). Holdings of the USNM and The University of Southwestern Louisiana Zoological Collections (USLZ) were the source for comparative materials of *L. louisianensis* from the Gulf of Mexico and *L. siriboia* from Brazil, as well as most examples of congeneric populations from the eastern Pacific. Comparison to the male holotype of *L. bocourti* was made while that specimen, MNHN Th. 64, was on loan to us from the Muséum National d'Histoire Naturelle, Paris. Comparison to what are possibly the eastern Pacific type specimens of *L. eiseni* was based upon examination of cataloged lot number MCZ 4370, provided on loan from the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; compelling evidence for these being the probable types was presented by Biffar (1972:69–70).

Systematics

Lepidophthalmus Holmes, 1904

Diagnosis.—See Manning & Felder, 1991.

Lepidophthalmus rafai, new species

Figs. 1a–h, 2a–h, 3a–i

Material examined.—Holotype: Beach at Playa Basura, Bahía de Buenaventura, Pacific coast of Colombia, 3°53′48″N, 77°05′12″W, 18 Oct 1991, coll. J. Tovar, 1 male (CL 6.0 mm), USNM 260797. Paratypes: Same location, date, coll., 1 male (CL 7.2 mm), ICN-MNH-Cr 1678; 3 females (CL 5.1, 6.6, 6.8 mm) USNM 259407.

Diagnosis.—Rostrum acute, flanked by low angular shoulders lateral to eyestalks. Branchiostegite with sclerotized boss in anterior ⅓. Ventral margin of cheliped merus strongly bicarinate. Dactyl of major chela in male with subrectangular prehensile tooth near ⅖ length, separated by notch from broad, subtriangular distal tooth. Second abdominal somite lacking sclerotized

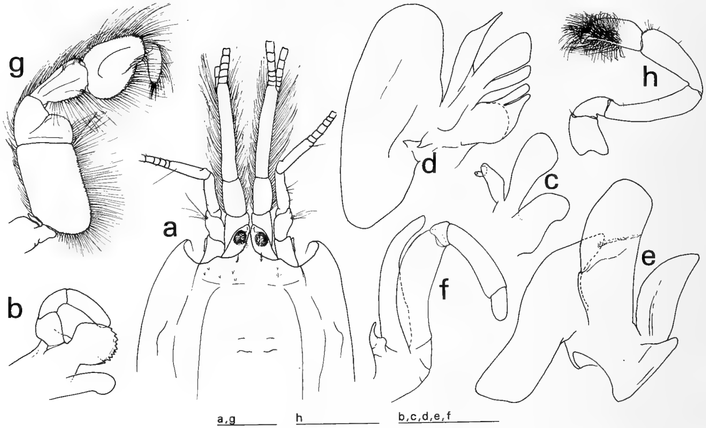

Fig. 1. *Lepidophthalmus rafai,* new species, holotype male from Bahía de Buenaventura, Pacific coast of Colombia, USNM 260797 (CL 6.0 mm): a, anterior carapace, eyestalks and antennae, dorsal surface; b, right mandible and paragnath, external surface, setation not shown; c, right first maxilla, external surface, setation not shown; d, right second maxilla, external surface, setation not shown; e, right first maxilliped, external surface, setation not shown; f, right second maxilliped, external surface, setation not shown; g, right third maxilliped, external surface; h, right fifth pereiopod, external surface. Scale lines indicate 1.0 mm.

ventromedial plate. Appendix interna of male second pleopod small, not reaching to end of endopod. Second through fifth pleopods lacking distolateral spine on anterior surface of basis. Telson broad, subovoid, posterior margin not strongly trilobate. Uropodal endopod broadly suboval to subrhomboid, about 1.5 times longer than broad.

Description.—Frontal margin of carapace with acute, narrow rostral spine flanked laterally by low, weakly angular shoulders (Fig. 1a), apices of which are immediately lateral to eyestalks; rostral spine directed anteriorly, extending about ¾ length of eyestalks in dorsal view, base of spine ventrally with tuft of setae, longest of which extend anteriorly between eyestalks beyond cornea. Carapace anterior to dorsal oval with several pairs of short setose punctae on either side of midline and scattered smaller punctae laterally, some longer setae plumose; dorsal oval well defined, smooth, usually with pair of widely separated setal punctae anterior to midlength, length of oval slightly more than $^{9}/_{10}$ of postrostral carapace length; marginal suture of oval diminished at anterior midline, stronger and with sclerotized articulation to cardiac region at posterior midline; branchiostegite with low, sclerotized boss in anterior ⅓.

Eyestalks subtriangular in dorsal view, reaching to or beyond ¾ length of basal antennal article; anterolateral margins tapered to thin, arcuate flange, dorsomesial margin thickened to form low marginal ridge or poorly defined tubercle in distal ¼, ridge extending to blunt terminal protuberance of eyestalk (Fig. 1a); distinct, pigmented cornea centered on dorsal surface, area of pigmentation often broader than faceted surface. Antennular peduncle longer and slightly heavier than antennal peduncle; basal article dorsally invaginated to form statocyst occluded by setae, overlain by eyestalk; length of second article subequal to that of basal article, third article about 2.5 times length of second; second and third articles with dense, ventromesial and ventrolateral rows of long, ventrally directed setae; rami of flagellum slightly longer than third article of peduncle, ventral ramus slightly longer, narrower, and with much denser, longer setation than dorsal ramus, subterminal articles of dorsal ramus much broader than those of ventral ramus and fringed with short, dense ventral setae. Antennal peduncle reaching barely beyond midlength of third article of antennular peduncle; basal article with dorsolateral carina strong proximally, forming lip above excretory pore, ventrally with setose distomesial protuberance; second article with distal field of long setae on lateral boss; third article elongate, slightly shorter than combined lengths of first two, slightly shorter than fourth, laterally with few long setae; fourth article narrower than others, setation limited to few long subterminal setae; flagellum with sparse short setae, about 3 times length of antennular flagella.

Mandible (Fig. 1b) with large, setose, 3-segmented palp, elongate third article of palp compressed distally, becoming subspatulate, weakly truncate terminally; gnathal lobe of mandible with weakly angular distolateral shoulder, incisor process with well-defined corneous teeth on cutting margin, concave internal surface with lip giving rise to molar process with a corneous tooth proximal and internal to incisor teeth; thin, rounded paragnath set against proximal convex surface of molar process. First maxilla (Fig. 1c) with endopodal palp narrow, terminal article deflected at poorly defined articulation; proximal endite with mesial margin sinuous, distal endite elongate, terminally broadened and with dense spiniform setation; exopodite low, rounded. Second maxilla (Fig. 1d) with margins setose, endopod narrowed terminally, first and second endites each longitudinally subdivided, exopod forming large, ovoid scaphognathite. First maxilliped (Fig. 1e) with margins setose, endopod rudimentary, overlain by distal endite; proximal endite angular, coarsely setose distomesial corner directed to internal side of endite; distal endite subovoid, narrowed distally, proximal ³⁄₅ of external surface with longitudinal carina, mesial half densely setose; exopod incompletely divided by oblique suture, lateral margin near midlength offset to form slightly produced corner at intersection with suture, mesial margin with comb of close-set long setae, external face with dense field of mesially directed setae distal to oblique suture; epipod large, broad, anterior end strongly tapered. Second maxilliped (Fig. 1f) with margins setose, endopodal merus and propodus arcuate, both slightly broader distally than proximally, flexor margin of merus with comb of long setae, internal surface produced distally to form rounded lobe extending over internal surface of short carpus; merus length 3.0–3.5 times width; propodus length about ⅔ length of merus, longest setae originating on extensor margin and distal half of external surface; dactylus almost twice as long as broad, terminally rounded, distal half bearing stiff setae; exopod narrow over most of length, width at ¾ length about ½ of width at ¼ length, overreaching endopodal merus, arcuate, terminally rounded; bilobed epipod with broad basal lobe, narrow tapered, weakly hooked distal lobe. Third maxilliped (Fig. 1g) with small, naked, terminally acute, rudimentary exopod and large setose endopod; endopodal ischium subrectangular, length less than 2 times width, internal surface with weak, unarmed longitudinal carina, strongest proximally; merus subtriangular, broader than long, mesial margin forming a distinct rounded lobe; carpus subtriangular, longer than broad; terminal articles twisted, directing tip of dactyl toward posterior; propodus large, subovoid, slightly longer than broad; dactylus narrow, arcuate proximally, long setae of extensor and distal margins including a few long stiff bristles at terminus.

Branchial formula as reported for congeners (Lemaitre & Rodrigues 1991:625,

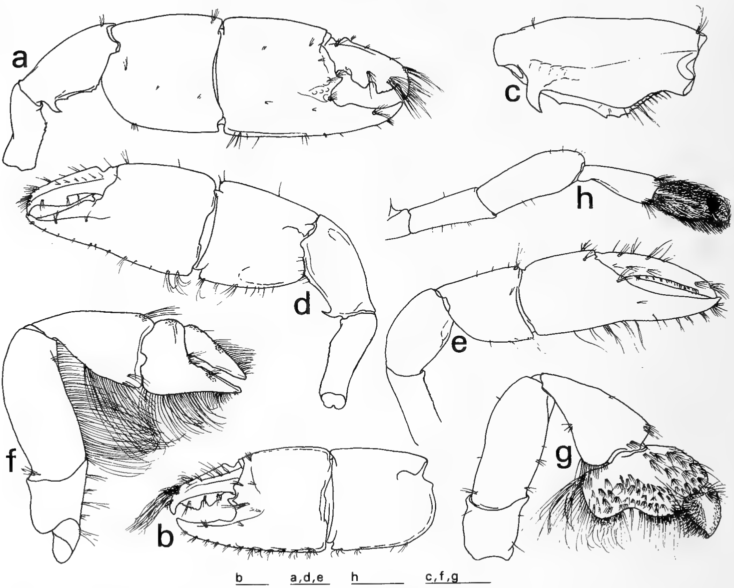

Fig. 2. *Lepidophthalmus rafai,* new species, type specimens from Bahía de Buenaventura, Pacific coast of Colombia. Holotype male, USNM 260797 (CL 6.0 mm): a, major cheliped, external surface; b, major chela, internal surface; c, merus of major chela, external surface; f, right second pereiopod, external surface; g, right third pereiopod, external surface. Paratype female, USNM 259407 (CL 6.6 mm): d, major chela, internal surface; h, right fourth pereiopod, external surface. Paratype male, ICN-MNH-Cr 1678 (CL 7.2 mm): e, minor cheliped, external surface. Scale lines indicate 1.0 mm.

Felder & Rodrigues 1993:363, 369–370); endopods and epipods as described above, branchiae limited to single rudimentary arthrobranch on second maxilliped, pair of arthrobranchs on third maxilliped, and pair of arthrobranchs on each of the first through fourth pereiopods.

Major cheliped located on either right or left side of body, shape and ornamentation sexually dimorphic. Major cheliped of male (Fig. 2a–c) massive, more strongly armed than that of female; ischium slender, superior margin sinuous, row of small denticles on proximal ⅔ of inferior (flexor) margin, row usually terminated distally with a few stronger, sometimes hooked teeth; merus (Fig. 2c) with broad, shallow notch in proximal ⅕ of superior margin, inferior (flexor) margin subangular, with strong proximal hook at base of bicarinate keel, external carina unarmed, internal carina forming inferior margin bearing (usually 4–6) small distally directed or slightly hooked denticles, most of which are positioned near or distal to angular bend of inferior margin; external surface of article weakly eroded above proximal hook; carpus broad, subquadrate, superior and inferior margins keeled, near parallel to weakly convergent in distal half, terminated distally in angular corners. Propodus of male major chela broad, heavy, length of fixed finger markedly exceeding

½ length of palm; inner surface of palm (Fig. 2b) smooth proximally, with few setose punctae along unarmed carina extending onto fixed finger; outer surface (Fig. 2a) with short unarmed longitudinal carina and adjacent weakly tuberculate depression extending proximally from gape of fingers; distinct keel of superior propodal margin terminating just short of distal articulation with dactylus, keel of inferior margin distinct proximally, extending onto fixed finger, distally diminished and overlain by setose punctae; subtriangular, superodistally directed tooth at proximal end of gape, tooth undercut by broadly U-shaped notch at base of fixed finger, notch terminated distally by low prehensile tooth near ⅓ length of fixed finger; fixed finger with well defined separation of inner and outer prehensile margins, inner margin unarmed; dactylus with hooked tip, superior margin with erect tubercle at proximal end, inferior surface with unarmed, weakly developed inner margin, outer prehensile margin usually with two large, variously subdivided prehensile teeth, subrectangular proximal tooth centered near ⅖ length, separated by a U-shaped notch from broad, often subtriangular distal tooth, distal shoulder of which is typically cut into a series of small teeth running distally.

Major cheliped of female less massive (Fig. 2d), less strongly armed than that of male; merus with weak distal dentition on outer inferior carina than in male; outer prehensile margins of fixed finger and dactylus weakly serrate, dactyl relatively less massive and fixed finger broader than in males, notch at base of fixed finger very narrow; superior and inferior margins of propodus distinctly converging distally, inferior margin broadly sinuous; when fingers closed, dactyl usually overreaching fixed finger, tips slightly crossing, gape filled except for deepest part of notch at base of fixed finger.

Minor cheliped (Fig. 2e) sparsely armed; ischium with row of minute denticles or tubercles on most of flexor margin; merus unarmed; carpus with angular distal corners. Minor chela with fixed finger bearing tufts of short setae on proximal ⅗ of outer prehensile margin, prehensile surface lacking excavate area of dense setation, gape between fingers narrow; dactylus with inferior (prehensile) surface mostly unarmed over proximal ⅗, subterminally with minute corneous serrations on outer prehensile margin, fingers terminating in corneous tips.

Second pereiopod (Fig. 2f) chelate, flexor margins of merus and distal ⅔ of carpus lined with evenly spaced long setae, inferior margin of propodus weakly concave, with setae long proximally, reduced in length to short bristles distally, subterminally with separated minute tuft of short, stiff bristles; middle ⅓ of fixed finger with patch of short, stiff bristles just outside prehensile margin; tips and prehensile margins of both fingers corneous; granulated superior margin of dactylus with stiff, arched bristles reduced in length distally. Third pereiopod (Fig. 2g) merus length about 2.4 times width; propodus with inferodistal margin bilobate and separated from articulation of dactylus by external furrow, lobes demarcated by furrows on internal surface, distal margins of both lobes with bristles longest on weakly scalloped margins, those in distal half of upper lobe partially concealing 1–2 prominent, corneous, distally directed teeth arising from margin; longest setae on inferior margin of lower lobe, patterned tufts of lighter setae on outer face of article; dactylus subtriangular, superior margin granulated, weakly sinuous, narrowed distally to short ventrolaterally directed corneous tooth, outer surface with row of stiff bristles lining inferior margin, fields of finer setae above. Fourth pereiopod (Fig. 2h) weakly subchelate, inferodistal process of propodus (= fixed finger) a weak angular lobe extended distally about ⅓ length of dactylus, lower margin of lobe with usually 3–4, well developed, articulated corneous spines, often obscured by dense brush of stiff setae, dactylus subtriangular, superior margin arched, narrowed distally to short ventrolaterally directed corneous tooth. Fifth pereiopod (Fig. 1h) minutely chelate, opposable surface of minute dactylus spooned, terminally rounded, cupping short blunt fixed finger to form beak-like chela obscured by dense fields of setation on distal ⅔ of propodus and superior surface of dactylus.

Abdominal somites mostly smooth dorsally, glabrous; first abdominal tergite thin and translucent dorsally, enclosed anteriorly and laterally by narrow marginal sclerite, arms of which diverge toward posterior of somite; marginal sclerite articulated anterolaterally to narrow arched lateral carina, extending anteroventrally toward thorax; second tergite poorly sclerotized, small tuft of long setae at posterolateral extreme; third-fifth tergites each encompassing a finely setose, lateral, membranous subcircular or suboval area below a weak posterolateral suture, that of the third tergite larger, more circular and more posterolaterally positioned than in the fourth and fifth tergites; sixth tergite (Fig. 3i) with 2 posterolateral lines of short setae anterior to posterolateral groove from which transverse suture originates, longest line adjacent and subparallel to transverse suture, weakly defined posterior suture directed anteriorly, tufts of stiff setae on posterolateral corners, and usually as 4 short lines or tufts of stiff setae on posterior margin. Ventral surfaces of abdominal somites without conspicuous armor of plates or tubercles.

First pleopod of male and female uniramous, composed of 2 articles; in male, weak suture separating articles (Fig. 3a–c), appendage length about ½ that of second pleopod, proximal article less than 2 times length of terminal article, terminal article flattened, bifurcate, anterolaterally directed tip with several terminal denticles, both tips with long subterminal setae (bases of which are densely fouled by small fungal hyphae in holotype); in female (Fig. 3d), extended length subequal to that of second pleopod, proximal article slightly shorter and heavier than terminal article, terminal article narrowed to spatulate blade beyond midlength, both articles bearing long setae. Second pleopod of male and female biramous, with appendix interna on endopod; appendix interna of male (Fig. 3e, f) small, not reaching to tip of endopod, terminally subacute, subterminal shoulder with field of minute, rudimentary hooked setae (fouled by longer fungal hyphae in holotype); in female (Fig. 3g), both rami setose, appendix interna small, slightly elongate. Basis of second through fifth pleopods with, at most, a low tubercle or tooth on anterior surface at articulation with exopod. Third to fifth pleopod pairs forming large, posteriorly cupped fans when cross-linked by hooked setae of appendices internae on opposed margins of endopods; endopod of each subtriangular (Fig. 3h) articulation of stubby appendix interna embedded into mesial margin. Telson (Fig. 3i) broad, subovoid, width about 1.4 times length, posterior margin weakly to indiscernibly trilobate, median lobe most pronounced; dorsal surface usually with pair of setal tufts near midlength; lateral margins typically with pair of setal tufts near midlength, posterior margin with distinct tuft on each of weak posterolateral lobes. Uropod (Fig. 3i) with short, angular, posteriorly directed prominence on protopod and short, posteromesially directed tooth on proximal article of exopod, both abutting or overreaching anterior margin of extended endopod; endopod broadly ovoid to subrhomboidal, about 1.5 times longer than broad, rounded terminus bearing marginal fringe of long setae, posteromesial margin with isolated tufts of setae; exopod with anterodorsal plate falling well short of distal endopodal margin, posterodistal edge of plate with short, thick, spiniform setae grading to thinner, dense, elongate setae of exopod margin; distal margin of exopod with dense fringe of setation, longest posteriorly.

Size.—Apparently smaller than known congeners, on the basis of present materials which appear to be mature or nearly so. In postorbital length, measured after preservation, the largest male is CL 7.2 mm, TL 30.5 mm; the largest female CL 6.8 mm,

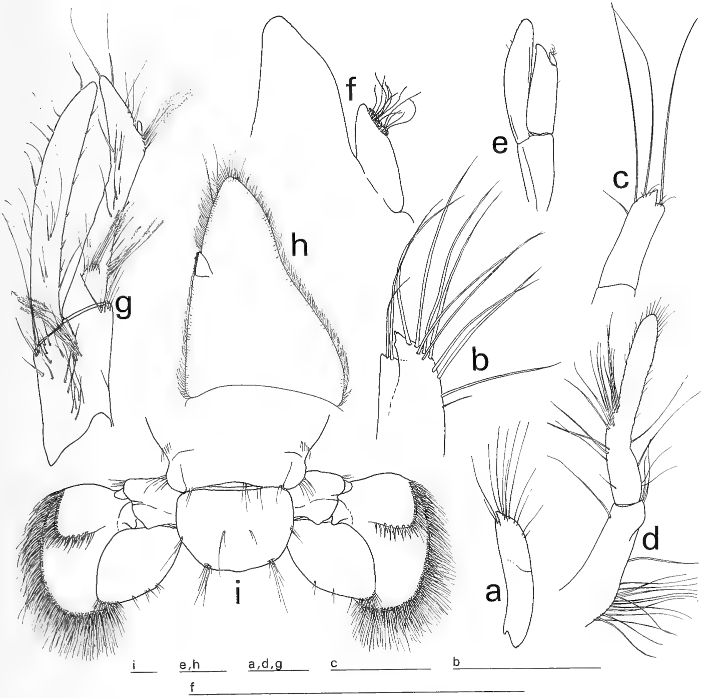

Fig. 3. *Lepidophthalmus rafai,* new species, type specimens from Bahía de Buenaventura, Pacific coast of Colombia. Holotype male, USNM 260797 (CL 6.0 mm): a, right first pleopod (gonopod), external surface; b, right first pleopod (gonopod), terminus; e, right second pleopod, posterior surface; f, right second pleopod, appendix interna and terminus of endopod; i, sixth abdominal somite, telson and uropods, dorsal surface. Paratype male, ICN-MNH-Cr 1678 (CL 7.2 mm): c, left first pleopod (gonopod), external surface. Paratype female, USNM 259407 (CL 6.6 mm): d, right first pleopod, external surface; g, right second pleopod, posterior surface; h, endopod of right third pleopod, anterior surface. Scale lines indicate 0.5 mm.

TL 30.0 mm. Egg size is unknown, as no ovigerous specimens have been collected to date. Sampling conducted by J. Tovar at the type locality was limited to the upper 20 cm of sediment (G. E. Ramos, Universidad del Valle, Cali, Colombia, pers. comm.), and larger individuals of the population thus may not have been captured.

Habitat.—Known from only the type locality at Playa Basura (meaning "Garbage Beach" in English), Bahía de Buenaventura, Pacific coast of Colombia. According to notes furnished by G. E. Ramos (Universidad del Valle, Cali, Colombia, pers. comm.), the low-gradient intertidal habitat is very muddy and heavily contaminated by organic material from a nearby sewage outfall ("aguas negras" in Spanish) from the nearby city of Buenaventura. The area has also been impacted previously by cutting of mangroves and dredging of a port for tourist traffic. Subsequently, walls to retard erosion have been constructed along 300–400 m of coastline here, and sandy materials have begun to accrue which have somewhat indurated selected areas of the muddy substrate.

Etymology.—The species is named in recognition of many contributions by our friend and colleague, Rafael Lemaitre, to the study of decapod crustaceans. Known to many friends by the nickname "Rafa", Dr. Lemaitre's extensive publications and generous assistance to colleagues have substantially improved systematic understanding of many decapod assemblages, in both his native Colombia and abroad.

Remarks.—Lepidophthalmus rafai differs from known populations of congeneric eastern Pacific species in lacking a strongly trilobate posterior margin on the telson, such as was figured by Bott (1955: fig. 7g) and Biffar (1972: fig 17a). In addition it lacks well developed sclerotized plating on membranous ventral surfaces of the anterior abdominal somites, which is particularly evident in the absence of a large ventromedial plate on the second abdominal somite. Such plates, varying from subquadrate to near hourglass in shape, are conspicuously evident in the very large (CL 24.5 mm) male holotype specimen of *L. bocourti* (A. Milne Edwards, 1870) (MNHN Th. 64) from "La Union" (likely the shores of Golfo de Fonseca, El Salvador) and in the comparably large (CL 25.0–26.0 mm) male and female probable type specimens of *L. eiseni* Holmes, 1904 (lot number MCZ 4370) from the southern tip of the Baja California peninsula. This ventral abdominal plating was also perviously described in part for specimens of *L. eiseni* reported from El Salvador (Holthuis 1954:12–13).

Such plates and other extensive ventral sclerotization are evident on close inspection of recently collected smaller individuals that we assign to either of the aforementioned species, including several specimens which are comparable in size to the type series of *L. rafai.* Additionally, the first through fifth pleopods in *L. rafai* lack a distolateral spine on the anterior surface of the basis, a characteristic feature of adults and juveniles in both sexes of *L. bocourti.*

Provided that presently available small specimens of *L. rafai* accurately represent the approximate mature size and configuration of secondary sexual structures, males of this new species may also differ from both *L. bocourti* and *L. eiseni,* as well as from other undescribed eastern Pacific specimens of the genus available to us, in the diminutive size of the appendix interna on the second pleopod. In both *L. bocourti* and *L. eiseni,* the appendix interna of this appendage is usually comparable in size to the terminal lobe of the endopod and is adorned with elongate terminal setae, much as in the Caribbean species *L. jamaicense* (Schmitt 1935) (Felder & Manning 1997: fig. 1h). However, at sizes comparable to our small specimens of *L. rafai,* specimens of *L. bocourti* and *L. eiseni* do not always exhibit secondary sexual characters of mature form.

Over the full size range of available specimens, including sizes comparable to the types of *L. rafai,* specimens of both *L. bocourti* and *L. eiseni* appear to have smaller, narrower uropodal endopods (relative to exopods) than do specimens of *L. rafai.* In addition, *L. rafai* has a very strongly developed bicarinate, rather than weakly bicarinate or single, ventral margin on the merus of the major cheliped. While such bicarination of the meral margin is also evident in type materials of *L. eiseni* and most other congeneric eastern Pacific materials that we have seen (the chela is lacking in the type of *L. bocourti*), it is often poorly defined or limited to the anterior or posterior half of the ventral margin, especially in specimens comparably sized to those of *L. rafai.*

Absence of the ventral abdominal plating also distinguishes *L. rafai* from the Caribbean species *L. jamaicense, L. sinuensis, L. richardi* Felder & Manning, 1997, and an undescribed population from the southwestern Gulf of Mexico. However, it shares the absence of such armor with at least *L. louisianensis* from the northern Gulf of Mexico and *L. siriboia* from Brazil, antitropically distributed western Atlantic species that closely resemble *L. rafai* and perhaps shared a common lineage with this eastern Pacific form preceding their separation from it by the Panamanian Isthmus. *L. rafai* further resembles *L. siriboia* in having a distinct bicarinate ventral margin on the merus of the major cheliped, forming a longitudinal groove between the carinae. It differs from *L. siriboia* and many other congeners in sculpture of the major chela, the dactylar dentition of which most resembles that of *L. louisianensis,* and in having a pronounced mesial lobe on the merus on the third maxilliped.

The materials of *L. rafai* were discovered by J. Tovar in the course of a search for bioindicator species in a heavily contaminated environment. It is noteworthy that other members of the genus are also known to flourish in such richly organic and hypoxic environments (Felder 1979, Felder et al. 1995, Nates & Felder 1998), where they apparently tolerate or perhaps derive some benefit from elevated concentrations of reduced minerals or nutrients, sometimes to the apparent detriment of animals in the overlying water layer (Nates & Felder 1998). Recent evidence of an intrinsic ability for sulfide metabolism in several eastern Atlantic thalassinid genera (*Calocaris, Callianassa,* and *Jaxea*), and the suggestion that this mechanism may provide an ancillary energy source for those burrowing animals (Johns et al. 1997) raises the likelihood that such pathways could also operate in members of *Lepidophthalmus,* including *L. rafai.* We are aware of no other callianassid genus that so readily invades, colonizes, and deeply burrows into organically rich estuarine sediments, including those that are strongly hypoxic and sometimes sulfidic. Much as eastern Atlantic mudshrimp are among the few species to survive in sediments of sea lochs where placement of commercial fish cages has intensified hypoxia and hypercapnia (Atkinson 1987), members of the genus *Lepidophthalmus* can be expected to sometimes survive and perhaps thrive as a dominant macrofaunal form in those coastal American habitats subject to organic and nutrient loading from sewage effluents, maricultural operations, and other sources of eutrophication (Felder & Griffis 1994, Nates & Felder 1998).

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Eohalimede sandersi, the correct name for the species described as *Eohalimede saundersi* Blow & Manning, 1997 (Crustacea: Decapoda: Xanthidae)

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The species name of the fossil xanthid crab that we dedicated to Albert E. Sanders of The Charleston Museum (Blow & Manning 1997:177) was incorrectly spelled *saundersi* in the original description. We regret this lapsus and apologize to Dr. Sanders for this unfortunate error on our part.

The correct name of the species is *Eohalimede sandersi* Blow & Manning, 1997.

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A new species of *Geophis* of the *sieboldi* group (Reptilia: Squamata: Colubridae) from northern Honduras

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Abstract.—A new species of *Geophis* from northern Honduras is described. It is a member of the *sieboldi* group, the largest and most geographically extensive of the seven species groups currently recognized in the genus. With the inclusion of this species, the *sieboldi* group now contains 15 species, which range from Michoacán, Mexico, to Colombia. The new species can be distinguished from the other members of the *sieboldi* group by the combined presence of 15 rows of smooth scales throughout the body, six supralabials, one supraocular, one postocular, dark gray dorsum with reddish-orange markings, and a white venter with a gray band on the anterior edge of each scale. The new species seems to be most closely related to *G. brachycephalus.*

The snake genus *Geophis* is a prominent component of the Middle American herpetofauna. Currently, 41 species are recognized in seven species groups (*chalybeus, championi, dubius, latifrontalis, omiltemanus, semidoliatus,* and *sieboldi* groups), which are distributed from Tamaulipas and Chihuahua, Mexico, to northwestern Colombia. Downs (1967) revised the genus and the following papers add to our knowledge of its species: Bogert & Porter (1966), Smith & Holland (1969), Dixon & Thomas (1974), Campbell & Murphy (1977), Webb (1977), Savage (1981), Campbell et al. (1983), Restrepo & Wright (1987), Pérez-Higareda & Smith (1988), Smith & Chiszar (1992), Lips & Savage (1994). Field work in the region of Cerro Texíguat, a wildlife refuge situated in the departments of Atlántida and Yoro in northern Honduras, has produced a single specimen of the *sieboldi* group that represents a new species, which we name below.

Methods

For ease of comparison, the methods of this paper essentially follow those of Lips & Savage (1994). The numbers in parentheses following capitalized color names in the section on coloration in life refer to the color codes in Smithe (1975).

Systematics

Geophis damiani, new species
Figs. 1, 2

Holotype.—National Museum of Natural History (USNM) 498356, an adult male from 2.5 airline km NNE La Fortuna (15°26′N, 87°18′W), 1750 m elev., Departmento de Yoro, Honduras, collected 26 Jul 1995 by D. Almendarez, J. R. McCranie, K. L. Williams, and L. D. Wilson. Original number LDW 10505.

Diagnosis.—This new taxon is a member of the *sieboldi* group, based on Downs' (1967:137–145) characterization (see Relationships) and its further explication by Lips & Savage (1994:413–414). This group of 14 species (Downs 1967, Campbell & Murphy 1977, Restrepo & Wright 1987, Smith & Chiszar 1992, Lips & Savage 1994) ranges from the southern edge of the

Mexican Plateau in Michoacán to Colombia. *Geophis damiani* can be distinguished from three of the members (*G. dunni, G. nasalis, G. sieboldi*) by having 15 dorsal scale rows, instead of 17, and smooth scales throughout the body, as opposed to some degree of keeling. *Geophis damiani* is further distinguished from all three of these species by possessing a dark gray dorsum with reddish-orange markings and a banded gray and white venter. *Geophis dunni* has a pale yellow dorsum with dark brown dorsal crossbands and an immaculate venter. Both *G. nasalis* and *G. sieboldi* have a dark brown or gray dorsum that is darkest middorsally and palest laterally, and ventrals that are white or yellowish white with brown lateral edges. The remaining 11 species (*G. betaniensis, G. brachycephalus, G. hoffmani, G. laticollaris, G. nigroalbus, G. petersi, G. pyburni, G. russatus, G. sallei, G. talamancae,* and *G. zeledoni*) all agree with *G. damiani* in having 15 dorsal scale rows. *Geophis damiani* differs in color pattern from all of these species, save for some specimens of *G. brachycephalus*. *Geophis betaniensis* has a reddish-brown dorsum with a black lateral stripe and a greenish-yellow venter bordered laterally with brown; furthermore, it is the only species in the group with two postoculars, instead of one. *Geophis brachycephalus* has distinctly keeled dorsal scales, except on the neck. *Geophis hoffmanni* has a uniformly dark brown to grayish-black dorsum, with a pale collar in juveniles, five supralabials (six in *G. damiani*), keeled dorsal scales above the vent, and 147–168 ventrals + subcaudals (177 in holotype of *G. damiani*). *Geophis laticollaris* has weakly keeled scales except on the neck, which are smooth, 162 ventrals + subcaudals, a dark dorsum (nearly black medially, brown laterally), except for a broad white nuchal collar, and an immaculate white venter. *Geophis nigroalbus* has tubercles on the anterior one-third of the dorsum and keeling on the posterior half, and the supraocular and postocular scales are separated by an anterior extension of the parietal (postocular and supraocular in contact in *G. damiani*). *Geophis petersi* and *G. pyburni* are distinguished from *G. damiani* in having the scales above the vent keeled and an immaculate cream to creamish-white venter. In *G. petersi* the dorsum is brown medially and pale yellowish brown laterally; in *G. pyburni* it is dark brown medially becoming somewhat paler laterally. *Geophis russatus* has weakly keeled dorsal scales on the posterior two-thirds of the body, a brick red dorsum with irregular black bars, and ≤129 ventrals (136 in the holotype of *G. damiani*). *Geophis sallei* has distinctly keeled dorsal scales, except on the neck, 156–170 ventrals + subcaudals (177 in *G. damiani*), a grayish-brown to brownish-black dorsum in which the scales of the lateralmost row of each side possess pale centers, and a usually immaculate yellowish-white venter. *Geophis talamancae* has distinctly keeled scales on the posterior half of the dorsum, a uniformly iridescent black dorsum, and a transversely banded venter in which each scale is white anteriorly and black posteriorly. Finally, *G. zeledoni* has the scales above the vent lightly keeled, a uniformly grayish-black dorsum, and a mostly black venter with scattered irregular pale markings.

Description of holotype.—Head not distinct from neck; snout elongate, rounded in dorsal outline; rostral not extending posteriorly between internasals, its length from above about ¼ its distance from frontal; internasals large, slightly shorter than suture with prefrontal; prefrontals short, their median suture about ½ length of frontal; frontal slightly wider than long, almost hexagonal, in contact with prefrontals, supraoculars, and parietals, distinctly angulate anteriorly; parietals moderately long, broad, their median suture almost equal to length of frontal; parietal separated from prefrontals by supraocular; one postocular and one supraocular in contact with the parietal on each side of the head (Fig. 2).

Nasal divided, postnasal slightly larger than prenasal, their combined length about

Fig. 1. *Geophis damiani,* holotype (USNM 498356), overall length 327 mm.

110% length of loreal; loreal relatively elongate, slightly less than ½ length of snout, about 1⅔ times eye diameter; eye contained about 4 times in snout length (tip of snout to anterior border of eye), its diameter about ⅔ distance of eye from lip line; supralabials 6-6, 3rd and 4th in contact with orbit on both sides, 5th in contact with parietal; posterior temporal directly about 6th supralabial, not fused with nuchal along parietal margin.

Mental rounded anteriorly, broader than long, separated from chin shields by first pair of infralabials; infralabials 6-6, first 3 and anteromedial tip of 4th in contact with anterior chin shields; anterior chin shields definitely longer than broad, longer than posterior chin shields; posterior chin shields short, separated for their length by a medial gular; 3 gulars separating chin shields (including the one separating the posterior chin shields) from first ventral.

Dorsal scale rows 15-15-15, smooth throughout, without apical pits on dorsum. Ventrals 136; vent plate entire; subcaudals 41, not including terminal scale. Ventrals + subcaudals 177. Standard length (snout-to-vent) 267 mm, tail length 60 mm, tail length 18.3 percent of total length.

Color in life: Dorsal portions of body and tail Blackish Neutral Gray (82) with 24 Flame Scarlet (15) crossbands or laterally offset pairs of half crossbands on body; first nine bands complete, next twelve divided (or almost so) and the halves offset from one another along the longitudinal axis, and final three complete; seven similar markings (both crossbands and laterally offset markings) on tail that become increasingly faint towards its tip; head Blackish Neutral Gray (82); each ventral scale Glaucous (79) on anterior portion and white on posterior portion; underside of tail Glaucous (79); iris Jet Black (89).

Color in alcohol: Dorsally very dark gray with pale red-orange markings; each ventral scale dark gray anteriorly and yellowish cream posteriorly; underside of tail colored as is venter, except that dark gray color is more extensive.

Hemipenis: Bilobed, distal portion of organ strongly capitate, calyculate, spinulate; sulcus spermaticus intermediate between centrifugal and centrolineal (Myers & Campbell 1981), bifurcation at point of capitation, each branch reaching apex; naked basal pocket on asulcate side; central portion of organ with large spines in oblique rows.

Maxilla: Extending anteriorly to middle

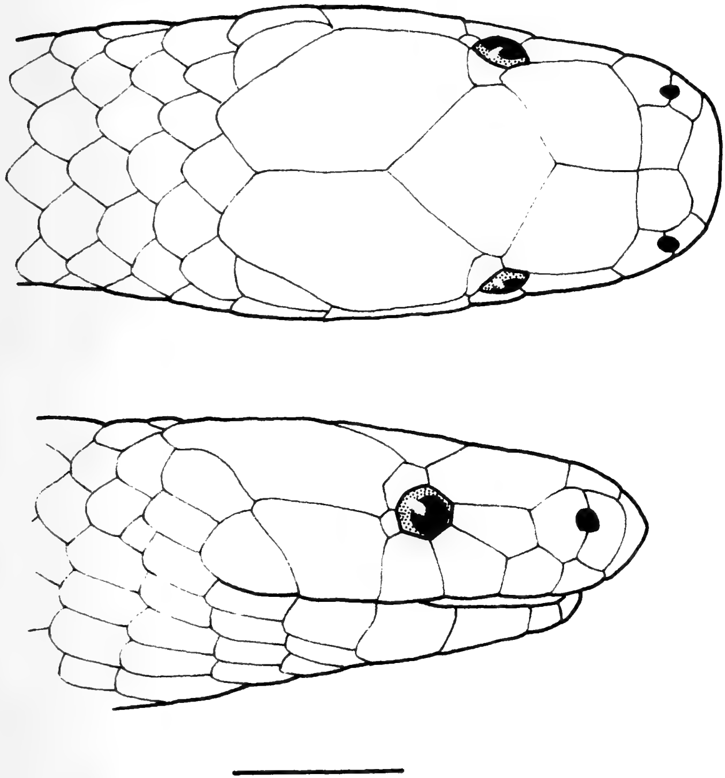

Fig. 2. Semidiagrammatic representation of dorsal and lateral head scutellation for the holotype (USNM 498356) of *Geophis damiani.* Line equals 3 mm.

portion of second supralabial, bearing 10 subequal teeth; anterior tip of maxilla toothless.

Distribution and natural history notes.—*Geophis damiani* is known only from the type locality within the limits of the Refugio Silvestre Cerro Texíguat. It was found beneath an illegally sawn mahogany plank on a steep incline in the Lower Montane Wet Forest formation (Holdridge 1967). The ground below the plank was damp. Also collected from underneath mahogany planks in the area were several specimens of the salamander *Oedipina gephyra.*

Remarks.—The description of *G. damiani* brings to three the number of species of *Geophis* known from Honduras (see Wilson et al. 1998). The other two are *G. fulvoguttatus,* a member of the *dubius* group, found in western Honduras near the Sal-

Table 1.—Some distinguishing features of the members of the *Geophis sieboldi* group. Abbreviations used are: DSR = dorsal scale rows; DS = dorsal scale; SL = number of supralabials; PO = number of postoculars.

Species	DSR	DS condition	SL	PO	Dorsal coloration	Ventral coloration
Mexican group						
G. laticollaris	15	weakly keeled except on neck	6	1	nearly black medially, browner on sides, white nuchal collar present	immaculate white
G. petersi	15	smooth except keeled above vent	6	1	brown grading to pale yellowish brown laterally	immaculate white
G. pyburni	15	smooth except keeled above vent	6	1	dark brown, paler brown laterally	immaculate creamish white
G. russatus	15	weakly keeled on post ⅔ of body	6	1	red with irregular, short, black transverse bars	immaculate cream
G. sallei	15	distinctly keeled except on neck	6	1	grayish brown to brownish black, first row of scales with pale centers	usually immaculate yellowish white
G. sieboldi	17	keeled on post. ½ of body	6	1	dark gray or brown, first row of scales with pale centers	scutes white or yellowish white with brown lateral edges
Northern Central American group						
G. damiani	15	smooth throughout	6	1	dark gray with reddish orange markings	scutes white with gray bands on anterior edges
G. dunni	17	distinctly keeled except on neck	6	1	dark brown crossbands on pale yellow ground color	immaculate yellowish white
G. nasalis	17	distinctly keeled except on neck	6	1	dark brown or gray, paler laterally	scutes white or yellowish white with brown lateral edges
Southern Central and South American group						
G. betaniensis	15	smooth throughout	6	2	reddish brown, black lateral stripe on 1st and 2nd dorsal rows, diffuse pale collar	scutes greenish yellow with brown lateral borders
G. brachycephalus	15	distinctly keeled except on neck	6	1	brown to black, uniform, or with pale lateral blotches, crossbands, or stripes	usually white to gray, post. ½ of scutes usually banded with bark anterior edges
G. hoffmanni	15	smooth except keeled above vent	5	1	uniform dark brown to grayish black	scutes immaculate yellowish white or with dark anterior edges

Table 1.—Continued.

Species	DSR	DS condition	SL	PO	Dorsal coloration	Ventral coloration
G. nigroalbus	15	keeled on post. ½ of body, tubercles on ant. ⅓	6	1	black[1]	white[1]
G. talamancae	15	strongly keeled on post. ½ of body	6	1	uniform iridescent black	white with black bands on post. edges of scutes
G. zeledoni	15	smooth except lightly keeled above vent	6	1	uniform grayish black	black, with scattered irregular pale markings

[1] Data from Boulenger, 1908.

vadoran and Guatemalan borders, and *G. hoffmanni,* another member of the *sieboldi* group, distributed from eastern Honduras to western Panamá. Thus, *G. damiani* is the only member of the genus currently restricted to Honduras. It can be added to an increasing list of endemic taxa known from the Cordillera Nombre de Dios in northern Honduras (a discussion of the herpetological and conservation significance of this region is in Wilson et al. 1998).

The discovery of *G. damiani* makes even more poignant and disturbing the pace of habitat destruction in the Cerro Texíguat wildlife refuge. We have made three trips to the area above La Fortuna since 1991, and with each succeeding trip, we have witnessed continued conversion of undisturbed forest into crop fields and scarred remnants of logging operations. Although established as a wildlife refuge in 1987, there is presently no indication that the Cerro Texíguat area is protected. There are no signs indicating refuge limits, no personnel assigned to oversee the area, and no housing or research facilities for scientific study. Until these measures are implemented, we expect that habitat destruction within this paper-protected area will continue until it is complete.

The resemblance of the color pattern of *Geophis damiani* to the bicolor ringed pattern of *Micrurus nigrocinctus* from the same area is striking, and suggests that the former may be involved in a mimicry complex with the latter, as is also the case with the local population of *Pliocercus elapoides* (Wilson, et al., 1996).

Relationships.—Geophis damiani is a member of the *sieboldi* group based on the following features (Downs 1967, Lips & Savage 1994): snout long, projecting well beyond lower jaw, rounded in dorsal outline; rostral not produced posteriorly between internasals; internasals short, their greatest length 61% of suture between prefrontals; postnasal short, width about 47% of height; prefrontals and loreals elongate; supraocular forming about posterior half of dorsal margin of orbit; no anterior temporal; rounded mental; maxilla extending forward to middle portion of second supralabial, with 10 subequal teeth, anterior tip of maxilla toothless; hemipenis capitate with naked basal pocket on asulcate side.

Based on our study, as well as those of Smith & Chiszar (1992) and Lips & Savage (1994), the *sieboldi* group contains 15 species and is the largest in the genus. Six of these species are restricted to Mexico (*G. laticollaris, G. petersi, G. pyburni, G. russatus, G. sallei,* and *G. sieboldi*), one is restricted to Guatemala and adjacent Chiapas, Mexico, (*G. nasalis*), one is endemic to Honduras (*G. damiani*), one is known only from Nicaragua (*G. dunni*), two are endemic to Costa Rica (*G. talamancae* and *G. zeledoni*), and one is endemic to Colombia (*G. betaniensis*). Each of three species is distributed in more than a single country: *G. brachycephalus* (Costa Rica, Panama, and Colombia), *G. hoffmani* (eastern Honduras to western Panama), and *G. nigroalbus* (eastern Panama and Colombia). The distribution of this species group makes it the most geographically extensive in the genus.

Relationships among the 15 species comprising the *sieboldi* group are poorly understood, perhaps due to the mosaic of features used to discriminate among them (Table 1). The species listed in Table 1 follow the geographical groups established by Downs (1967) and expanded by current treatment. The *sieboldi* group is the most morphologically diverse, with members possessing smooth or variably keeled dorsal scales in 15 or 17 rows, and a dorsal coloration that is patternless, with dark markings on a pale background, or pale markings on a dark background.

Based on the distribution of the morphological features indicated in Table 1, *G. damiani* apparently is not closely related to the other Nuclear Central American members of the group (*G. dunni* and *G. nasalis*), both of which have 17 rows of distinctly keeled (except on the neck) dorsal scales (15 rows of smooth scales in *G. damiani*). *Geophis dunni* has a dorsal coloration of dark brown crossbands on a pale yellow ground color and an immaculate yellowish-white venter, whereas *G. nasalis* has a dark brown or gray dorsal coloration and a venter that is pale, mottled, or edged with brown (*G. damiani* has a dark gray dorsum with reddish-orange markings and a white and gray banded venter).

Among the remaining twelve species, *G. damiani* seems to resemble most closely *G. brachycephalus* from Costa Rica, Panama, and Colombia. Both taxa possess 15 dorsal scale rows, six supralabials, and one postocular. In addition, some *brachycephalus* have dorsal and ventral patterns similar to those found in *G. damiani. Geophis brachycephalus,* however, has the dorsal scales distinctly keeled except on the neck, as opposed to the smooth dorsals seen in *G. damiani.*

Similar relationships are those linking *Duellmanohyla salvavida* and *D. soralia* to the other members of the predominately lower Central American red-eyed hylas formerly allocated to the *Hyla uranochroa* group and now residing within the genus *Duellmanohyla* (Wilson & McCranie 1985, McCranie & Wilson 1986), and *Hyla insolita* to the lower Central American members of the *lancasteri* group (*H. calypsa* and *H. lancasteri*; see McCranie et al. 1993, Wilson et al. 1994, Lips 1996).

Etymology.—The specific name *damiani* is a patronym honoring our friend and field companion Damian Almendarez, a resident of El Díctamo, Olancho, Honduras, whose assistance in recent field seasons has been indispensable.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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Type locality and taxonomic status of *Saltator plumbiceps* "Baird, MS." Lawrence, 1867 (Aves: Passeriformes: Cardinalidae)

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Abstract.—Due to an error in the published type locality for *Saltator plumbiceps* "Baird, MS." Lawrence, 1867, this name has long been considered a synonym of *S. coerulescens vigorsii* Gray. It is, in fact, an older available name for the subspecies currently known as *S. coerulescens richardsoni* van Rossem. Van Rossem's *richardsoni* thus becomes a junior objective synonym of Lawrence's *plumbiceps.*

The populations of the Grayish Saltator, *Saltator coerulescens* Vieillot, inhabiting the Pacific slope of Mexico were originally known as *Saltator plumbiceps* "Baird, MS." Lawrence, 1867. In Lawrence's original description, USNM 29372 was designated as the holotype, with Mazatlan, Mexico indicated as its locality. This name was applied to birds ranging from Sinaloa to Oaxaca (Ridgway 1901), and can still be found on labels of USNM specimens collected prior to 1910.

Van Rossem (1931) discovered an older name applicable to this Pacific coast form, *Saltator vigorsii* G. R. Gray, 1844 (a renaming of preoccupied *Saltator rufiventris* Vigors, 1839, type locality unknown), and *plumbiceps* became a synonym of *S. coerulescens vigorsii* Gray (Hellmayr 1938). When this taxon was split into northern and southern forms (van Rossem 1938), the type locality of *vigorsii* (the northern form) was restricted to Mazatlan. This action retained *plumbiceps* as a synonym of *vigorsii,* with the southern form being named *Saltator grandis richardsoni* van Rossem, 1938, type locality Plains of Colima, Colima, Mexico (holotype BM 1894.7.1.1180). These two subspecies are still recognized as *S. coerulescens vigorsii* Gray, ranging from Sinaloa to northern Jalisco, and *S. coerulescens richardsoni* van Rossem, ranging from central Jalisco to western Oaxaca (Paynter & Storer 1970).

Although Lawrence (1867) published the locality of USNM 29372 as Mazatlan, Mexico, there is no evidence to support this assertion. The specimen is an adult male collected by John Xantus (field number 53) in January 1863. His original field catalog, the original specimen label, and the museum ledger entry all indicate "Plains of Colima" as the locality. Deignan (1961) made note of Lawrence's error, but did not mention the taxonomic consequences. Clearly, Lawrence's earlier name applies to van Rossem's southern form *richardsoni,* which has the same type locality. Thus, the subspecies of Grayish Saltator that occurs from central Jalisco to western Oaxaca should be properly recognized as *S. coerulescens plumbiceps* Lawrence.

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Taxonomic notes on hummingbirds (Aves: Trochilidae). 1. *Eriocnemis dyselius* Elliot, 1872 is a melanistic specimen of *Eriocnemis cupreoventris* (Fraser, 1840)

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Abstract.—*Eriocnemis dyselius* Elliot, 1872 is hypothesized to be a melanistic specimen of *Eriocnemis cupreoventris* (Fraser, 1840), a puffleg hummingbird restricted to the Andes Mountains of Colombia and Venezuela.

Among the families of birds, the systematics of the Trochilidae are the most confused, in absolute numbers, by hybrids, genetic variants, and the problems associated with taxa described from unique specimens (e.g., Berlioz & Jouanin 1944; Banks & Johnson 1961; Greenway 1978; Bleiweiss 1988; Graves 1990, 1993, 1996, 1997a, 1997b; Hinkelmann et al. 1991). One such questionable taxon is *Eriocnemis dyselius* Elliot, 1872 a puffleg hummingbird of indeterminate origin. Salvin (1892:369) suggested that the black-plumaged specimen was "perhaps a melanism of *E. cupreiventris,*" an inhabitant of forest borders and shrubby slopes (1950–3000 m) of the Venezuelan Andes and the Eastern Cordillera of the Colombian Andes (Hilty & Brown 1986, Fjeldså & Krabbe 1990). Salvin did not elaborate on this proposal. Subsequent authors (Cory 1918, Berlioz & Jouanin 1944, Peters 1945, Greenway 1978, Fjeldså & Krabbe 1990) agreed with Salvin but likewise provided no further support for this hypothesis. Consequently, the taxonomy of *E. dyselius* is still uncertain. Here I present evidence that supports Salvin's (1892) conjecture that the holotype of *E. dyselius* is a melanistic specimen of *Eriocnemis cupreoventris* (Fraser, 1840).

Materials and Methods

The unsexed holotype of *Eriocnemis dyselius* (Fig. 1), a partially relaxed taxidermy mount with glass eyes, is adult as judged by the lack of striations on the maxillary ramphothecum (see Ortiz-Crespo 1972). Previously housed in both the Bourcier and Elliot collections (see Greenway 1978), the specimen is now catalogued in the American Museum of Natural History (AMNH 38452). I studied the specimen taking the approach outlined in Graves (1990) and Graves & Zusi (1990). In determining the scope of the species pool to be investigated, Elliot's (1872: 294) description offers little guidance:

> "Four specimens, precisely alike, were, as I was informed, contained in the small collection of birds from which my example was taken; and, although no locality was given, it is supposed that Ecuador is the habitat of the species."

The existence of four similar specimens of unknown origin should not be interpreted as evidence of a differentiated population. Millinery dealers in the 19th century sorted and high-graded shipments of hummingbird skins for unusual specimens to offer to collectors of natural history specimens. Although the circumstances of Elliot's acquisition of *E. dyselius* are unknown, the four black-plumaged specimens could have been gleaned from commercial lots consisting of tens of thousands of specimens (Doughty 1975). For the purpose of analysis, the holotype of *E. dyselius* may have originated anywhere in northwestern South America (see Berlioz &

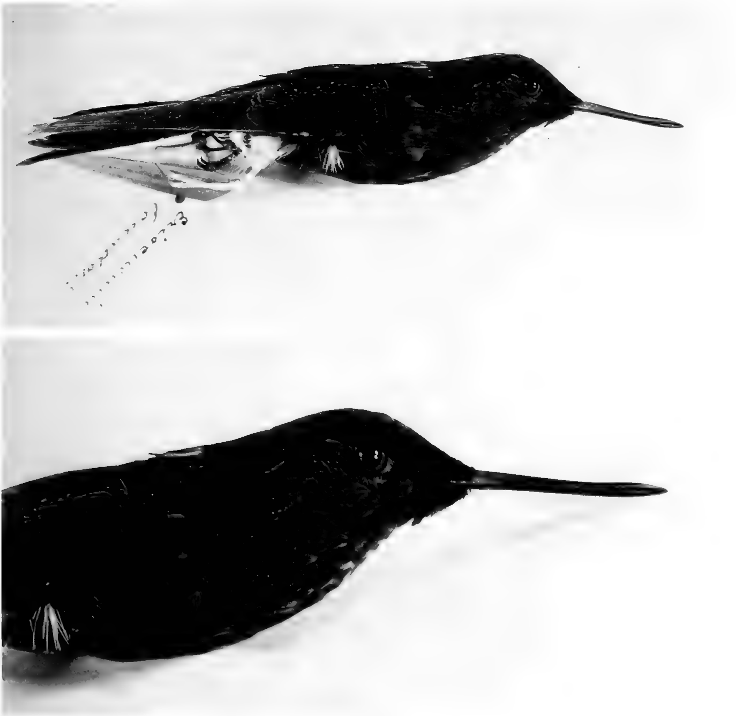

Fig. 1. Holotype of *Eriocnemis dyselius* Elliot, 1872 (AMNH 38452).

Jouanin 1944), a region inhabited by more than 150 species of hummingbirds (Hilty & Brown 1986, Graves 1990).

I considered Salvin's hypothesis as the most likely, a priori. The possibility of hybridization was judged to be negligible because the plumage of *E. dyselius* is substantially darker and less reflective than that of any potential parental species in northwestern South America (i.e., *Coeligena prunellei, Eriocnemis nigrivestis, Heliangelus zusii, H. regalis*).

The downy tibial puffs and body proportions of *E. dyselius* clearly mark it as a member of *Eriocnemis*. I took standard measurements (rounded to the nearest 0.1 mm) of adult male and female specimens of *Eriocnemis cupreoventris, E. nigrivestis,* and *E. vestitus* (the three species most similar in size and shape to the holotype of *E. dyselius*) with digital calipers: wing chord; lengths of rectrices (from point of insertion of central rectrices); and bill length (from anterior extension of feathers) (Table 1). Color comparisons were made under natural light; the plumage was examined under 10× magnification (Appendix).

I used principal components analysis

Table 1.—Ranges and means (± standard deviation) of measurements (mm) of *Eriocnemis cupreoventris, E. vestitus,* and the type specimen of *Eriocnemis dyselius* Elliot, 1872.

	cupreoventris		*vestitus*		
	♂♂ (*n* = 15)	♀♀ (*n* = 6)	♂♂ (*n* = 15)	♀♀ (*n* = 11)	*dyselius*[a] AMNH 38452
Wing chord	59.6–63.8 61.6 ± 1.3	57.2–60.7 58.8 ± 1.1	57.8–61.3 59.4 ± 1.1	54.7–59.4 57.7 ± 1.4	58.8
Bill length	16.6–18.6 17.8 ± 0.5	17.0–19.6 18.5 ± 1.0	15.9–18.8 17.5 ± 0.8	17.4–19.2 18.5 ± 0.5	17.5
Rectrix 1	24.5–28.2 26.4 ± 1.1	24.6–26.6 25.8 ± 0.7	26.2–29.7 28.4 ± 1.1	29.7–32.8 31.1 ± 0.9	26.9
Rectrix 2	26.9–31.2 28.6 ± 1.3	26.1–28.2 27.4 ± 0.8	28.0–31.5 29.9 ± 1.1	31.3–35.1 32.9 ± 1.1	29.8
Rectrix 3	31.9–36.6 33.8 ± 1.5	30.7–33.3 32.1 ± 0.9	31.1–35.3 33.1 ± 1.4	33.5–37.7 35.9 ± 1.3	34.6
Rectrix 4	36.9–42.4 39.5 ± 1.8	34.8–38.5 37.0 ± 1.3	35.3–39.7 37.9 ± 1.5	35.9–41.0 38.9 ± 1.5	37.9
Rectrix 5	40.4–46.3 42.9 ± 1.7	36.0–40.1 38.6 ± 1.6	40.6–45.3 42.7 ± 1.4	37.6–42.2 39.7 ± 1.5	39.5

[a] All measurements on left side.

(PCA) on $\log_{10}$ transformed measurements to reduce the dimensionality of data. Unrotated principal components were extracted from covariance matrices (Wilkinson 1989). Factor scores were projected on a bivariate plot to illustrate the relationship of rectricial measurements in *Eriocnemis* (Table 2, Fig. 2). For brevity, the holotype of *E. dyselius* will be referred to as *dyselius* in the remainder of the paper.

Results and Discussion

Currently recognized species of *Eriocnemis* (Sibley & Monroe 1990, Graves 1996) exhibit areas of glittering or brilliant plumage which probably serve as signaling badges during agonistic and sexual displays. The dull black plumage of *dyselius* lacks glittering iridescence, an observation consistent with the hypothesis of melanism. Although melanism is thought to occur at a very low frequency in the Trochilidae (e.g., Salvin 1892, Greenway 1978), the fine structure of melanism in hummingbirds has not been formally investigated, and I will only briefly address the topic here. Iridescence in hummingbirds is caused by the interference of light reflected from the upper and lower surfaces of air-filled vacuoles in melanin granules, which are closely stacked in 7–15 layers in the outer keratin of the expanded dorsal flanges of feather barbules (Dorst 1951, Greenewalt et al. 1960, Lucas & Stettenheim 1972). Perceived colors vary according to the size of the vacuoles, the thickness of melanin granules, and the an-

Table 2.—Factor loadings from a principal components analysis (PCA) of rectricial measurements of *Eriocnemis cupreoventris, E. vestitus,* and the holotype of *Eriocnemis dyselius* Elliot, 1872.

Variables	PCA 1	PCA 2	PCA 3
Rectrix 1 (innermost)	0.0314	−0.0054	0.0076
Rectrix 2	0.0298	−0.0035	0.0005
Rectrix 3	0.0195	0.0055	−0.0102
Rectrix 4	0.0093	0.0150	−0.0071
Rectrix 5	0.0012	0.0228	0.0090
Percent variance explained	66.2%	23.1%	8.3%

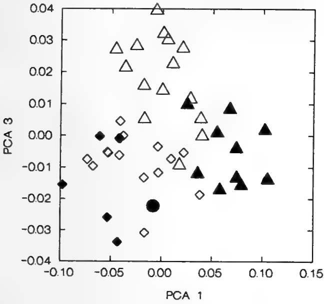

Fig. 2. Bivariate relationship of factor scores (PCA 1 & PCA 3, see Table 2) from a principal components analysis of rectricial measurements of *Eriocnemis cupreoventris* (diamonds: females = filled; males = empty), *E. vestitus* (triangles: females = filled; males = empty); and the holotype of *Eriocnemis dyselius* Elliot, 1872 (filled circle).

gle of observation. The intensity of color is enhanced by reflectance from multiple layers of granules. An overabundance and random placement of melanin granules in the keratin would lead to a disarrangement of the reflective layers, the absorption of light, and a damping of iridescent brilliance.

Eriocnemis cupreoventris and *E. vestitus* are remarkably similar in size and shape and melanistic specimens would be difficult to distinguish. The mean bill and wing lengths of the respective sexes of the two species differ by 0 to 3.7%. The difference in mean rectrix length varies from 0.4% to 7.5% in males and 5.1% to 20.9% in females. Comparison of raw measurements and inspection of bivariate plots of PCA variables extracted from rectricial measurements show that *dyselius* is most similar in size and shape to male *E. cupreoventris* (Table 1, Fig. 2). The bill length of *dyselius* (17.5 mm) falls outside the range of measurements for *E. nigrivestis* (males: $n = 15$; 14.4–15.8 mm, $\bar{X} = 15.1 \pm 0.5$, and females: $n = 6$; 15.6–16.5 mm, $\bar{X} = 16.0 \pm 0.3$; see measurements in Graves 1996), thus eliminating that species as a possibility.

Feather shape of *dyselius* provides additional clues as to its identity. The outermost rectrices and longest uppertail coverts of *E. cupreoventris* are slightly narrower and more attenuate than those of *E. vestitus* and *E. nigrivestis,* although some overlap occurs among the species. The shape of these feathers in *dyselius* is most similar to those of *E. cupreoventris.*

When viewed head-on under direct light, the throat of *dyselius* emits a dull plumbeous iridescence but exhibits no evidence of a centrally demarcated area corresponding to the gorget found in both sexes of *E. nigrivestis* and *E. vestitus. Eriocnemis cupreoventris* lacks a defined gorget. Instead, the entire throat and upper breast exhibits brilliant iridescence in both sexes. The gradation of feather size, shape, and reflectivity across the throat of *dyselius* resembles that of *E. cupreoventris.* Moreover, the pattern of melanization in *dyselius* corresponds precisely with the distribution of iridescent plumage in *E. cupreoventris.*

In summary, the holotype of *Eriocnemis dyselius* corresponds well in size to male *E. cupreoventris.* Subtleties of rectrix shape, the lack of a well-developed gorget, and the general pattern of melanization of *dyselius* also are consistent with Salvin's (1892) hypothesis that *dyselius* is a melanistic example of *E. cupreoventris,* and provide no reason to believe that *dyselius* represents either a hybrid or a valid species. Thus, the name *Eriocnemis dyselius* Elliot, 1872 correctly is placed in the synonymy of *Eriocnemis cupreoventris* (Fraser, 1840).

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Appendix

Description of *Eriocnemis dyselius* Elliot, 1872. The plumage of *dyselius* is entirely black (with the exception of tibial plumes), glossier on the crown (bluish sheen), with faint greenish reflections on the uppertail coverts and pronounced bronzy-green reflections on the innermost secondaries. Sides of the head, lores, and auriculars, are about same color as the hindneck and crown but lack the bluish sheen. Dorsal body plumage is subtly darker than ventral plumage; feather bases are grayish-buff, palest near the rachis. The throat lacks a structurally demarcated gorget; however, the terminal discs reflect a faint plumbeous iridescence in direct light (dull black in diffuse light). The basal margins of some throat feathers are buffy-white, imparting a somewhat mottled or scaled appearance to the throat. Undertail coverts are black with a bluish sheen. Primaries are dull black but paler than the dorsal body plumage. Rectrices are glossy bluish-black on the dorsal and ventral surfaces. The well-developed tibial "puffs" are white.

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Taxonomy and distribution of *Daeodon*, an Oligocene-Miocene entelodont (Mammalia: Artiodactyla) from North America

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Abstract.—*Dinohyus* Peterson, 1906, the widely used generic name of the giant Oligocene-Miocene entelodont from North America, is a junior subjective synonym of *Daeodon* Cope, 1879. *Ammodon* Marsh, 1893 also is a junior subjective synonym of *Daeodon.* Five species have been named that we assign to *Daeodon*; *D. shoshonensis* Cope, 1879, *D. leidyanus* (Marsh, 1893), *D. mento* (Allen, 1926), *D. hollandi* (Peterson, 1905b), and *D. minor* (Loomis, 1932), and we tentatively consider all to represent a single species, *D. shoshonensis* Cope, 1879. The type material of *D. leidyanus,* from the basal Kirkwood Formation near Farmingdale, New Jersey is of early Miocene (late Arikareean) age. Other *Daeodon* occurrences range in age from late Oligocene (Arikareean) to early Miocene (Hemingfordian).

Entelodontidae is a family of Holarctic Eocene-Miocene suiform artiodactyls. Entelodonts were always among the largest artiodactyls of their times, and the later forms became gigantic, some with skulls nearly one meter long. They appeared in North America during the late Eocene (Duchesnean) as immigrants from Asia (Brunet 1979, Emry 1981, Lucas 1992) and became relatively conspicuous members of latest Eocene-early Oligocene (Chadronian-Orellan) mammalian fossil assemblages in the western United States. They persisted through the late Oligocene into the early Miocene (Whitneyan-Hemingfordian) before becoming extinct. The giant genus, usually called *Dinohyus,* represents a later lineage of Asian entelodonts that immigrated into North America near the end of the Oligocene (Brunet 1979), and became geographically widespread in the early Miocene, though apparently never abundant.

Peterson (1905b) named *Dinohyus* for complete skeletal material from Nebraska that he later monographed (Peterson 1909). However, an entelodont from the Miocene of Oregon, *Daeodon* Cope, 1879, belongs to the same genus as *Dinohyus* and thus has priority. Furthermore, *Ammodon* Marsh, 1893, from the Miocene of New Jersey, also is a synonym of *Daeodon.* The purpose of this article is to establish the synonymy of *Daeodon, Ammodon* and *Dinohyus* and to summarize the distribution of *Daeodon,* which had a broad range in the United States (Fig. 1).

Abbreviations used.—In this article, AM refers to Amherst Museum, Amherst University, Amherst; AMNH to the American Museum of Natural History; CM to the Carnegie Museum of Natural History, Pittsburgh; LACM to the Natural History Museum of Los Angeles County; MCZ to the Museum of Comparative Zoology of Harvard University, Cambridge; UNSM to the University of Nebraska State Museum, Lincoln; SDSM to the South Dakota School of Mines, Rapid City; TMM to the Texas Memorial Museum, Austin; UCMP to the University of California Museum of Paleontol-

Fig. 1. Map of the United States showing distribution of fossils of the giant entelodont *Daeodon.* Localities are: 1. Unnamed unit above Haystack Valley Member, John Day Formation, Oregon. 2. Bolero Lookout local fauna, "Sespe Formation", Santa Ana Mountains, California. 3. Big Badlands, South Dakota. 4. Lusk-Hat Creek Breaks, Wyoming. 5, Pine Ridge escarpment, Nebraska. 6, Agate Springs quarry, Nebraska. 7, Washington County, Texas. 8, San Jacinto County, Texas. 9, Vicksburg Group, Conecuh River, Escambia County, Alabama. 10, Franklin Phosphate Pit, Florida. 11, Ashley River Phosphates, South Carolina. 12, Farmingdale, Monmouth County, New Jersey.

ogy, Berkeley; USNM to the National Museum of Natural History, Smithsonian Institution, Washington, D.C.; and YPM to the Yale Peabody Museum, New Haven.

Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Family Entelodontidae Lydekker, 1883
Genus *Daeodon* Cope, 1879

Daeodon Cope, 1879:77.—Loomis, 1932: 361, figs. 1–2.—Simpson, 1945:144.—Gallagher et al., 1995:257, fig. 2C–D.—Lucas et al., 1996:15.

Ammodon Marsh, 1893:409, pl. 9, figs. 2–3 [not *Ammodon* Marsh, 1893:410, pl. 9, fig. 4].—Peterson, 1909:67, figs. 20–21 [not *Ammodon*? Marsh, 1893:410, pl. 9, fig. 4].—Peterson, 1909:67, figs. 20–21 [not *Ammodon*?, Peterson, 1909:68, fig. 22.—Troxell, 1920:252, pl. 3, figs. C–D.—Brunet, 1979:90.

Dinochoerus Peterson, 1905a:212.

Dinohyus Peterson, 1905b:719 [replacement name for *Dinochoerus* Peterson, 1905a, preoccupied by *Dinochoerus* Glöger, 1841, p. 131].—Peterson, 1906:49, pls. 16–17.—Peterson, 1909:66, figs. 29–80, pls. 45–61.—Simpson, 1930:169, fig. 16.—Wilson, 1957:641, figs. 2–4, table 1.—Parris & Green, 1969:7, figs. 1–2, table 1.—Brunet, 1979:90.—Westgate, 1992:685, figs. 1–2.—[not *Dinohyus,* Schlaijker, 1935:157, pl. 21].

Dinohyus?—Allen, 1926, p. 450, pl. 1.

Type species.—Daeodon shoshonensis Cope, 1879.

Included species.—Only the type species.

Revised diagnosis.—Daeodon is the largest entelodont (LP_4 = 45–53 mm), also distinguished from other entelodonts by the following combination of autapomorphous characters: $I^1{}_1$ very small (possibly absent); $I^3{}_3$ larger than $I^2{}_2$; incisorcanine diastema very short or absent; diastemata between all premolars, largest between $P^1{}_1$ and $P^2{}_2$; lower molars lacking paraconids and with trigonids and talonids of subequal height; alveolar border of premaxillary very short; jugal flange relatively small (compared to *Archaeotherium*); infraorbital foramen above posterior portion of P^3; symphyseal tubercle very small or absent; large posterior tubercle (under P_4/M_1) on lower jaw; mandibular angle slopes gently posteriorly; trapezium absent; unciform completely separated from magnum by semilunar; metatarsal V absent; fibula and tibia co-ossified.

Distribution.—Late Oligocene-early Miocene of Oregon, California, South Dakota, Wyoming, Nebraska, Texas, Alabama, Florida, South Carolina and New Jersey (Fig. 1).

Discussion.—The holotype of *D. shoshonensis,* AMNH 7387 (Fig. 2), represents an individual slightly smaller than CM 1594, the holotype of *Dinohyus hollandi.* AMNH 7387 is a much damaged fragment of the mandiblular symphysis with the roots and/or alveoli of the incisors, canines and P_1's. The three incisors are procumbent and increase in size from I_1 to I_3. The canines are large and circular in cross section. A small diastema separates the canine and the P_1, and a larger diastema evidently separates the P_1 and the P_2. No diastema separates the I_3 and canine. The tooth crowns are broken and absent, so it is impossible to describe crown morphology or to use wear on the teeth to estimate the relative age of the individual. Chin tubercles are absent.

Several characteristics observable on AMNH 7387, including the relative size of incisors and diastemata and the lack of chin tubercle–do diagnose one genus of giant North American entelodonts to which the name *Dinohyus* is usually applied. The holotype (CM 1594) of *D. hollandi,* the type species of *Dinohyus,* displays all the features of the holotype of *Daeodon shoshonensis,* except that it has a very small tubercle on the chin. The size of the chin tubercle ranges from very small to absent in specimens that we assign to *Daeodon,* quite different from the large chin tubercle found in *Archaeotherium* and similar North American entelodonts (e.g., Peterson 1909). Therefore, we conclude that *Dinohyus* is a junior subjective synonym of *Daeodon.*

The holotype P_4 of *Ammodon leidyanus* (Fig. 3A–D) is very similar to the P_4 of the holotype of *Dinohyus hollandi* (Fig. 3G). The teeth differ only in the slightly larger size (about 15%), longer talonid (due to the larger posterior cingulid) and more prominent posterior ridges on the trigonid slope on the *A. leidyanus* holotype (also see Peterson 1909:68). The referred M_3 of *A. leidyanus* differs from that tooth in the holotype of *D. hollandi* only in being slightly longer (about 4%) and having a larger hypoconulid (Fig. 3E–G). We believe that these differences do not merit generic separation of the holotypes of *A. leidyanus* and *D. hollandi,* and they do not even merit separation at the species level (see below). We thus consider *Dinohyus* and *Ammodon* to represent a single genus, which should be termed *Daeodon.*

Simpson (1945:144) suggested that *Daeodon, Dinohyus* and *Ammodon* represent a single genus. Brunet (1979:90) also recognized the close similarity of the type material of *Ammodon* to that of *Dinohyus,* but preferred not to synonymize the two genera because *Dinohyus* is based on more nearly complete type material. We prefer to synonymize all three genera.

Daeodon shoshonensis Cope, 1879

Daeodon shoshonensis Cope, 1879:77.—Peterson, 1909:64, fig. 18.

Ammodon leidyanum.—Marsh, 1893:409, pl. 9, figs. 2–3.—Peterson, 1909:67, figs. 20–21.

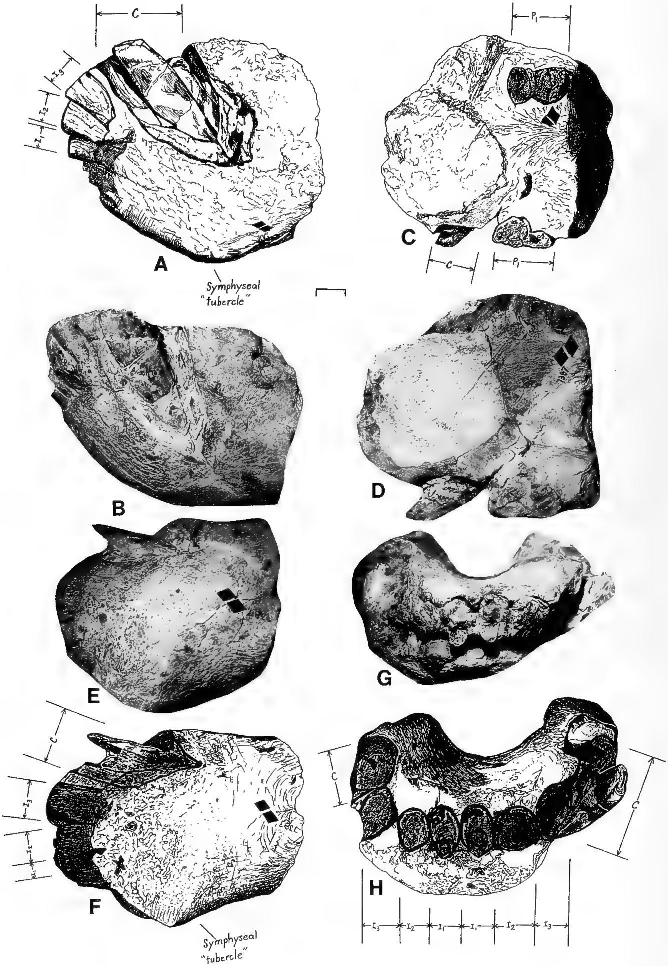

Fig. 2. Holotype of *Daeodon shoshonensis,* AMNH 7387, symphyseal fragment with roots, alveoli or partial crowns of left and right I_{1-3}, C and P_1. A–B, Labial views. C–D, Occlusal views. E–F, Ventral views. G–H, Anterior views. Bar scale = 20 mm.

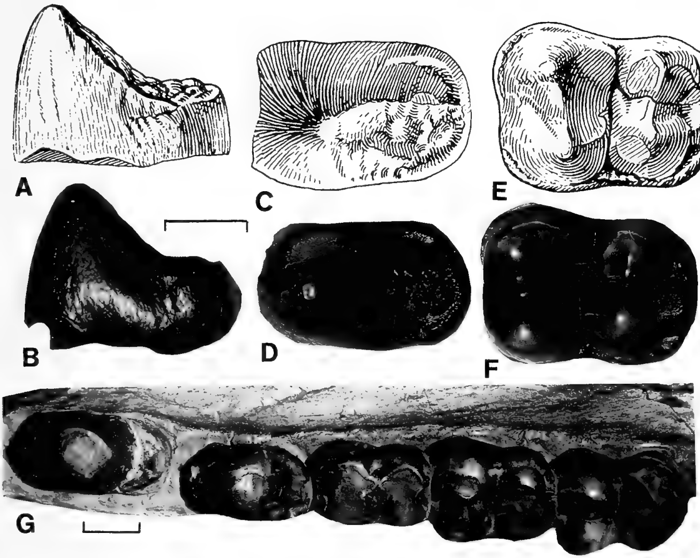

Fig. 3. Referred specimen and lectotype of *Ammodon leidyanus* (A–F), compared to holotype of *Dinohyus hollandi* (G). A–D, YPM 12040, right P_4, lingual (A–B) and occlusal (C–D) views. E–F, YPM 12041, left M_3, occlusal views. G, Occlusal view of left P_3-M_3 of CM 1594. Drawings from Peterson (1909). Bar scales = 20 mm.

Dinochoerus hollandi.—Peterson, 1905a: 212.

Dinohyus hollandi.—Peterson, 1905b: 719.—Peterson, 1906:49, pls. 16–17.—Peterson, 1909:66, figs. 29–80, pls. 45–61.—Wilson, 1957:641, figs. 2–4, table 1.—Brunet, 1979:90.

Not *Daeodon calkinsi.*—Peterson, 1909:64, fig. 19.

Ammodon leidyanus.—Troxell, 1920:252, pl. 3, figs. C–D.—Brunet, 1979:90.

Dinohyus (?) *mento.*—Allen, 1926:450, pl. 1.

Daeodon minor Loomis, 1932:361, figs. 2–3.

Dinohyus sp.—Parris & Green, 1969:7, figs. 1–2, table 1.

Dinohyus aff. *D. hollandi.*—Westgate, 1992:685, figs. 1–2. *Holotype.*—AMNH 7387, symphyseal fragment (Fig. 2). *Horizon and locality of holotype.*—John Day Formation, Bridge Creek, Wasco County, Oregon.

Principal referred specimens.—From the basal Kirkwood Formation near Farmingdale, New Jersey: holotype of *Daeodon leidyanus* (Marsh, 1893), YPM 12040, right P_4 (Fig. 3A–C); YPM 12041, left M_3 (Fig. 3E–F).

From the lower part of the Harrison Formation, Agate Spring fossil quarry, Sioux County, Nebraska: holotype of *D. hollandi* (Peterson, 1905a), CM 1594, a nearly complete skeleton (Peterson 1906, pls. 16–17; 1909, figs. 29–80, pls. 45–61).

From the lower part of the Harrison Formation, *Stenomylus* quarry near Agate, Nebraska: holotype of *Daeodon minor* (Loomis, 1932), AM 31–32, lower jaws with de-

Table 1.—Measurements (in mm) of lower cheek teeth of selected specimens of *Daeodon.*

	YPM 12040/12041	CM 1594	TMM 40224-1[1]	NM[2]
P_3L	—	53.6	60.1	55.0
P_3W	—	30.1	31.8	29.0
P_4L	52.3	46.9	55.0	46.0
P_4W	33.2	29.3	32.5	28.0
M_1L	—	42.7	50.7	42.0
M_1W	—	33.4	38.1	34.0
M_2L	—	47.3	55.0	49.0
M_2W	—	39.0	44.1	40.0
M_3L	52.4	50.0	55.2	55.0
M_3W	39.5	38.9	44.8	40.0

[1] From Sinclair (1905); measurements only to the nearest millimeter.

[2] From Wilson (1957).

ciduous dentition, an associated m1, associated deciduous upper teeth, and miscellaneous other associated skeletal elements.

From a Miocene? horizon in Ashley River phosphate deposits near Charleston, South Carolina: holotype of *Daeodon mento* (Allen, 1926), MCZ 17015, edentulous symphyseal region of lower jaw (Allen 1926, pl. 1).

For additional referred specimens from these and other localities see references cited in the synonymy above.

Description.—We redescribe here the holotype and only referred specimen of *D. leidyanus.* The holotype, AMNH 7387, a right P_4, is a submolariform tooth with a prominent talonid. The enamel of the tooth crown is rugose and lineated except for the occlusal tip of the trigonid cuspid. The trigonid is a single, bulbous, blunt cuspid much taller than the remainder of the tooth. The talonid is a low, semicircular posterior projection of the crown that occupies almost half of the occlusal area of the tooth. A thick, rugose cingulid surrounds the labial, lingual and posterior edges of the talonid. Two cuspidate ridges extend from near the apex of the trigonid down its posterior slope onto the talonid. The talonid between these ridges is rugose and cuspidate. Measurements are in Table 1.

The referred left M_3 (YPM 12041) is a rectangular tooth in occlusal view. Its enamel is rugose and lineated except for the cuspid occlusal tips. A cingulid surrounds the crown anteriorly and labially but is discontinuous lingually. The trigonid consists of a thick, blunt metaconid and a somewhat smaller and lower protoconid. A transverse lophid connects these two cuspids; it is lower than the cuspids and has a notch in the middle. A rudimentary paraconid/paracristid can be seen in a bulge between the metaconid and protoconid, above the cingulid, on the anterior face of the tooth. A deep, transverse notch separates the trigonid from the talonid. The posterior slope of the protoconid and the anterior face of the hypoconid most nearly bridge this notch. The hypoconid and entoconid are low, bulbous, blunt cuspids separated by a narrow notch in the lophid that connects them. This lophid is slightly oblique (i.e., the entoconid is slightly posterior to the hypoconid) to a transverse line through the tooth axis. Behind and slightly lingual to the hypoconid is a prominent, blunt hypoconulid. This hypoconulid is lower than the hypoconid and entoconid and forms a small posterior projection. Lingual to the hypoconulid are two, small cingulid cuspids behind the entoconid.

Discussion.—Hay (1902:656) correctly noted that mention of the name *Elotherium leidyanum* by Marsh (1871:10; 1874:534) did not constitute proper proposal of a new species. Indeed, Marsh's (1871, 1874) uses of the name do not even constitute an indication as defined in Article 12 of the International Code of Zoological Nomenclature. Rhoads (1903:237) thus quite correctly declared Marsh's (1871) *Elotherium leidyanum* a nomen nudum.

There are five named species based on specimens of *Daeodon:* the type species *D. shoshonensis* (Cope 1878), *D. leidyanus* (Marsh 1893), *D. hollandi* (Peterson 1905) *D. mento* (Allen 1926), and *D. minor* (Loomis 1932). Each species is known from one or a few specimens. Except for the ho-

Table 2.—Measurements (in mm) of upper cheek teeth of selected specimens of *Daeodon*.

	LACM 140397	CM 1594	SDSM 675[1]	TMM 40223-1[2]	USNM 25809[3]	UCMP 953
P^3L	43.9	43.5	48.0	—	—	37.5
P^3W	32.8	33.2	27.0	—	—	—
P^4L	39.6	37.2	34.0	41.0	38.2	25.5
P^4W	44.6	38.6	37.0	45.5	39.9	—
M^1L	47.6	42.9	42.0	45.8	45.5	31.5
M^1W	49.7	44.8	45.0	50.0	46.1	33.0
M^2L	48.4	45.2	46.0	—	—	33.0
M^2W	56.4	47.3	49.0	—	—	33.5
M^3L	45.5	42.7	—	—	—	31.0
M^3W	51.2	46.5	—	—	—	28.0

[1] From Parris & Green (1969); measurements only to the nearest millimeter.

[2] From Wilson (1957).

[3] From Westgate (1992).

lotype of *D. hollandi,* a complete skull and jaws, there is little morphological overlap among the holotypes of *Daeodon* species. Therefore, we find it difficult to evaluate the validity of these taxa and offer the tentative, conservative conclusion that they represent a single species. Measurements (Tables 1–2) and the relatively narrow range of meristic variation in the specimens that we assign to *Daeodon* support this conclusion.

The holotype of the type species of *Dinohyus, D. hollandi,* displays all the features of the holotype of *Daeodon shoshonensis,* except that it has a very small tubercle on the chin. Size of the chin tubercle ranges from very small to absent in specimens that we assign to *Daeodon,* quite different from the large chin tubercle found in adult *Archaeotherium* and similar North American entelodonts (Lucas et al. 1997). Therefore, we conclude that *Dinohyus* is a synonym of *Daeodon* (Lucas et al. 1996, 1997).

The holotype P_4 of *Ammodon leidyanus* Marsh, 1893 is very similar to the P_4 of the holotype of *Dinohyus hollandi* (compare illustrations in Marsh (1893) and Peterson (1909)). The teeth differ only in the slightly larger size (about 15%), longer talonid (due to the larger posterior cingulid) and more prominent posterior ridges on the trigonid slope on the *A. leidyanus* holotype (also see Peterson 1909:68). The referred M_3 of *A. leidyanus* differs from that tooth in the holotype of *D. hollandi* only in being slightly longer (about 4%) and having a larger hypoconulid. We believe that these differences do not merit species-level separation of the holotypes of *A. leidyanus* and *D. hollandi.*

Daeodon mento (Allen 1926) is based on an edentulous mandibular symphysis slightly larger than the holotype of *D. shoshonensis.* The two specimens are otherwise essentially identical, so we consider *D. mento* to be a junior subjective synonym of *D. shoshonensis.*

Daeodon minor (Loomis 1932) is based on the remains of a very young individual, consisting of lower jaws with deciduous premolars, an m1 thought to be associated, associated upper deciduous teeth and various postcranial elements. Loomis (1932: 361) listed the postcranial elements, but did not describe them because they were so young that the epiphyses were lacking. Loomis (1932:362) noted that the specimen is from the same area and same strata that produced the type and referred material of *D. hollandi*; however, because of its small size, complete lack of the anterior tuberosity on the lower jaw, and small size of the posterior tuberosity, Loomis gave the specimen a new species name and referred it to the genus *Daeodon.* Surely this is a juvenile individual of the same taxon previously called *Dinohyus hollandi,* considered here to be a synonym of *Daeodon shoshonensis.*

Dinohyus minimus Schlaijker, 1935, is based on the symphyseal region of a juvenile lower jaw (MCZ 2894) from the lower Harrison Formation of Wyoming (Schlaijker 1935:157–159, pl. 21). Note its similarity to *Archaeotherium trippensis* from the Turtle Butte Formation of South Dakota (Skinner et al. 1968:419–425, figs. 14–15). The holotypes of "*Dinohyus*" *minimus* and *Archaeotherium trippensis* both have small chin tubercles, but are juveniles, and in other diagnostic features resemble *Archaeothe-*

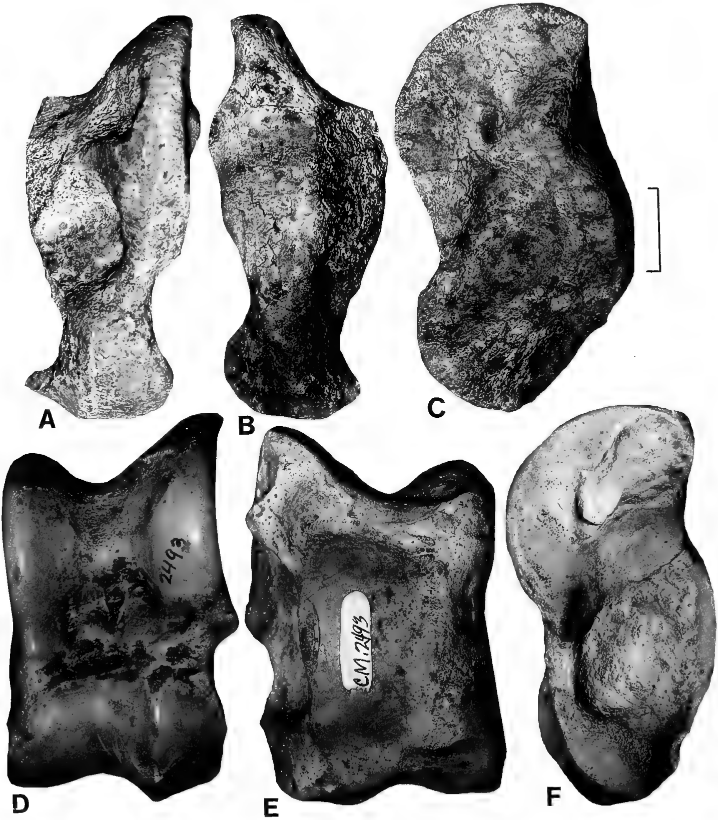

Fig. 4. Astragali of *Daeodon.* A–C, CM 1548, left astragalus, anterior (A), posterior (B) and lateral (C) views. D–F, CM 2493, left astragalus, anterior (D), posterior (E) and lateral (F) views. Bar scale is 20 mm long.

rium, not *Daeodon.* A small chin tubercle thus is a feature of juvenile, but not of adult, *Archaeotherium.* The three permanent incisors of MCZ 2894 are approximately the same size. Thus we believe that the species should be transferred to *Archaeotherium.*

Elotherium calkinsi Sinclair, 1905 is based on a skull and partial postcranial skeleton (UCMP 953) from the John Day Formation of Oregon. The specimen is of an old individual, and although the chin tubercle is small, the asociated tibia and fibula are unfused (Sinclair 1905:132–134, pl. 15). Thus we tentatively exclude it from *Daeodon.*

Peterson (1909:69, fig. 22) referred CM 1548, an incomplete left astragalus (Fig.

4A–C), to *Ammodon*?, even though it lacks any dental association. He noted that this astragalus is slightly larger, has a more convex sustentacular facet and a more anteriorly projecting distal trochlea than astragali of "*Dinohyus*" *hollandi* from the Agate Springs quarry (Fig. 4). These features strike us as minor postcranial differences of uncertain taxonomic significance, and we doubt that such minor features can be used to distinguish *Daeodon, Dinohyus* and *Ammodon* from each other.

Distribution

The type specimen of *Daeodon leidyanus* is part of the Farmingdale local fauna, a small assemblage of land mammals from the basal Kirkwood Formation in coastal New Jersey (Tedford & Hunter 1984, Gallagher et al. 1995). Based on sequence stratigraphy and marine micropaleontological biostratigraphy, Benson (1993) concluded that the lower Kirkwood Formation is slightly older than the "Shiloh marl." The "Shiloh marl" produced the single land mammal *Tapiravus validus* described by Marsh (1871) and is older than the Pollack Farm site in Delaware, which is approximately 18 Ma and can be confidently assigned to the early Hemingfordian based on its land-mammal fauna (Emry & Eshelman 1998). Sugarman et al. (1993) reported strontium-isotope age estimates of 20.0–20.3 Ma for the "Shiloh marl."

Besides *Daeodon leidyanus,* the Farmingdale local fauna includes the horse *Anchitherium* sp., the rhinos *Diceratherium matutinum* and *Menoceras* cf. *M. cooki,* the peccary *Hesperhyus antiquus,* and the protoceratid *Prosynthetoceras* (Tedford & Hunter 1984). Although Tedford & Hunter (1984) assigned the Farmingdale local fauna an early Hemingfordian age, it is more likely to be late Arikareean because: *Diceratherium* has its last record in the late Arikareean; and Sugarman et al. (1993) gave strontium-isotope age estimates for the lower Kirkwood of 19.2–22.6 ± 0.5 Ma, which are late Arikareean ages (Tedford et al. 1987). Gallagher et al. (1995) suggested that the Farmingdale local fauna was a mixed assemblage of reworked Arikareean and Hemingfordian fossils; such an interpretation seems unnecessary and unparsimonious, when none of the faunal evidence is inconsistent with a late Arikareean age.

In the United States, *Daeodon* first occurs during the early Arikareean (late Oligocene) and last occurs during the early Hemingfordian (early Miocene) (Tedford et al. 1987). This gives the genus a duration of about 11 million years, from 18 to 29 Ma. The oldest well-dated records of *Daeodon* are in the early Arikareean of South Dakota, Wyoming and Nebraska, though its occurrence in Alabama may be equally old (Westgate 1982). The youngest well-dated records are in the Hemingfordian of Oregon, California and Texas. The ages of *Daeodon* occurrences in South Carolina and Florida are weakly constrained.

Daeodon clearly had a broad distribution across the United States by the late Arikareean. This distribution is consistent with immigration of the genus from Asia via Beringia during the early Arikareean.

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Four new species of spiny rats of the genus *Proechimys* (Rodentia: Echimyidae) from the western Amazon of Brazil

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Abstract.—A total of eight species of spiny rats of the genus *Proechimys* are included within a collection of mammals assembled during a year-long survey of vertebrates along the Rio Juruá in the western Amazon Basin of Brazil. Four of these are the well-recognized taxa in western Amazonia, *P. simonsi, P. brevicauda, P. cuvieri,* and *P. steerei,* but the remaining four are new (*P. echinothrix, P. kulinae, P. pattoni,* and *P. gardneri*). The diagnoses and descriptions of the new taxa are provided herein on the basis of genetic (chromosomes and DNA sequences) and morphological data. The latter include bacular characters, qualitative and quantitative features of the cranium and external morphology.

Resumo.—Oito espécies de ratos-de-espinho do gênero *Proechimys* foram coletadas durante levantamento dos vertebrados terrestres realizado no Rio Juruá, no oeste da amazônia brasileira. Quatro dessas espécies, *P. simonsi, P. brevicauda, P. cuvieri,* e *P. steerei,* são bem conhecidas do oeste da Amazônia, enquanto as demais são novas (*P. echinothrix, P. kulinae, P. pattoni,* e *P. gardneri*). Nesse estudo apresentamos a descrição e o diagnóstico das espécies novas com base em dados genéticos (cromossomos e sequências de DNA) e morfológicos. Estes incluem o tamanho e a forma do baculum, caracteres qualitativos e quantitativos do crânio e da morfologia externa.

The genus *Proechimys* contains medium- to large-bodied rodents known as "spiny rats" due to the presence of wide, flattened and stiff aristiform hairs on their back. This is the most speciose genus of the rodent family Echimyidae and was described in 1899 by J. A. Allen. Traditionally it has been divided into two subgenera, *Trinomys* (restricted to the Atlantic forest of Brazil) and *Proechimys* (distributed from Honduras south to Paraguay in tropical forests below 1000 m; Woods 1993, Emmons & Feer 1997). More recently, Lara et al. (1996) have challenged this subdivision and elevated *Trinomys* to generic status based on phyletic relationships among extant genera of echimyids derived from mtDNA sequences. Here, I use *Proechimys* in the restricted sense, excluding *Trinomys.*

Despite high diversity, large geographic range, and local abundance, spiny rats are taxonomically one of the least understood of all Neotropical mammals. To date, only a few published studies have succeeded in defining local taxonomic groups (e.g., Moojen 1948, Patton & Gardner 1972) and describing character trends over large geographic areas (Gardner & Emmons 1984, Patton 1987).

During a year-long survey of the vertebrates along the Rio Juruá (Projeto Rio Juruá; see Acknowledgments) in the western Amazon Basin of Brazil, we collected approximately 1200 specimens of *Proechimys* spp. After examination of other specimens in museum collections, inspection of holotypes in the Museu Nacional do Rio de Janeiro and of photographs (provided by J. L.

Patton) of the skulls of all holotypes in US museums as well as the British Museum, and review of the scientific literature, I identified the Rio Juruá sample as comprising eight species. Four of these are new to science and I present their descriptions here.

Materials and Methods

Specimens from the Rio Juruá collection received collector initials JLP, JUR and MNFS; they will be deposited either at the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil; the Museu Paraense Emilio Goeldi (MPEG), Belém, Brazil, or the Museum of Vertebrate Zoology (MVZ) of the University of California at Berkeley, where the entire collection is presently housed. All specimens from the Rio Urucu are deposited at INPA. Due to the special value and curation normally given to paratype specimens, and because the Rio Juruá collection will be divided and deposited in three different institutions, adult specimens in good condition were designated as paratypes. A list of all specimens examined is provided under the description of each of the new species.

The species described herein are identifiable on the basis of genetic (chromosomal, DNA sequence, and restriction enzyme data) and morphological characters, especially those of the phallus; qualitative features of the cranium (such as palatal characters and temporal ridge development), and counterfold patterns of the cheekteeth. Throughout this study, age categories assigned to specimens were based on the tooth-wear sequence established by Patton & Rogers (1983). The number of folds on the teeth were counted on both sides of the jaw; when a given tooth had different numbers of folds on the left and right side, the highest number was recorded; coalesced folds (those with a Y-shape) were counted as a range (e.g., tooth with one to two folds, two to three folds, etc.). Capitalized color terms refer to Ridgway (1912).

Cranial measurements (Fig. 1) were taken with digital calipers, and external measurements and weight are those recorded on the specimen label and field notes; measurements are in millimeters and weight (mass) in grams. Measurements (and their abbreviations) are as follow: total length (ToL), including tail; tail length (TaL); hind-foot (HF), including claws; ear (E), from notch; greatest length of skull (GSL), anterior-most projection of nasals to posterior-most projection of occipital region on mid line of skull; basilar length of Hensel (BaL), post margins of upper incisors to anterior edge of foramen magnum; condyloincisive length (CIL), anterior edge of upper incisors to posterior-most projection of occipital condyle; zygomatic arch breadth (ZB), greatest breadth across the zygoma; orbital constriction (IOC), least distance between bony orbits; rostral length (RL), diagonal measure from anterior edge of orbit lateral to lacrimal to anterior edge of nasals at mid line; nasal length (NL), greatest length of nasals at mid line; rostral breadth (RB), breadth of rostrum at arc of upper incisors; rostral depth (RD), least depth of rostrum; orbital length (OL), greatest length of orbits; diastema length (D), post margins of upper incisor to anterior edge PM4; maxillary tooth row length (MTRL), from anterior edge of PM4 at alveolus to posterior edge of M3 at alveolus; incisive foramina length (IFL), length of opening of foramina; palatal length ‘a’ (PLa), posterior edge of upper incisors to anterior edge of mesopterygoid fossa; palatal length ‘b’ (PLb), anterior edge of PM4 at alveolus to anterior edge of mesopterygoid fossa; postpalatal length (PPL), posterior margin of inner aspect of zygomatic arch to a line perpendicular and tangent to greatest projection of occipital region; bullar length (BuL), greatest anterior-posterior length of tympanic bullae; maxillary breadth (MaxB), greatest breadth of maxilla on outside of M1 or M2; occipital condyle width (OccW), width

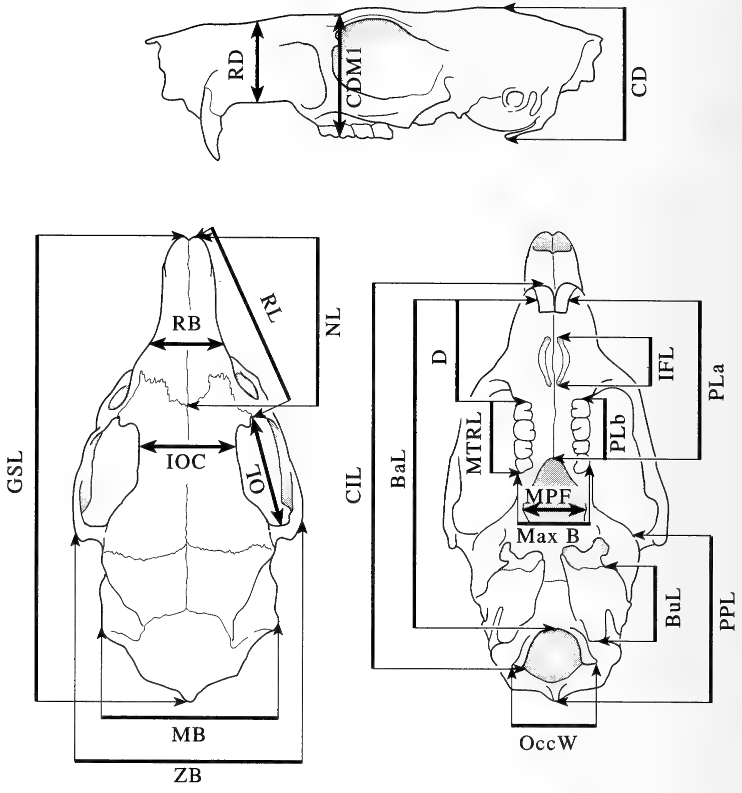

Fig. 1. Positions of 23 cranial dimentions taken on skulls of *Proechimys* spp (see Materials and Methods for explanation of dimensional abbreviations).

across outside margins of occipital condyles; mesopterygoid fossa width (MPFW), greatest width at junction of palatine and pterygoid bones; cranial depth (CD), depth of cranium using a slide resting on bullae (not paroccipital processes); cranial depth at M_1-M_2 (CDM_1). Table 1 summarizes the measurements of adult specimens (age classes 8–10) and Table 2 of the holotypes of the undescribed taxa from the Rio Juruá.

Male phalli were examined from specimens preserved in formalin in the field and maintained in 70% ethanol. Bacular measurements (Table 3) are in millimeters and were taken with a Vernier occular caliper in a dissecting microscope: length (L), greatest distance between anterior and posterior most projections; mid length (MiL), greatest length of baculum at mid line; proximal width (pW), greatest width at the anterior end; distal width (dW), greatest width at the posterior end.

Chromosome preparations followed the basic in vivo colchicine-hypothonic citrate sequence described by Patton (1967). Initially, animals were live trapped in their natural habitats and injected intraperitoneally with colchicine (0.05 grams % - 0.01 ml/g body weight). Cells from dividing bone marrow from the shafts of the femora were then treated in hypotonic KCl prior to fixation in acetic acid-methanol. Back from the field, the cells were resuspended and slides were prepared either by flame or air drying. Diploid numbers were established by counting at least 20 complete cells per individual. Fundamental number is used to designate only the number of autosomal arms, thus excluding the sex pair. The cell suspensions and chromosome slides for all karyotyped specimens are deposited in the MVZ collection, as are tissue samples preserved either in 95% ethyl alcohol or frozen at −76°C. Duplicates of tissue samples preserved in 95% ethyl alcohol will also be maintained at INPA.

To assess the evolutionary independence and relationships of the several species of *Proechimys* identified on the Rio Juruá, I examined the sequence of the first 798 base pairs (266 codons) of the mitochondrial cytochrome b gene. The initial data set included 47 individuals belonging to the four undescribed species, one individual of another unidentified species (but not from the Rio Juruá), and representatives of five of the species-groups of *Proechimys* recognized by Patton (1987), including *P. brevicauda, P. cuvieri, P. simonsi,* and *P. steerei* from the Juruá drainage. Sequences of *Trinomys, Dactylomys, Euryzygomatomys,* and *Thrichomys* as well as *Cavia* and *Coendou* were used as outgroups (Lara et al. 1996). Phylogenetic analyses were performed employing maximum parsimony using PAUP, version 3.1.1 (Swofford 1993). Because saturation was observed in the ingroup taxa at third positions of the codon, all searches were performed excluding third-position transitions. A heuristic search with 10 replicates of random addition of taxa was initially performed including all 58 individuals mentioned above. Subsequently, in order to maximize computer time, haplotypes of a given clade that were less than 1% divergent were pruned. The final analyses presented here includes 21 individuals of *Proechimys* with *Dactylomys* as the outgroup. Methods for DNA extraction, amplification by the polymerase chain reaction (PCR), and sequencing, as well as oligonucleotide primers used in the PCR reactions follow those given in Lara et al. (1996) and da Silva (1995). Sequences for the outgroups are available in Genbank; those for all individuals of *Proechimys,* as well as some of the initial analyses, are presented in da Silva (1995).

Restriction endonucleases were also used to define restriction sites in the mitochondrial cytochrome b gene that could be used as markers to identify specimens of the new taxa for which the cyt b sequences or karyotype were not available. Using the computer program MacDNASIS Pro (v1.0), 246 enzymes were searched for specific restriction sites in approximately 800 bp of the cytochrome b of three to five individuals of each species. Twenty seven restriction sites were identified on those sequences, but just one, N1a IV, generated fragments of distinct sizes and patterns that would discriminate among the species. Amplified PCR products using the primer pair MVZ05-MVZ16 were obtained for a total of 64 specimens. Following the double strand amplifications, the DNA samples were incubated for approximately three hours at 37° in a mixture containing 10× NEB buffer 4, BSA (1000 ng/μl) and the enzyme N1a IV (5 units/μl; New England Biolab). After the digestion, the samples were run in a 1.5% agarose gel with a 100 base pair ladder as a marker. Each of the three species examined had unique restriction fragments. One had fragments of approximately 70, 316 and 439 base pairs (bp; for the individuals from Condor) or 212,

Table 1.—Selected measurements (in millimeters) of males and females adult specimens (age classes 8 through 10; Patton & Rogers 1983) of spiny rats of the genus *Proechimys,* including the mean ± one standard error and range with sample size (see text and Fig. 1 for explanation of variable abbreviations).

Variable	*P. echinothrix* $n = 27$	*P. kulinae* $n = 39$	*P. gardneri* $n = 31$	*P. pattoni* $n = 26$
ToL	382.3 ± 7.0	289.1 ± 4.9	310.1 ± 5.0	305.7 ± 3.1
	(317–440)	(252–328)	(242–353)	(278–328)
	$n = 20$	$n = 17$	$n = 25$	$n = 20$
TaL	171.8 ± 4.3	120.2 ± 2.3	127.7 ± 2.8	126.1 ± 2.0
	(126–209)	(107–140)	(88–152)	(106–141)
	$n = 18$	$n = 17$	$n = 25$	$n = 20$
HF	48.3 ± 0.5	41.0 ± 0.3	40.6 ± 0.5	40.9 ± 0.4
	(41–54)	(38–44)	(32–45)	(37–43)
	$n = 27$	$n = 26$	$n = 31$	$n = 22$
E	24.2 ± 0.4	20.2 ± 0.3	20.8 ± 0.3	20.4 ± 0.3
	(19–28)	(17–23)	(18–24)	(18–23)
	$n = 26$	$n = 24$	$n = 28$	$n = 22$
GSL	55.3 ± 0.5	46.0 ± 0.4	47.6 ± 0.5	46.6 ± 0.4
	(50.0–61.3)	(42.1–51.2)	(42.0–55.0)	(43.0–50.2)
	$n = 23$	$n = 36$	$n = 28$	$n = 22$
BAL	38.5 ± 0.4	32.1 ± 0.3	33.3 ± 0.4	32.4 ± 0.3
	(34.8–42.6)	(27.7–35.8)	(29.5–38.3)	(29.6–34.5)
	$n = 24$	$n = 36$	$n = 27$	$n = 23$
CIL	44.3 ± 0.4	37.4 ± 0.3	38.8 ± 0.5	37.7 ± 0.3
	(39.8–49.0)	(33.9–42.5)	(34.5–46.1)	(34.8–40.1)
	$n = 24$	$n = 36$	$n = 28$	$n = 24$
ZB	25.2 ± 0.2	21.9 ± 0.2	22.5 ± 0.2	22.4 ± 0.2
	(22.5–27.1)	(20.4–24.4)	(20.8–24.5)	(21.4–23.9)
	$n = 24$	$n = 37$	$n = 29$	$n = 23$
MB	20.0 ± 0.1	17.9 ± 0.1	18.4 ± 0.2	17.8 ± 0.1
	(18.8–21.3)	(16.6–19.6)	(16.9–19.9)	(16.9–18.9)
	$n = 25$	$n = 37$	$n = 28$	$n = 23$
IOC	11.7 ± 0.2	9.9 ± 0.1	10.3 ± 0.1	9.8 ± 0.1
	(10.3–13.2)	(8.9–11.7)	(9.1–11.4)	(8.6–10.9)
	$n = 26$	$n = 38$	$n = 29$	$n = 26$
RL	22.0 ± 0.3	17.8 ± 0.2	18.7 ± 0.2	18.1 ± 0.2
	(17.6–25.3)	(15.7–20.1)	(16.6–22.2)	(16.5–19.8)
	$n = 25$	$n = 39$	$n = 30$	$n = 24$
NL	20.2 ± 0.3	16.6 ± 0.2	17.5 ± 0.3	17.1 ± 0.2
	(15.6–23.4)	(14.7–18.9)	(15.4–20.5)	(15.1–19.0)
	$n = 25$	$n = 39$	$n = 29$	$n = 24$
RB	7.8 ± 0.1	6.9 ± 0.1	7.2 ± 0.1	7.0 ± 0.1
	(7.1–9.4)	(6.1–7.3)	(6.4–8.0)	(6.2–8.1)
	$n = 26$	$n = 39$	$n = 31$	$n = 26$
RD	10.3 ± 0.1	8.7 ± 0.1	8.9 ± 0.1	8.6 ± 0.1
	(9.2–11.7)	(7.7–9.9)	(7.9–9.8)	(7.9–9.9)
	$n = 27$	$n = 39$	$n = 30$	$n = 26$
OL	14.0 ± 0.1	11.9 ± 0.1	12.3 ± 0.1	12.0 ± 0.1
	(13.0–15.2)	(11.0–13.8)	(11.3–13.4)	(10.4–12.8)
	$n = 24$	$n = 38$	$n = 29$	$n = 26$
D	11.6 ± 0.2	9.4 ± 0.1	9.8 ± 0.1	9.1 ± 0.1
	(9.2–13.9)	(8.4–11.0)	(8.6–11.4)	(7.3–10.1)
	$n = 26$	$n = 39$	$n = 31$	$n = 26$
MTRL	8.3 ± 0.1	7.1 ± 0.1	7.5 ± 0.1	7.2 ± 0.0
	(7.6–9.2)	(6.3–8.6)	(6.9–8.2)	(6.7–7.5)
	$n = 27$	$n = 39$	$n = 31$	$n = 25$

Table 1.—Continued.

Variable	*P. echinothrix* *n* = 27	*P. kulinae* *n* = 39	*P. gardneri* *n* = 31	*P. pattoni* *n* = 26
IFL	5.3 ± 0.1	4.0 ± 0.1	4.1 ± 0.1	4.0 ± 0.1
	(4.0–6.1)	(3.0–5.1)	(3.4–5.0)	(3.0–4.8)
	n = 26	*n* = 39	*n* = 31	*n* = 26
PLA	18.8 ± 0.3	14.8 ± 0.2	15.8 ± 0.2	15.0 ± 0.2
	(14.9–21.0)	(13.0–18.1)	(13.5–18.4)	(13.7–16.5)
	n = 26	*n* = 39	*n* = 31	*n* = 26
PLB	7.8 ± 0.1	5.9 ± 0.1	6.5 ± 0.1	6.3 ± 0.1
	(6.3–9.1)	(5.3–6.9)	(5.6–7.7)	(5.6–7.9)
	n = 27	*n* = 39	*n* = 31	*n* = 26
PPL	22.2 ± 0.2	19.0 ± 0.2	19.4 ± 0.2	18.8 ± 0.4
	(20.3–24.6)	(17.1–21.5)	(17.0–21.9)	(10.5–20.4)
	n = 25	*n* = 37	*n* = 29	*n* = 24
BUL	10.2 ± 0.1	9.7 ± 0.1	9.9 ± 0.1	9.6 ± 0.1
	(9.3–11.0)	(8.7–10.3)	(9.0–10.6)	(7.3–10.9)
	n = 26	*n* = 39	*n* = 30	*n* = 26
MAXB	8.3 ± 0.1	7.2 ± 0.1	7.3 ± 0.1	7.1 ± 0.1
	(7.6–9.6)	(6.4–8.6)	(6.5–8.2)	(6.3–8.0)
	n = 26	*n* = 39	*n* = 31	*n* = 25
OCCW	9.3 ± 0.7	8.2 ± 0.1	8.6 ± 0.1	8.1 ± 0.1
	(8.7–9.9)	(7.5–9.1)	(8.0–9.4)	(7.3–9.0)
	n = 24	*n* = 39	*n* = 28	*n* = 22
MPFW	5.4 ± 0.1	4.0 ± 0.1	4.3 ± 0.1	3.9 ± 0.1
	(4.9–6.1)	(3.0–4.6)	(3.7–5.3)	(3.1–4.8)
	n = 23	*n* = 38	*n* = 29	*n* = 22
CD	17.9 ± 0.1	15.0 ± 0.2	16.0 ± 0.1	15.8 ± 0.1
	(16.6–19.4)	(13.1–17.5)	(15.0–17.1)	(14.5–16.6)
	n = 24	*n* = 37	*n* = 29	*n* = 23
CDM1	14.1 ± 0.1	11.9 ± 0.1	12.3 ± 0.1	12.0 ± 0.1
	(12.6–15.2)	(11.1–14.0)	(11.3–13.1)	(11.1–12.7)
	n = 24	*n* = 38	*n* = 29	*n* = 24

297, and 316 bp (those from Barro Vermelho). Sequences of the other two species resulted in two fragments of approximately 316/509 bp, and 103/722 bp, respectively.

Proechimys echinothrix, new species

Etymology.—Gr. *echinos,* hedgehog or sea urchin; *thrix,* hair. Named for the unusually stiff and broad dorsal aristiforms.

Holotype.—INPA 2550 (Instituto Nacional de Pesquisas da Amazônia - Coleção de Mamíferos, Manaus, Amazonas, Brazil), adult female, collected on 29 May 1992 by M. N. F. da Silva (original number MNFS 1703); skin, skull and mandibles in good condition, plus karyotype and tissue sample preserved in ethyl alcohol.

Type locality.—Brazil, Amazonas: Colocação Vira-volta, left bank Rio Juruá on Igarapé Arabidi, affluent of Paraná Breu, 66°14′W, 3°17′S. Obtained in terra firme (or upland, non-seasonally flooded) forest.

Diagnosis.—A medium- to large-sized spiny rat with dorsum covered by extremely heavy, broad and long aristiform hairs having distinctly strong and blunt tips that are very conspicuous to the eye and touch. The ears are large. The tail is moderately long, approximately two-thirds of body length and bicolored with sharply defined white venter and dark dorsum; the hair on the tail is very abundant, almost completely hiding scales. The top of hind-foot is nearly unicolored white in most specimens, and without a dark band on the ankle joint. The cranial features include weakly-developed pos-

Table 2.—Selected measurements (in millimeters) of holotypes of four new species of spiny rats of the genus *Proechimys* (see text and Fig. 1 for explanation of variable abbreviations).

Variable	*P. echinothrix* (INPA 2550)	*P. kulinae* (INPA 2553)	*P. gardneri* (INPA 2559)	*P. pattoni* (INPA 2565)
ToL	380	308	342	322
TaL	159	131	142	130
HF	46	40	41	41
E	23	21	22	22
GSL	53.8	45.4	49.6	47.1
BAL	37.7	32.2	35.0	32.7
CIL	43.6	36.8	40.0	38.2
ZB	24.9	22.0	24.1	23.0
MB	19.2	17.9	19.6	18.3
IOC	11.0	9.7	10.6	10.0
RL	21.0	17.4	18.8	17.9
NL	18.9	16.4	17.0	17.0
RB	8.3	7.1	7.1	7.1
RD	10.1	8.8	8.3	8.3
OL	14.0	11.9	12.9	12.5
D	11.3	9.3	10.1	9.4
MTRL	8.0	7.3	6.9	7.3
IFL	5.6	4.2	4.6	4.2
PLA	17.7	15.0	16.2	15.0
PLB	7.2	6.2	6.7	6.2
PPL	22.3	18.6	20.9	20.1
BUL	9.8	9.5	10.5	9.9
MAXB	8.4	6.9	7.9	7.2
OCCW	9.4	8.4	8.7	9.0
MPFW	5.0	3.8	4.3	3.7
CD	17.5	15.3	16.1	16.3
CDM1	13.6	12.4	12.9	12.5

terior portion of the temporal ridges; ovate to lyrate incisive foramen with an expanded and long contribution of the premaxillary portion in contrast to the attenuate flanges and attenuate maxillary portion which also lacks a keel. The baculum is broad and short with well developed apical wings defining a deep medial notch. Karyotype is 2N = 32 and FN = 60.

Distribution.—The known range of *P. echinothrix* is restricted to the western Brazilian Amazon in the lower Rio Juruá drainage (known from two localities on the left and one on the right bank) and to the east from the alto Rio Urucu, in the state of Amazonas (Fig. 2). However, the group of species to which *P. echinothrix* belongs has a much wider distribution. Recently, *P. echinothrix*-like animals were collected throughout the Parque Nacional do Jaú,

Table 3.—Mean and range of bacula measurements (in millimeters) of *Proechimys echinothrix, P. kulinae, P. pattoni,* and *P. gardneri* (see Material and Methods for explanation of variable abbreviations).

Variable	*P. echinothrix* $n = 2$	*P. kulinae* $n = 6$	*P. gardneri* $n = 8$	*P. pattoni* $n = 5$
L	8.4 (8.3–8.6)	6.7 (5.4–8.2)	7.7 (6.5–8.6)	8.3 (7.4–9.4)
MiL	7.0 (6.7–7.3)	6.7 (5.4–8.2)	6.9 (6.0–7.8)	6.3 (4.7–8.0)
pW	5.1 (4.8–5.4)	1.6 (1.6–2.1)	4.0 (3.3–5.0)	4.7 (4.2–5.1)
dW	4.6 (4.2–5.1)	1.7 (1.7–2.6)	3.4 (2.7–4.1)	3.8 (3.1–4.2)

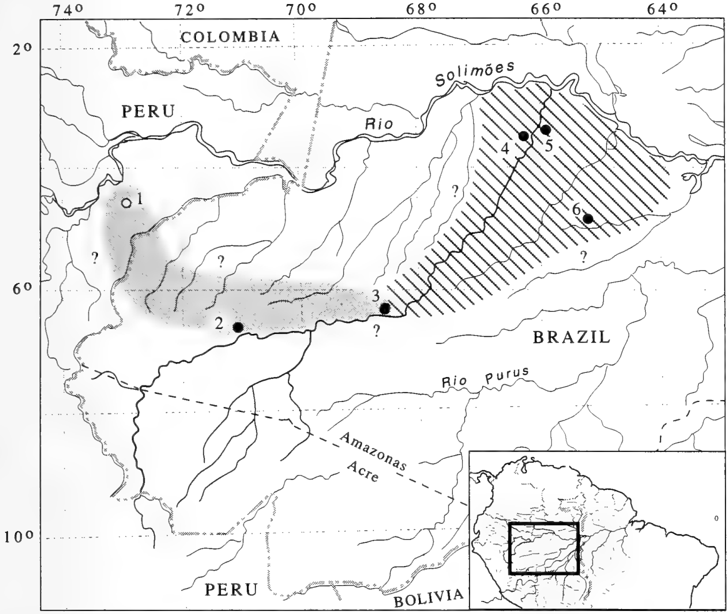

Fig. 2. Geographic distribution of the spiny rats *Proechimys echinothrix* (cross hatched) and *P. kulinae* (stipples). Localities from which samples were examined are indicated by the dots; solid ones are those for which 801 base pairs of cytochrome b sequences were examined; the open dot represents the locality for which no cyt b sequence is available. Localities are numbered according to the locality list in Appendix 1 and text.

northwest of the mouth of the Rio Negro in the central Amazon. Preliminary analyses of these materials suggest this is a new species, which will be described elsewhere, but closely related to *P. echinothrix*. J. L. Patton (pers. comm.) examined some specimens from Río Vaupés, in Amazonian Colombia, in the collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia in Bogotá that have the strongly developed aristiform dorsal hairs and that he also believes to be related to *P. echinothrix*.

Description

External features.—This is one of the most readily distinguishable species of *Proechimys* and one of the largest species of spiny rats occuring in western Brazil. In overall size *P. echinothrix* corresponds to individuals of the *P. goeldii* and *P. simonsi* groups (as defined by Patton, 1987). In general morphology these animals are robust, have long tail and ears (mean 24 mm), and large hind-feet (mean 48 mm; see Tables 1 & 2). The length of the tail is about two-thirds that of the head and body; it is distinctly bicolored, the dark skin and hairs of the dorsum make a sharp contrast with the white skin and hairs of the ventrum. Individual hairs on the upper surface of the tail extend from the distal portion of the scales for the length of five to seven annuli (annuli

Table 4.—Length and width (in millimeters) of individual aristiform hair from the mid-back of adult specimens (age classes 8 through 10; Patton & Rogers 1983) of the new species of spiny rats genus *Proechimys*, including the mean ± one standard error and range with sample size. Measurements were taken with a Vernier occular caliper in a dissecting microscope.

Variable	*P. echinothrix*	*P. kulinae*	*P. gardneri*	*P. pattoni*
Length	21.8 ± 0.6 (19.3–24.1) *n* = 10	18.1 ± 0.4 (16.4–20.0) *n* = 9	17.0 ± 0.2 (15.4–19.9) *n* = 45	14.9 ± 0.1 (13.2–15.9) (*n* = 40
Width	1.4 ± 0.0 (1.2–1.6) *n* = 10	0.9 ± 0.0 (0.8–1.0) *n* = 9	0.8 ± 0.1 (0.7–1.0) *n* = 45	0.6 ± 0.0 (0.5–0.8) *n* = 40

of scales narrow, with 12–15 per centimeter); the hair tends to completely hide the scales giving an almost brushy aspect to the tail, when compared to other species of *Proechimys*. Overall, the color of the body is uniform from head to rump, varying between Sanford's Brown to Auburn among individuals, and coarsely streaked with varying amounts of black both on the dorsum and sides; the interspersed heavy dark-brown guard hair give the mid dorsum a somewhat darker aspect, but there is no sharp color contrast with the sides of the body. Aristiforms are long and much broader than those of all other species of spiny rats found along the Rio Juruá (see Table 4 & Fig. 3), and have distinctly strong and blunt tips especially in the mid dorsum. The color of the venter, chin, sides of the upper lips, spot at base of vibrissae (when present, sometimes confluent with the upper lips and chin), under surfaces of forelimbs, and hind limbs is pure white. The hind-feet are long and narrow, mostly white above. The pure white color of the under surface of the hind limbs extends across the tarsal joint and over the outer surface of the hind-feet to the base of the digits; in a few specimens, the distal portion of all, or some digits is dark-brown. In the Rio Urucu specimens, however, most of the top of the hind-foot is pure white, although the tarsals, the entire first and second digits, or just the distal end of all digits may have dark-brownish hair. The juvenile pelage varies from uniformly grayish-brown (age class 1) to pale-brown mixed with Sanford Brown (age class 6). One specimen of age class 1 from the Rio Juruá is uniformly grayish-brown on the dorsum and with slightly paler sides; the venter, the chin and the sides of the upper lips are pure white. Two specimens from the Rio Urucu of age classes 4 and 5 are similar except that they show some rusty hair around the ear lobes; at those ages, spines on the back are conspicuous to the eye and the hair on the sides of the body is a little streaky; two specimens of age class 6 from that same locality have adult-like, heavy spines in a patch on the middle of the back, and soft streaked adult hair on the face; a third specimen from the Rio Juruá of age class 6 has adult pelage throughout the mid and lower back, with the sides of the body and thighs showing soft juvenile hair (gray at the base and Sanford's Brown of varying amounts on the tips). A few adult specimens of age class 9 from both drainages retain soft grayish juvenile-like hair on the rump, although in the great majority, adult pelage covers the entire body.

Plantar surface of hind-foot.—The plantar surface of the hind-feet has six tubercules; the lateral metatarsal tubercule (lmt; fifth postdigital tubercule, sensu Hershkovitz 1960:524–525) is weakly to moderately-developed (but always visible), and short when compared to the medial metatarsal tubercule (mmt); the position of the medial and lateral metatarsal tubercules with first and fourth postdigital tubercules is close-set and arranged as points of a square or rect-

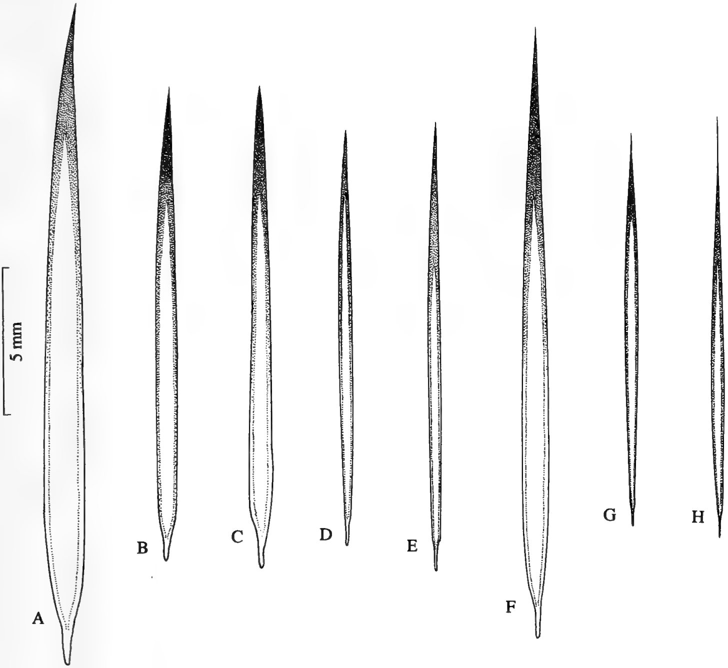

Fig. 3. Mid dorsal aristiform hairs of all eight species of *Proechimys* found in the Rio Juruá: (A) *P. echinothrix* (INPA 2551); (B) *P. kulinae* (MVZ 187193); (C) *P. gardneri* (MVZ 187204); (D) *P. pattoni* (MPEG 25509); (E) *P. brevicauda* (MNFS 1159); (F) *P. cuvieri* (JLP 15463); (G) *P. simonsi* (MNFS 1468); and (H) *P. steerei* (JLP 15388). Note the large size of *P. echinothrix* and the delicate and whip-like tip of the hair of *P. steerei* relative to the others.

angle; the distance between mmt and first postdigital tubercule is equal to or less than the width of mmt; the hallux extends to the posterior margin or to the middle of second postdigital tubercule; the distance between the heel and the first postdigital tubercule is approximately equal to the distance between first postdigital tubercule and the end of third digit.

Cranial features.—The skull is relatively large, with a long and narrow rostrum (see Table 1 & Fig. 4). The supraorbital ridge is well developed extending along the orbits but discontinuous across the parietals; the anterior portion of this crest is almost at the same level as a somewhat weakly-developed posterior portion. The postorbital process of the zygoma is either absent or very weakly-developed, and rather rounded; this process consists either of the squamosal (9 out of 22 individuals) or of an approximately equal contribution of both the squamosal and jugal bones (i.e., shows a suture at the apex of the process in 8 individuals; in four individuals the process is formed mostly by the jugal). The ventral canal on

Fig. 4. Dorsal, ventral, and lateral views of cranium of the holotype of *Proechimys echinothrix*, new species, INPA 2550, adult female (original number MNFS 1703).

the floor of the infraorbital foramen has weakly to moderately-developed lateral flanges (among 26 specimens only two had a smooth medial floor and weakly-developed flanges; all others showed a well-defined groove); specimens from the Rio Urucu have slightly less-developed flanges than those from the Rio Juruá. The overall shape of the incisive foramen is ovate to lyrate, with posterolateral margins mostly flat, sometimes with very weakly-developed flanges and grooves extending onto the anterior palate (which is smooth, without a medial ridge); the premaxillary portion of the septum is long and narrow, usually extending from ½ to ⅔ the length of the foramen; the maxillary portion ranges from attenuate to expanded anteriorly and is usually in tenuous to no contact with the premaxillary portion (in 11 of 26 specimens these two portions were not in contact); the vomer is visible in most specimens (completely enclosed in 2 of 25 specimens). The mesopterygoid fossa is shallow to moderately deep, and broad, with angle of indentation into posterior margin of palate averaging 70.5° (62–74°) and extending to the anterior one-half of M3 in 13 out of 26 specimens; to the posterior one-half of M3 in 10 specimens, and barely reaching the posterior margins of M3 in three specimens. The number of folds in the lower cheek teeth varies with pm4 presenting the higher numbers, with either three or four folds (in 9 and 15 individuals respectively); m1 with two or three folds (in 8 and 17 individuals respectively); m3 with two folds (23 out of 25 individuals; the others have three and three to four folds, depending how the Y-shaped fold is counted); in all upper teeth the modal number of folds is three (in 24 out of 26 individuals; the other two have two or two to three folds in M3).

Phallus.—The glans penis (three adult specimens examined) is long, and sub-cylindrical with almost straight dorsal and lateral margins (Fig. 5). The mean length (measured on the dorsal side from the prepuce to tip) is 16.3 mm, mean greatest width is 6.8 mm, and index of robustness (greatest diameter/length) is 0.41, on average. The dorsal surface of the glans above the baculum is smooth to slightly striate and becomes more corrugated towards the side and tip. In the area above the depression between the apical extensions of the baculum (see below), there is a small hollow, filled in some specimens by a mass of tissue, that converges as a longitudinal slit towards the tip (present in two out of three specimens). The ventral surface is corrugated and has a prominent swelling at about mid length; from near the base to the apex, it is bisected by a fine and discontinuous keel-like midventral ridge. No enlarged lip protrudes from the dorsal rim of the glans.

Baculum.—The baculum is massive and relatively short; its shaft is broad with a thick and expanded base; mean and range of measurements are presented in Table 3. The distal end has a pair of divergent apical extensions separated by a shallow median depression (Fig. 6). This baculum is most similar in shape and size to that of *P. cuvieri* (figured in Patton, 1987).

Karyotype.—2N = 32 and FN = 60 (Fig. 7). Chromosome preparations are available for 29 individuals (14 males and 15 females). The autosomes comprise two pairs of very large metacentrics; eight pairs of medium-sized to small metacentrics and submetacentrics; one pair of large and four pairs of small to medium-sized subtelocentrics. The X-chromosome is a small acrocentric and the Y-chromosome is a smaller acrocentric. The karyotype of *P. echinothrix* is similar to that of *P. simonsi,* which also has 2N = 32, but differs by having one extra pair of small subtelocentrics and lacking the large pair of acrocentric chromosomes (see Patton & Gardner 1972).

Paratypes.—Seven specimens listed by locality as numbered in the map, Fig. 2: Brazil—Amazonas: (3) Barro Vermelho, left bank Rio Juruá, 68°46′W, 6°28′S—MVZ 187167, adult male, skin and skull plus glans, tissue sample, and karyotype; MVZ 187168, adult female, skin and skull plus tissue sample; INPA 2551, adult male, skin and skull plus glans, tissue sample, and karyotype; INPA 2552 adult female, skin and skull plus tissue sample and karyotype; MPEG 25500, adult female, skin and skull plus tissue sample and karyotype; (4) type locality—MVZ 187169, adult male, in fluid with skull removed plus tissue sample and karyotype; (5) Lago Vai-quem-quer, right bank Rio Juruá, 66°01′W, 3°19′S—MPEG 25501, adult male, in fluid with skull removed plus tissue sample and karyotype.

Other specimens examined.—Brazil, Amazonas: (3) Barro Vermelho, left bank Rio Juruá, 68°46′W, 6°28′S—JLP 15816; JUR 188; (4) type locality—JUR 430; MNFS 1694, 1698, 1699, 1704, 1714, 1715, 1716, 1719, 1723, 1724; (5) Lago Vai-quem-quer, right bank Rio Juruá, 66°01′W, 3°19′S—JUR 273, 287, 290, 298, 301, 319, 324, 336, 342, 343, 356, 357, 358, 360, 361, 363, 364, 374, 375, 377,

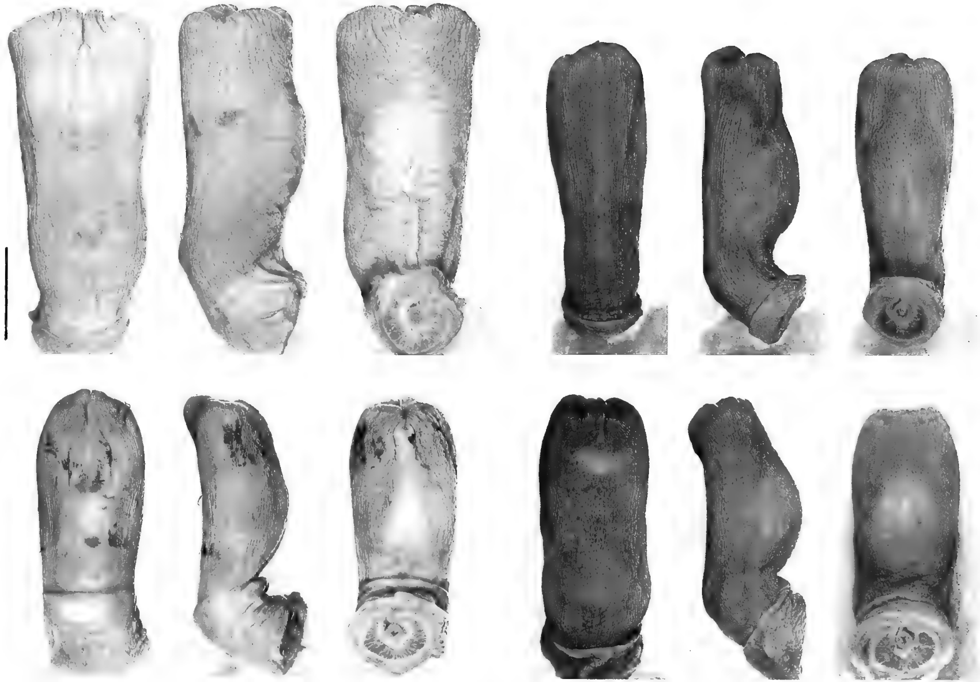

Fig. 5. Dorsal, lateral, and ventral views of the male phallus of (upper left) *Proechimys echinothrix* (MVZ 187167), (upper right) *P. kulinae* (MVZ 187192), (lower left) *P. pattoni* (MPEG 25511), and (lower right) *P. gardneri* (MPEG 25514). Line = 5 mm.

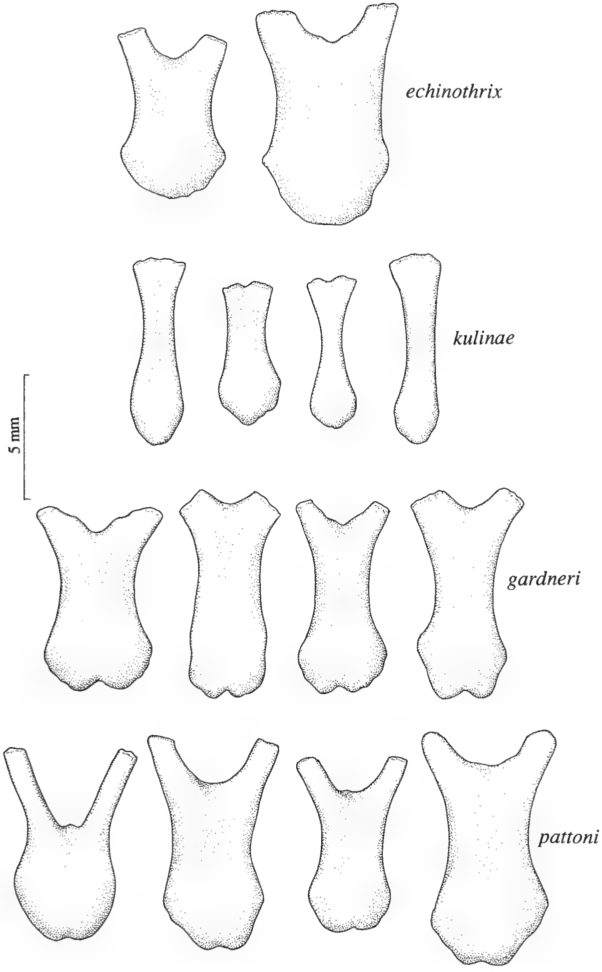

Fig. 6. Representative bacula of members of (from top to bottom and left to right) *Proechimys echinothrix* (MVZ 187167 and INPA 2551—Brazil: Amazonas, Barro Vermelho, left bank Rio Juruá, 68°46′W, 6°28′S); *P. kulinae* (MPEG 25502, INPA 2557, INPA 2553 [holotype], and INPA 2555—Brazil: Amazonas, Condor, left bank Rio Juruá, 70°51′W, 6°45′S); *P. gardneri* (INPA 2566, INPA 2565 [holotype], MVZ 187203, and INPA 2567—Brazil: Amazonas, Altamira, right bank Rio Juruá, 68°54′W, 6°35′S), and *P. pattoni* (MPEG 25509, INPA 2560, MVZ 187194, and INPA 2564—Brazil: Amazonas, Porongaba, right bank Rio Juruá, 72°47′W, 8°40′S).

Fig. 7. Karyotypes of (from top to bottom) *Proechimys echinothrix* (JUR 395; male, 2N = 32, FN = 60); *P. kulinae* (MPEG 25505; male, 2N = 34, FN = 52); and *P. pattoni* (MNFS 1428; female, 2N = 40, FN = 56); *P. gardneri* (MNFS 121; male, 2N = 40, FN = 56).

378, 390, 395, 396, 401, 403, 404, 406; (6) alto Rio Urucu, 65°16′W, 4°51′S—JLP 14773; MNFS 17, 30, 31, 45, 68, 78, 80, 81, 113, 115, 121, 126, 132, 133, 142, 165, 175, 169, 191.

Proechimys kulinae, new species

Etymology.—Named after the Kulina, an Arawakan-speaking indigenous people of the Juruá and Purus drainages of western Amazonia. The type specimen was collected near a Kulina indigenous reserve on the central Rio Juruá.

Holotype.—INPA 2553 (Instituto Nacional de Pesquisas da Amazônia - Coleção de Mamíferos, Manaus, Amazonas, Brazil), adult male, collected on 21 Sep 1991 by M. N. F. da Silva (original number MNFS 560); skin with skull and mandibles in good condition, plus glans preserved in ethyl alcohol and liver tissue preserved both deep frozen and in ethyl alcohol.

Type locality.—Brazil: Amazonas; Seringal Condor, left bank Rio Juruá, 70°51′W, 6°45′S. Obtained in terra firme forest.

Diagnosis.—This is a small rat with a short tail (ca. 40% of body length); the tail is almost naked, distinctively bicolored with dark-brown dorsum and white ventrum; the hind-foot is short (<44 mm) and narrow, mostly white above; lateral metatarsal tubercule on plantar surface of hindfoot mostly absent (in 12 out of 16 specimens); ears are small (not larger than 23 mm). The dorsal color is relatively uniform (Sanford's Brown to Auburn), coarsely streaked with varying amounts of black, both on the dorsum and sides; the heavy dark-brown aristiform hair on dorsum form a darker band that contrasts with the color of the sides of the body; aristiforms are relatively wide and long; the skull is small and narrow with a short rostrum; the incisive foramen is evenly tapered to moderately lyrate, with weakly-developed posterolateral margins; the mesopterygoid fossa is moderately deep and narrow, extending to the anterior one-half of M3 (angle ranges from 50 to 69°); karyotype is 2N = 34 and FN = 52.

Distribution.—Currently known only from two localities on the left bank of the central portion of the Rio Juruá in the Brazilian state of Amazonas and one locality in the Peruvian department of Loreto (Fig. 2).

Description

External features.—*Proechimys kulinae* is one of the smallest species of spiny rats to occur on the Rio Juruá (average total length 291 mm). In general morphology these animals are relatively delicate, have small ears (less than 23 mm), and a moderately short tail and hind-feet (see Tables 1 & 2). The tail is approximately 40% of body length and has a distinct dark dorsal stripe and white undersurface. The scales on the tail are conspicuous to the eye, with about 11 annuli per centimeter; they are covered by three strands of hair each approximately two annuli long and generally positioned at the central distal end of the scale and on each side on the proximal margin. Ventral tail hairs are white and very fine; on the dorsal surface this fine hair mixes with heavier dark-brown hair. Overall, the color of the body appears uniform (Sanford's Brown to Auburn), coarsely streaked with varying amounts of black both on the dorsum and sides; the interspersed heavy dark-brown guard hair of the dorsum forms a broad darker stripe that contrasts with the sides of the body. The venter, chin, and undersurfaces of fore and hind limbs are pure white; the upper lip is dark with little or no white hair; the tarsal joint is either encircled by dark and rusty hair, or the tarsal ring is broken by a strip of white hair confluent with that of the undersurface of the hind limbs in equal number of specimens; the hind-foot, including digits, is white, with some golden tones in most individuals. The pelage of juvenile specimens (all from Condor, locality 2; Fig. 2) varies from dark grayish-brown (age class 2) to pale-brownish mixed with rusty hair (age class 5). One specimen of age class 3 has uniformly grayish-brown guard hair on the dorsum, soft streaky hair slightly paler on the sides that contrasts sharply with the white hair of the venter; it also has an almost pure white stripe approximately 2 cm long and almost half centimeter wide extending from the nose to the top of the head and several other white stripes around the shoulders with some of them extending to the middle of the back. One individual of age class 4 and three of age class 5 are mostly covered by soft hair, predominantly streaked with a dark-brown band and rusty tips; two of the three older individuals have adult pelage on the face and a patch with heavy spines on the middle of the back. In one specimen of age class 7, most of the body is covered by adult pelage, except the shoulders that are covered by juvenile pelage. Five individuals from Quebrada Blanco, northern Perú, also have a dark ankle, three with mostly white hind-feet, and two with uniformly brownish and whitish hair over the upper surface of the foot.

Plantar surface of hind-foot.—The description is based on dried skins only (no fluid specimens are available). The majority (12 of 16) specimens have five tubercules, lacking the lateral metatarsal tubercule; the remaining four specimens have six tubercules. The hallux (with claws) is relatively short, reaching the posterior half of the second postdigital tubercule in most specimens, extending to the anterior half only in two.

Cranial features.—The skull is relatively small, with short and narrow rostrum (Fig. 8). The supraorbital ridge is well developed above the orbits and on the anterior portion of the parietals, but discontinuous with the posterior portion of the crest weakly-developed to absent. The postorbital process of the zygoma is well developed; in nine specimens the process is formed mostly by the squamosal, in six by the jugal, or by both bones in five individuals. The overall shape of the incisive foramen is squarish to slightly ovate or lyrate, with the posterolateral margins nearly flat, sometimes with an attenuate flange; no groove extends onto the anterior palate, but in some specimens the maxillary portion of the foramen is expanded and extends anteriorly, forming a shelf that gives the appearance of a weakly-developed groove; the palate is smooth, lacking a medial ridge; the premaxillary portion of the septum is short, extending for less than half the length of the foramen; the maxillary portion is attenuate to expanded anteriorly and usually in contact with the premaxillary portion (in only 1 of 17 specimens these two portions did not touch); the vomer is either completely enclosed or barely visible. The ventral canal on the floor of the infraorbital foramen is smooth in most specimens (14) or weakly-developed (four of 18). The mesopterygoid fossa is broad with an angle of indentation into posterior margin of palate averaging 57° (50–69°), and moderately deep, extending to the anterior one-half of M3 in 16 of 18 specimens; in two others it reaches the posterior half of M3 (see Patton 1987). The lower cheek teeth are more variable than the uppers in number of counterfolds: pm4 with either three or four folds in equal number of specimens (n = 16); m1 the most variable with the folds ranging from two to four (3 specimens with two folds, 9 with three, 3 with two to three, and 2 with three to four); m2 with either two folds (4 specimens), three folds (10 specimens) or two to three folds (4 specimens); m3 with two folds in 17 specimens and three folds in only 1. All upper teeth but M3 have three folds in all specimens (in four of 18 M3 have two folds).

Phallus.—The glans penis (five adults examined) is moderately large, elongate, and tubular with nearly straight dorsal and lateral margins (Fig. 5). The mean length (measured on the dorsal side from the prepuce to tip) is 11.1 mm, and mean greatest width is 3.8 mm; index of robustness (greatest diameter/length) averages 0.34. The external surface is slightly corrugated

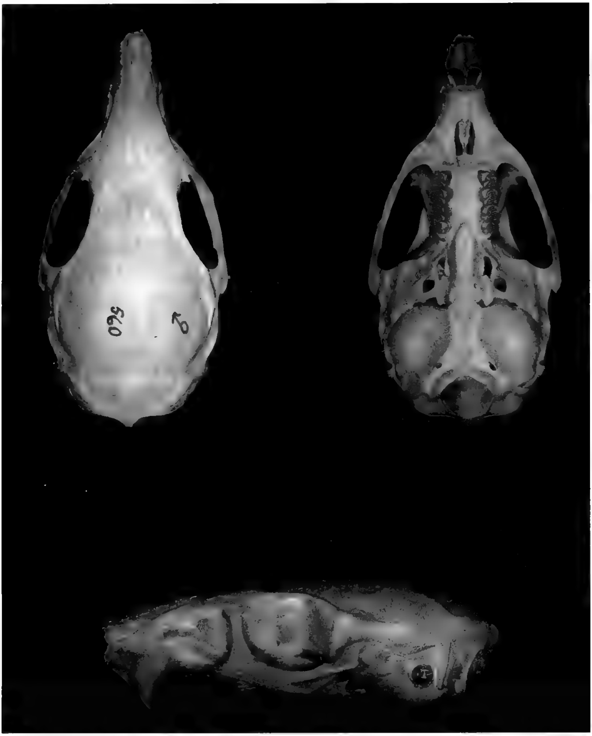

Fig. 8. Dorsal, ventral, and lateral views of cranium of the holotype of *Proechimys kulinae,* new species, INPA 2553, adult male (original number MNFS 560).

and sparsely covered with spines usually recessed deep into the wrinkles, especially on the dorsum and sides. A dorsal mound at the tip of the glans contains the urethral aperture, which opens almost at the rim of the glans but still within the ventral side of the mound between smooth, well-developed non-spinuous plaits of tissue. The most prominent feature of the glans is an ampulla-shaped mass, situated approximately midway along the ventral surface, covered by either serrate or single-pointed spines buried in small and irregular pits, and bordered by deep troughs that are widely separated but converge towards the tip.

Baculum.—The baculum is elongate and relatively narrow, with moderately-developed apical wings (Fig. 6). The proximal and distal ends are about equal in width for all specimens examined (Table 3). In overall shape it is similar to the bacula of *P. simonsi* and *P. steerei* (Patton 1987), which are absolutely bigger (mean L = 8.6 and 7.4 mm, respectively).

Karyotype.—2N = 34; FN = 52 (Fig. 7). Chromosomal preparations were examined for 19 individuals (9 males and 10 females); modal diploid number is 34. The preparations were not uniformly good and the following description is based on the best examples. The autosomes comprise one pair of very large metacentrics; six pairs of medium-sized to small pairs of metacentrics and submetacentrics; one pair of large and one pair of medium-sized subtelocentrics, of which the latter has a secondary constriction on the longer arm; and one pair of large and five pairs of small to minute acrocentrics. The X-chromosome is a moderately small metacentric and the Y-chromosome is a minute submetacentric. This is the first *Proechimys* reported with 34 chromosomes.

Paratypes.—Sixteen specimens listed by locality as numbered in the map, Fig. 2: Brazil—Amazonas: (2) type locality—INPA 2554, adult female, skin and skull plus tissue samples and karyotype; INPA 2555, adult males, skin and skull plus glans, tissue samples and karyotype; INPA 2556, adult female, skin and skull plus tissue samples and karyotype; INPA 2557, adult male, skin and skull plus glans, tissue samples; MPEG 25502 adult male, skin and skull plus glans, tissue samples and karyotype; MPEG 25503, sub-adult female, skin and skull plus tissue samples and karyotype; MPEG 25504, adult female, skin and skull plus tissue samples and karyotype; MPEG 25505, adult male, skin and skull plus glans, tissue samples and karyotype; MPEG 25506, adult female, skin and skull plus tissue samples; MVZ 187184, adult female, skin and skull plus tissue samples; MVZ 187185, adult male, skin and skull plus tissue samples; MVZ 187186-7, adult females, skin and skull plus tissue samples; MVZ 187188, adult female, skin and skull plus tissue samples and karyotype; (3) Barro Vermelho, left bank Rio Juruá, 68°46′W, 6°28′S—MVZ 187193, adult male, skin and skull plus glans, tissue samples; INPA 2558, adult female, skin and skull plus tissue samples.

Other specimens examined.—Brazil, Amazonas: (2) type locality—JLP 15534, 15562, 15602, 15660, 15680; JUR 178, 179, 180, 181, 182, 185; MNFS 546, 552, 554; (3) Barro Vermelho, left bank Rio Juruá, 68°46′W, 6°28′S—JUR 186. Perú, Loreto: (1) Quebrada Blanco, just outside the Reserva Comunal Tamshiyacu-Tahuayo—field numbers: E, 042, 063, 088, 100, 138, 141, 150, 208, 269, 275, 310, 335, 345, 360. These Peruvian specimens were kindly made available by Michael Valqui and collected by himself and Cesar Reyes (Universidad Nacional de la Amazonia del Perú).

Systematic remarks.—Despite a uniform morphology and chromosome complement, sequence divergence between the two Juruá populations of *P. kulinae* is extensive (10.1%). Here, I have considered them to represent a single species primarily because of the lack of possible comparisons of the two Juruá populations other than by sequence data only, and by virtue of the limited sample size (locality 2, Condor: 30 specimens examined, three individuals sequenced; and locality 3, Barro Vermelho: only three specimens available, two individuals sequenced), which precludes a realistic assessment of morphological variation between these populations; and the lack of cytochrome b sequence from Quebrada Blanco in northern Perú (locality 1), hindering its placement relative to either Juruá localities (see below & da Silva 1995).

The geographic distance between Condor and Barro Vermelho is approximately 200 km, a short distance within the confines of the Amazon Basin, but also small relative to the size of the Rio Juruá drainage itself. Future field and laboratory work is needed to determine the levels of genetic and morphologic variability within and between these and other populations.

Proechimys pattoni, new species

Etymology.—Named after James L. Patton for his invaluable contribution to the systematics of neotropical small mammals, particularly for clarification of patterns of geographic and non-geographic variation in spiny rats. The name also honors Jim for his friendship and continuous support.

Holotype.—INPA 2559 (Instituto Nacional de Pesquisas da Amazônia - Coleção de Mamíferos, Manaus, Amazonas, Brazil), adult female, collected on 24 Feb 1992 by M. N. F. da Silva (original number MNFS 1292); skin, skull and mandibles in good condition, plus karyotype and tissue samples preserved both deep frozen and in ethyl alcohol.

Type locality.—Brazil: Acre; Igarapé Porongaba, right bank Rio Juruá, 72°47′W, 8°40′S. Obtained in terra firme forest.

Diagnosis.—A small rat with relatively short tail (60% to 83% of body length) covered by fine hair; the tail is dark-brown above, and pale-brown to white below, with conspicuous scales. The head is small, relatively narrow and with a pointed snout; ears small (less than 23 mm). The hind-foot is narrow and short (less than 43 mm), mostly white with a dark band around the ankle; plantar surface with 5 to 6 pads and a long medial metatarsal tubercule. The color of the body is relatively uniform and without a sharp contrast between the dorsum and the sides, except for the upper back where the dark-brown heavy spines give it a somewhat darker aspect. The maxillary tooth row is very short (less than 7.5 mm) and the teeth are tiny. The postorbital process of the zygoma is always present and relatively developed, and pointed in shape. The ventral canal on the floor of the infraorbital foramen is mostly smooth. The incisive foramen is ovate to slightly squarish, with weakly-developed to almost flat posterolateral margins; the mesopterygoid fossa is shallow to moderately deep, with an acute angle of indentation into posterior margin of palate (50–60°), and penetrating to near the middle of M2. The glans penis is moderately large and thick (mean length 9.26 mm; mean greatest width 4.73 mm); the urethral mound is divided with the opening of the meatus urinarius at its base, which is guarded ventrally by a flap-like urethral process. The baculum is massive and relatively long; distal end with a relatively long pair of divergent apical extensions separated by a wide and deep median depression. Karyotype is 2N = 40 and FN = 56.

Distribution.—The current known range of *P. pattoni* is restricted to five localities in western Amazonia: two in the headwaters region of the Rio Juruá (both on the right and left banks) in the state of Acre, Brazil, and three localities in southeastern Perú in the departments of Ucayali, Madre de Dios and Puno (see Other Specimens Examined and map of Fig. 9).

Description

External features.—*Proechimys pattoni* is one of the smallest species of spiny rats presently known (mean total length 306 mm, as opposed to 380 and 404 mm for the larger sympatric species *P. simonsi* and *P. steerei,* respectively). In general morphology individuals of *P. pattoni* are slim, have relatively short ears (less than 23 mm) and tail (tail approximately 70% of body size on average), and small hind-feet (shorter than 43 mm) (Tables 1 & 2). The dark-brown dorsal surface of the tail does not contrast sharply with the paler brown to cream color of the ventral side; the scales on the tail are relatively small with approximately 10 to 12 annuli per centimeter, and with three strands of hair extending over the central distal portion of each scale for the length of nearly five annuli. Overall, the color of the body is uniform, between Sanford's Brown and Auburn, coarsely streaked with varying amounts of black both on the dorsum and sides; the gray base of the soft hair also contribute to the streaked aspect of the pelage; the heavy dark-brown guard hairs interspersed over the dorsum give it a somewhat darker aspect; however, the dorsum and sides do not contrast sharply. Animals from the Rio Juruá and from Putina Punco, the northern and southernmost localities, are reddish in color; specimens

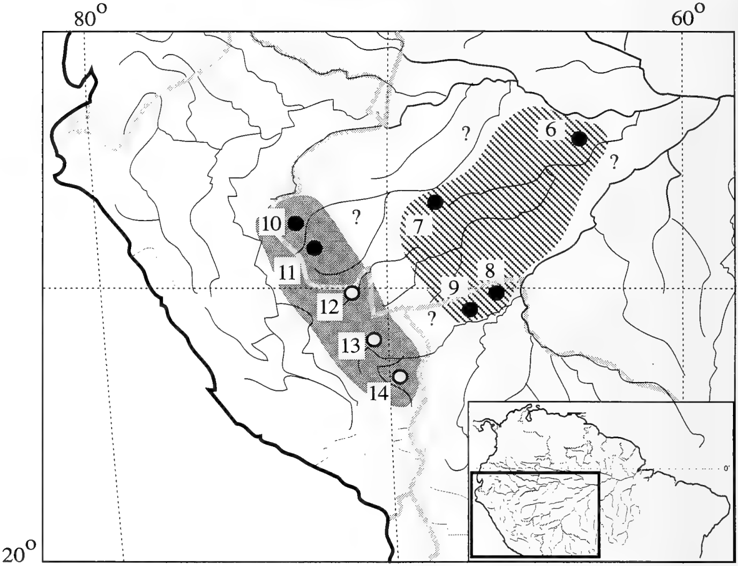

Fig. 9. Geographic distribution of the spiny rats *Proechimys pattoni* (dotted) and *P. gardneri* (cross hatched). Localities from which samples were examined are indicated by the dots; solid ones are those for which 801 base pairs of cytochrome b sequences were examined; the open dots represent the localities for which no cyt b sequence is available. Localities are numbered according to the locality list in Appendix 1 and text.

from Balta seem more yellowish in relation to those, but more reddish when contrasted with the specimens from the Río Manu, which have distinctly more yellowish tones than those from any other locality. The color of the venter and chin as well as the upper lips, usually with a spot at the base of vibrissae is pure white (in 11 of 13 specimens from the Rio Juruá); specimens from Balta and Pakitza also have white upper lips and/or a white spot at the base of the vibrissae. The white undersurface of the hind limbs ends at the tarsal joint where a dark band forms a ring surrounding the ankle. The dorsal surface of the hind-feet is entirely white in most specimens, although in a few the entire hind-foot is more golden than pure white; in some, the color of the hind-foot is brownish on the sides, including the third and fourth digits, or across the entire mid dorsum. The juvenile pelage is uniformly grayish-brown (age class 3). One specimen of age class 6 and one of age class 7 from the Rio Juruá have adult, aristiform hair on the mid back, and soft juvenile hair streaked with black and fulvus tips on the sides of the body, shoulders and rump.

Plantar surface of hind-foot.—It normally has six tubercules but in three out of 14 individuals the lateral metatarsal tubercule (lmt) is weakly-developed or fused with the 4th postdigital tubercule. Relative to other species of *Proechimys* on the Rio Juruá, the medial metatarsal tubercule (mmt) is long, about ⅓ to ⅔ of the distance between the

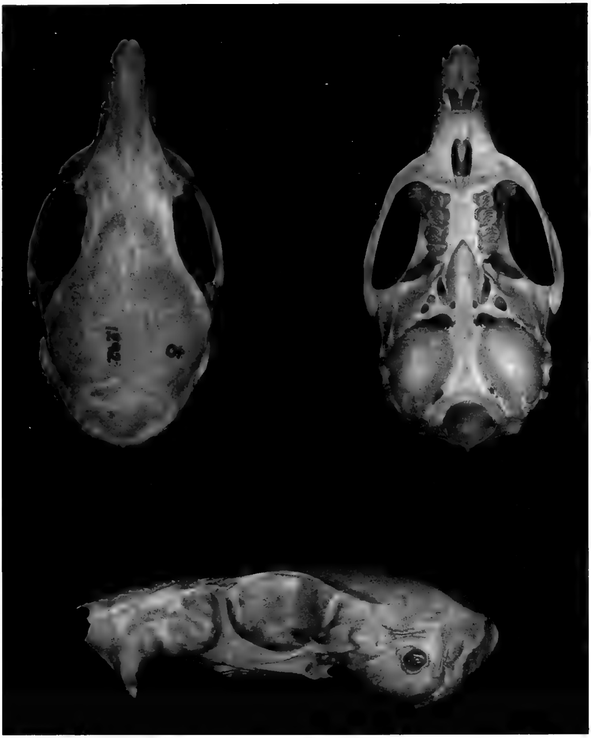

Fig. 10. Dorsal, ventral, and lateral views of cranium of the holotype of *Proechimys pattoni,* new species, INPA 2559, adult female (original number MNFS 1292).

calcaneum and the first postdigital tubercule; the distance between mmt and the first postdigital tubercule is equal or slightly less than the width of mmt; the hallux (with claw) extends to the posterior half of the second postdigital tubercule; in two of 11 specimens the hallux extends to the anterior half of the second postdigital tubercule; the distance between the heel and the first postdigital tubercule is approximately equal to the distance between the first postdigital tubercule and the end of third digit.

Cranial features.—The skull is relatively small and delicate (Fig. 10). The supraorbital ridge is beaded above the orbits but is discontinuous and weakly-developed over the parietals. The postorbital process of the zygoma is consistently present, relatively well-developed, bluntly pointed (Fig. 11), and formed mostly by the squamosal (19 of 24 individuals) or by equal contributions of squamosal and jugal (5 specimens). The floor of the infraorbital foramen is mostly smooth, with obvious flanges to the canal present in only one specimen from Balta. The incisive foramen of this species was

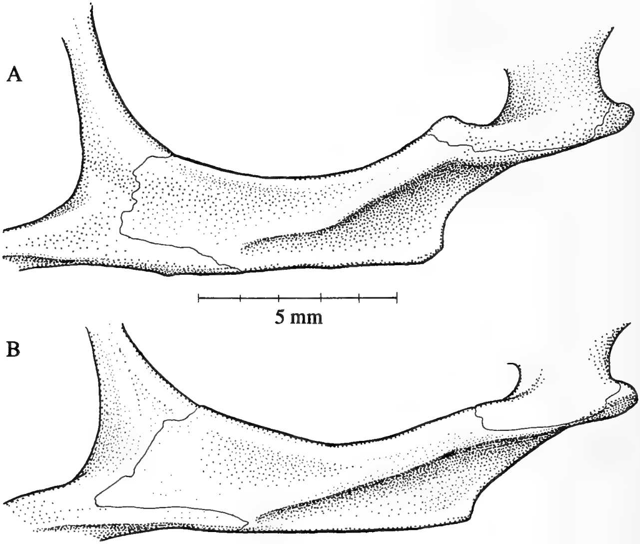

Fig. 11. View of postorbital process of the zygomatic arch of (A) *Proechimys pattoni*, new species (holotype, INPA 2559); and (B) *P. gardneri*, new species (MVZ 187207).

figured by Patton (1987: fig. 14d). Its overall shape is ovate to slightly squarish; the posterolateral margins are primarily flat, but sometimes with weak flanges which may from a weakly-developed, shallow groove; the maxillary portion is either attenuate or dorsoventrally compressed along its extension into the opening of the incisive foramen; the premaxillary portion of the septum is broad and short, and equal to or less than half the length of the foramen; in six of 11 specimens it either does not touch or is connected by a very attenuate keel to the maxillary portion; in the remaining specimens, the maxillary portion broadens to a spatule-like shape where it contacts the premaxillary bone; the vomer is not visible on the ventral margin of the septum; the palate is smooth, lacking a medial ridge; the mesopterygoid fossa is long and narrow, the angle of indentation on the posterior margin of palate is acute, averaging 54° (50–60°) and penetrates to near the middle of M2 in 8 out of 11 specimens, to the anterior one-half of M3 in 2, and to the posterior half of M3 in 1 specimen. The counterfold pattern on the lower cheek teeth is more variable than on the upper: pm4 with three folds in most specimens (16 of 23), the others with four or three to four folds; m1 with three folds in 12 specimens and two to three folds in 7, the remaining specimens with either four or two folds; m2 with either three or two to three folds on the same number of specimens (11 out of 23; 1 specimens with two folds); m3 of most specimens presented two folds (11 out of 21), the others had two to three folds (respectively in 6 and 4 specimens). All upper teeth of 19 specimens had three folds; in two other specimens PM4 and M3 had two folds, and in another M3 had two to three folds. The specimens from Balta are slightly more variable in relation to the shape and size of the incisive foramen, and in one specimen the foramen is more constricted posteriorly giving it a lyrate format (Patton & Gardner 1972). The incisive foramen of the two specimens from Puntina Punco are more squarish. In spite of some variation, specimens from all populations are similar, especially in their relative small cheek teeth, angle of indentation and penetration of the mesopterygoid fossa, development of the supraorbital ridge, and the canal on the floor of the infraorbital foramen.

Phallus.—The glans penis (four adult specimens examined) is relatively small and thick, with a slightly barrel-like shape (Fig. 5). The mean length (measured on the dorsal side from the prepuce to tip) is 9.3 mm, and mean greatest width is 4.7 mm; average index of robustness (greatest diameter/length) is 0.51. Glans size varies greatly among adult specimens of similar age class, apparently in relation to differences in reproductive state. The external surface of the entire glans is corrugated, sparsely covered with serrate spines. On the dorsal side, the area above and between the apical extensions of the baculum (see below) forms a rounded depression (of size equivalent to almost one-third of the glans), bordered by deep troughs that converge towards a deep longitudinal slot at the distal end that divides the urethral mound into two lobes. Immediately ventral to the medial mound is the meatus urinarius, which opens at the level of the proximal end of the split and is guarded ventrally by a urethral process in the form of a flap; no enlarged lip protrudes from the dorsal rim of the glans. The ventral side is characterized by a prominent swelling at about mid length, with surface sparsely covered by spines buried in small and irregular pits, and by a pair of asymmetric pleats that coalesce towards a small split at the center of the distal tip, subdividing the rim of the glans into four major lobes.

Baculum.—The baculum was figured by Patton & Gardner (1972), based on specimens from Balta, Perú. I examined six additional specimens from the Rio Juruá. The baculum is massive and relatively long (Fig. 6). It is characterized by a distal end with an unusually long pair of divergent apical extensions separated by a wide and deep median depression. It has a broad shaft with a thick and expanded base.

Karyotype.—2N = 40; FN = 56 (Fig. 7). Individuals from both the headwaters of the Rio Juruá and the Rio Urucu have the same chromosome number and morphology as the one from Balta, eastern Perú, illustrated and described by Patton & Gardner (1972). The autosomal complement includes seven pairs of medium-sized to small metacentrics and submetacentrics with one pair minute, two pairs of moderately small subtelocentrics, the smallest of which bear secondary constrictions on the long arms, and tree pairs of medium-sized and seven pairs of small acrocentrics. The X chromosome is a moderately small acrocentric and the Y is a small acrocentric.

Paratypes.—The following specimens are identified as paratypes (localities numbered as in Fig. 9): Brazil: Acre: (11) type locality—INPA 2560, adult male, skin and skull plus tissue sample and karyotype; INPA 2561, adult female, skin and skull plus tissue sample and karyotype; INPA 2562, adult male, in fluid with skull removed plus tissue sample and karyotype; INPA 2563, adult female, in fluid plus tissue sample and karyotype; INPA 2564, adult male, skin and skull plus tissue sample and karyotype; MVZ 187194, adult male, skin and skull plus glans, tissue sample and karyotype; MVZ 187195, adult male, skin and skull plus glans, tissue sample and karyotype; MVZ 187199, adult female, in fluid plus tissue sample and karyotype; MVZ 187201, adult female, in fluid plus tissue sample and karyotype; MVZ 187202, adult male, in fluid plus tissue sample and karyotype; MPEG 25507, adult female, skin and skull plus tissue sample and karyotype; MPEG 25508, adult female, skin and skull plus tissue sample and karyotype; MPEG 25509, adult male, skin and skull plus tissue sample and karyotype; MPEG 25510, adult female, in fluid plus glans, tissue sample and karyotype; MPEG 25511, adult male, skin and skull plus glans, tissue sample and karyotype.

Other specimens examined.—Brazil, Acre: (11) type locality—MNFS 1087, 1088, 1096, 1111, 1131, 1138, 1167, 1198, 1220, 1290, 1291, 1311; (10) Sobral, left bank Rio Juruá, 72°49′W, 8°22′S—MNFS 1428; Perú: (12) Depto. Ucayali; Río Curanja, Balta—LSU 9275, 12424, 14425, 14430, 14432, 16759; (13) Depto. Madre de Dios, Río Manu, Pakitza, 340 m—MUSM 7061, 7105, 7106, 7118; (14) Depto. Puno, Puntina Punco—MUSM 5141, 5144.

Remarks.—Patton & Gardner (1972) referred specimens of this species from Balta, Perú, to *P. guyannensis,* while Patton (1987) listed it as *Proechimys* sp., placing it provisionally in his *P. 'cuvieri'* species group.

Proechimys gardneri, new species

Etymology.—The name honors Alfred L. Gardner for his pioneering and elucidating work on the systematics of spiny rats and his many contributions on other neotropical mammals.

Holotype.—INPA 2565 (Instituto Nacional de Pesquisas da Amazônia - Coleção de Mamíferos, Manaus, Amazonas, Brazil), adult male, collected on 18 Nov 1991 by J. L. Patton (original number JLP 16085); skin, skull and mandibles in good condition; glans preserved separately in 70% ethyl alcohol; plus chromosomes and liver tissue preserved in ethyl alcohol.

Type locality.—Brazil: Amazonas; Altamira, right bank Rio Juruá; 68°54′W, 6°35′S. Obtained in terra firme forest.

Diagnosis.—A small spiny rat with relatively long tail (67% to 81% of body length), dark-brown above and cream to white below, covered by hair but with scales visible; small and narrow hindfeet (32 to 45 mm), mostly white with a dark band around the ankle; six tubercules present on the plantar surface of hind-foot; ears small (18 to 24 mm); the sides of the body colored like the dorsum, except for the dark-brown aristiform hair that give to the dorsum a darker aspect. The skull is small, with relatively narrow rostrum; the maxillary tooth row is shorter than 8.2 mm; the incisive foramen is ovate to lyrate, with mainly flat posterolateral margins; the postorbital process of the zygomatic arch is absent to very weakly-developed, and the floor of the infraorbital foramen is smooth without evidence of a distinct canal. The glans penis is moderately large (mean length 13.0 mm; mean greatest width 5.4 mm), with the opening of the meatus urinarius at the level of the rim of the glans and enveloped by the urethral processes. The baculum is massive and relatively long, with very short apical extensions at the distal end separated by a shallow medium depression. The karyotype is 2N = 40 and FN = 56.

Distribution.—Known from two localities in western Amazonia of Brazil and one in northern Bolivia. The distribution may be delimited by the Rio Juruá on the west and the Rio Madeira to the east, and south of the Amazon River into northern Bolivia (Fig. 9).

Description

External features.—*Proechimys gardneri* is small, relatively slim, with short ears, long tail, and small hind-feet (Tables 1 & 2). The dark-brown dorsal side of the tail contrasts with the cream to white color of the ventrum; the scales are small with approximately 12 to 14 annuli per centimeter; two or three strands of hair extend from the central distal portion of each scale and extend from three to five annuli. The color of the body is uniform, between Sanford's Brown and Auburn, coarsely streaked with varying amounts of black both on the dorsum and sides; the gray base of the soft hair also contributes to the streaked aspect of the pelage depending upon how much it shows through; the dorsum looks darker due to the presence of the heavy dark-brown aristiform hair. The venter and chin are pure white. In 12 of 26 specimens, the sides of the upper lips, sometimes confluent with a spot at base of vibrissae, are also white; specimens from the Rio Urucu tended to show more white in this area of the muzzle. At the latter locality, in 12 of 25 individuals, the white undersurface of the legs terminates at a dark band across the tarsal joint that forms a dark ring surrounding the ankle. This ring is incomplete in 7 of 13 Rio Juruá specimens, where the pure white of the undersurface of the legs extends along the hind-foot, although the color of the hind-foot is replaced by a not-so-clear white as on the venter and thighs. In some specimens the first and second digits of the hind-foot, in combination with or not with the distal portion of the digits, are brownish. The pelage of seven juvenile specimens from the Rio Urucu and one from the Rio Juruá of age classes 2 to 7 were examined. In all, the chin and venter are pure white and the tail is dark above and light bellow. The entire body of individuals of age class 2 is covered by soft grayish-brown hair, with the sides of the body slightly paler and with some fulvous tip hair; the sides sharply contrast with the pure white chin and venter; one of two specimens has a white spot at the base of the vibrissae; the hind-foot is whitish in both specimens, but the sides of the foot and the first and second digits are brown, the remaining parts of the hind-foot are pure white in one specimen and cream in the other. At age class 4, the grayish-brown juvenile pelage still covers the entire body, but the fulvous tips of the hair are slightly more conspicuous on the sides of the body and neck; the hind-foot is mostly brown, with some cream on the proximal to middle portion. The actual age of two individuals assigned to age class 5 apparently are not the same based on the amount of adult hair present on both skins, unless the onset of molt varies greatly. One of the specimens was just acquiring soft adult pelage, especially on the face and sides of the body, while the dorsum was still covered with juvenile dark-brown aristiform hair; the foot is cream to pale-brown, slightly darker on the sides and first digit. The second specimen of age class 5 has soft adult pelage on the head, sides of the body, but a round patch of heavy adult aristiform hair on the mid dorsum; the foot is mostly cream to pale-brown with a dark ankle. By age class 6, adult pelage covers most of the body, except for some pale grayish-brown juvenile hair found on the shoulders, flanks, and rump; the foot is cream to pale-brown on the side and there is a dark ring around the ankle. The one specimen of age class 7 is totally covered by adult pelage; its foot is white to cream to pale-brown; a dark ring is present around the ankle.

Plantar surface of hind-foot.—The plantar surface of the hind-feet has six tubercules in all 13 specimens examined; lateral metatarsal tubercule (lmt) weakly-developed and short when compared to medial metatarsal tubercule (mmt); distance between mmt and first postdigital tubercule less than width of mmt; hallux very short, extending (with claw) to the posterior third of the second postdigital tubercule; distance between heel and first postdigital tubercule equal to slightly shorter than the distance between first postdigital tubercule and end of third digit.

Cranial features.—The skull is small to medium-sized relative to that in other species of *Proechimys,* with a moderately long and narrow rostrum (Table 1 & Fig. 12); the supraorbital ridge is beaded above the orbits but discontinuous and weakly-developed over the parietals. The postorbital process of the zygoma is weakly-developed or obsolete in all but one specimen, contrasting with the condition found in *P. pattoni,* described above (Fig. 11); the process is formed mostly by the squamosal (4 speci-

Fig. 12. Dorsal, ventral, and lateral views of cranium of the holotype of *Proechimys gardneri,* new species, INPA 2565, adult male (original number JLP 16085).

mens of 23), or mostly by the jugal (9 specimens), or by approximately equal contribution of both bones (10 specimens). The floor of the infraorbital foramen is smooth, lacking a ventral canal. The shape of the incisive foramen is ovate to slightly lyrate with posterolateral margins flat to slightly flanged and forming a weakly-developed groove in some specimens; the maxillary portion of the septum is dorso-ventrally compressed posteriorly and narrower anteriorly, it is visible over almost half the length of the incisive foramen and fully contacts the premaxillary (34 of 36 specimens); the premaxillary portion of the septum is broad, usually equal to or less than half the length of the foramen; the vomer is not visible on the ventral margin of septum; the palate is smooth, typically without a medial ridge; the mesopterygoid fossa is long and narrow, with an acute angle of indentation into the posterior margin of palate averaging 61° (54–70°) and penetrating to the anterior half of M3 to near the middle of M2 in 28 of 32 specimens (the remaining four specimens were old and the angle of penetration was very shallow, not extending to the posterior one-half of M3). The counterfold pattern on the lower cheek teeth is more variable than on the upper. In most specimens pm4 has four folds (16 of 29 specimens), the other with three or three to four folds (respectively in 7 and 6 specimens); m1 with three folds in 17 specimens and two to three folds in 12 specimens; m2 with either three or two to three folds (respectively in 10 and 18 specimens; one specimen with two folds); m3 of most specimens with two folds (20 out of 29), with two to three folds (8 specimens), or with three folds. Upper teeth had three folds in all 30 specimens examined, except for one with four folds in M2 and another with two folds in M3.

Phallus (Fig. 5).—The glans penis (five adult specimens examined) is moderately large, and sub-cylindrical. The mean length (measured on the dorsal side from the prepuce to tip) is 13.0 mm, and mean greatest width is 5.4 mm; index of robustness (greatest diameter/length) is 0.42, on average. The external surface of the entire glans is rugose and slightly corrugated at the distal tip, and covered by great number of small spines. In the dorsal side, the area above and in-between the apical extensions of the baculum (see below) forms a very small and shallow depression, without pleats around it. Distal to this depression, instead of a longitudinal slit, thickened tissue forms a midventral ridge that continues almost to the tip of the urethral mound, which slightly protrudes from the dorsal rim of the glans in some specimens. Immediately ventral to the urethral mound is the meatus urinarius, which opens at the level of the rim of the glans. The most prominant feature of the ventral surface is an ampulla-shaped mass at about mid length, which extends towards the proximal base and to the distal tip, and is bordered laterally by a pair of well-separated, parallel and discontinuous (especially in the mid portion) troughs.

Baculum.—Seven specimens from the Rio Juruá (holotype INPA 2565, INPA 2566, INPA 2567, MPEG 25514, MVZ 187203, MVZ 187206, JLP 16036) and two from the Rio Urucu (MNFS 123 and 177) were examined. The baculum is massive and relatively long, with very short apical extensions at the distal end separated by a shallow median depression. The shaft is relatively broad with a thick and expanded base (see Fig. 6 & Table 3).

Karyotype.—2N = 40; FN = 56 (Fig. 7). This species has the same karyotype as *P. pattoni* (see above).

Paratypes.—Fourteen specimens listed by locality as numbered in the map, Fig. 9: Brazil: Amazonas: (7) type locality—INPA 2566, adult male, skin and skull plus glans and tissue samples; INPA 2567, adult male, skin and skull plus glans, tissue sample and karyotype; INPA 2568, adult female, skin and skull plus tissue samples; INPA 2569, adult female, skin and skull plus tissue samples; MVZ 187203, adult male, skin and skull plus glans, tissue sample and karyotype; MVZ 187204, adult female, skin and skull plus tissue samples and karyotype; MVZ 187205, adult female, skin and skull plus tissue sample and karyotype; MVZ 187206, adult male, skin and skull plus glans, tissue sample and karyotype; MVZ 187207, adult female, skin and skull plus tissue samples and karyotype; MPEG 25512-3, adult females, skin and skull plus tissue samples; MPEG 25514, adult male, skin and skull plus glans, and tissue sample; MPEG 25515, adult female, skin and skull plus tissue sample; MPEG 25516, adult female, skin and skull plus tissue samples.

Other specimens examined.—Brazil, Amazonas: (7) type locality—JLP 16036, 16037, 16039, JUR 192; MNFS 853, 854; (6) alto Rio Urucu 65°16′W, 4°51′S—MNFS 13, 14, 18, 19, 33, 34, 42, 71, 83, 84, 88, 90, 95, 123, 177.

Systematic remarks.—Morphologically, *P. pattoni* and *P. gardneri* are difficult to distinguish. Both have short toothrows and a similar pattern to the incisive foramen (although with much individual variation). The ventral color of their tail is less brilliantly white than, for example, *P. simonsi,* but the tail is still bicolored in most specimens, more so in *P. gardneri* than in *P. pattoni.* In *P. pattoni,* the color of the dorsum and ventral sides of the tail does not contrast sharply; in fact, the ventral side of the tail is browner in several specimens and have relatively larger scales and less hair than specimens of *P. gardneri.* Both also have relatively narrow and small white hind-feet with a dark ring around the ankle. Despite these similarities, subtle differences are present. For example, *P. pattoni* is slightly smaller than *P. gardneri* (see Table 1); the aristiform hair of *P. pattoni* is narrower but stiffer to the touch; the postorbital process of the zygomatic arch of *P. pattoni* is slightly but consistently more spinose (Fig. 11); the maxillary and premaxillary portions of the incisive foramen are either separated or connected by an attenuate keel in about half the specimens of *P. pattoni,* whereas these bones are in firm contact in nearly all *P. gardneri.* In addition to these differences, the shape of the baculum (Fig. 6) and the external morphology of the glans are very distinct, even if generally similar, between these two species (Fig. 5).

The assignment of specimens from Balta, Puntina Punco, and Pakitza to *P. pattoni,* for which no cytochrome b data are available, presented varying degrees of difficulties. The Balta specimens are allocated to *P. pattoni* primarily on the similarity of the shape and size of the baculum and glans, as figured by Patton & Gardner (1972). Identification of the specimens from Pakitza and Puntina Punco presented more difficulties, in part because of the lack of both genetic and phallic/bacular information for specimens from these localities. Morphologically, they have distinct pelage, both in color and softness, and have skull characters that are similar to both species. They are assigned to *P. pattoni* primarily on geographic grounds, as well as by my perception of the morphological variation within and between these groups of organisms. Future field and laboratory studies should verify the validity of my taxonomic assignments.

Ultimately, *Proechimys pattoni* and *P. gardneri* are recognized as separate species because they form well-supported, and highly differentiated haplotype clades that are also morphologically diagnosable. They also have relatively wide geographic distributions that at present appear allopatric (Fig. 9). Future studies in areas of contact between these two species in western Amazonia will be the ultimate test to the degree of independence of these two very distinct lineages.

Molecular Systematics of *Proechimys* from the Rio Juruá

Species limits as well as geographic distributions of taxa within *Proechimys* are still being clarified, and molecular data may help understand the actual diversity of species within this genus.

Sequence analyses of the mitochondrial cytochrome b gene based on Kimura 2-parameter molecular distance (Kimura 1980) show that divergences within geographic units of species-groups of *Proechimys* (as defined by Patton 1987) are low, ranging from 0% to 4%. Within species-groups, comparisons among geographic units are higher, ranging from 7% to 14%, and largely overlap comparisons among species-groups, which range from 10% to 18%. Comparisons of taxa within *Proechimys* and the outgroups range from 16% to approximately 30%.

The parsimony analysis for *Proechimys* specimens collected throughout the Rio Juruá basin generated one shortest tree with minimal length of 293 steps. All terminal branches are long, internodal distances are short, and most internodes linking the various taxa have bootstrap values below 50%. Figure 13 shows the eight monophyletic

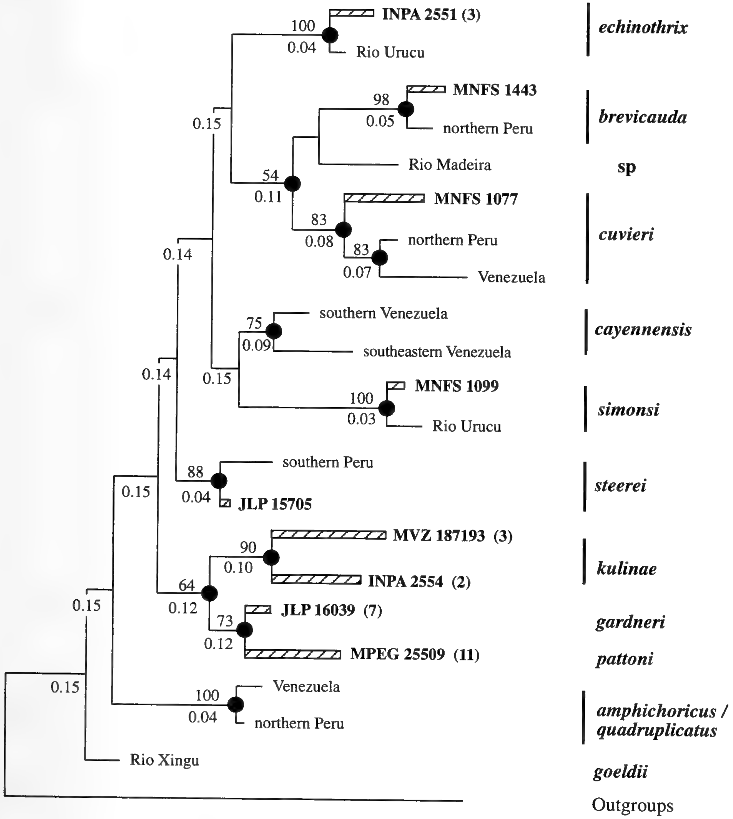

Fig. 13. Maximum parsimony cladogram, excluding 3rd position transitions, for the first 798 bp of the cytochrome b gene for species of the spiny rat *Proechimys*. Branch lengths are proportional; hatched ones correspond to Juruá samples for each of the eight spiny rat species followed by specimen number (and locality number for the new taxa). Circled numbers at specific nodes are bootstrap values (based on 100 iterations) above 50%; numbers below the branches correspond to sequence divergence based on Kimura 2-parameter distance.

clades of *Proechimys* in the Juruá basin that are recognized as separate species by virtue of monophyly and unique karyotype and morphology. Four of these conform to named forms already well known in the limited literature on the genus (*P. brevicauda, P. cuvieri, P. simonsi* and *P. steerei*). The other four are described in the sections above. Although the cytochrome b data do support the strong differentiation of all taxa of spiny rats represented at the species level, there is little support for any relationship at the deeper nodes of the tree. The only exceptions are the trichotomy of the *P. brevicauda* and *P. cuvieri* groups, with an unidentified species from the upper Rio Madeira, and of three of the new species, associations which are weakly supported by bootstrap analyses (respectively 54% and 64%). In the latter case, despite the monophyly of the clade, which is not totally surprising considering the similarities among the taxa in question, species recognition is given because, in addition to cytological and morphological differences (see descriptions above), the branches are very long and levels of sequence divergence among them are high (12% on average), equivalent to values observed among other species of *Proechimys* (15% on average). In Fig. 13 the terminal branches correspond to one or more geographic units within the species-groups represented. Our studies on the molecular phylogeography of Neotropical mammals suggest that, when determined by well-supported monophyletic groups that are also highly differentiated, these geographic units correspond to species differences (da Silva & Patton 1993, 1998; Patton et al. 1997). Within *Proechimys* this is certainly the case for the *P. goeldii*-group; for example, specimens of *P. steerei* captured along the Rio Juruá are quite divergent (11–15%), and morphologically distinct from specimens found north of the Rio Solimões and east of the Rio Negro or in southeastern Amazonia, to which the respective names *P. amphichoricus* and *P. goeldii* apply (see Fig. 13, da Silva 1995, da Silva & Patton 1998).

The lack of resolution within *Proechimys* is in part due to the high and similar levels of sequence divergence among them. Although these unresolved patterns might be due to the lack of characters or result from evolutionary traits specific to the cytochrome b gene of echimyids, they may in fact reflect the almost simultaneous diversification of clades within *Proechimys,* a pattern similar to the diversification within the family Echimyidae (Lara et al. 1996).

Interspecific comparisons of *Proechimys* from the Rio Juruá

In external appearance, species of spiny rats are confusingly similar. They follow the general pattern of having aristiform dark-brown hair on the dorsum, forming a poorly-defined dark band on the mid back, which contrasts with the sides of the body in varying degrees; the color of the adult soft pelage also has varying amounts of red and yellow tones and is generally streaked with black; the color of the tail is dark above and white to creamy below, normally sparsely covered by fine hair and with scales visible to the eye. The length of the tail relative to body size varies among species, but its maximum length is slightly less than the length of the head and body; the ears are mostly large; the hind-feet are narrow and long. Although differences in relative size and coloration may be useful in identifying species of spiny rats, these differences are not discrete and have contributed to the confusion in the taxonomy of *Proechimys.* Here, I compare morphological characters, with emphasis on the external anatomy, of the eight taxa of *Proechimys* found along the Rio Juruá hoping to facilitate their distinction. Patton & Gardner (1972), Gardner & Emmons (1984), and Patton (1987) present more detailed descriptions of the four previously recognized taxa.

Body size, in association with other morphological characters, is helpful in distinguishing adult specimens of the eight species of spiny rats from the Rio Juruá. *Proechimys kulinae, P. pattoni,* and *P. gardneri* are among the smallest of the known species of spiny rats. In addition to small body size (the total length of *P. gardneri,* the relatively larger species, is 310 mm, on average), they have tiny teeth and short tooth rows (maxillary tooth row length approximately 7 mm for all three species, on average); mostly white and small feet (absolute size not longer than 41 mm on average); short and bicolored tails. Despite karyological and DNA differences, the morphological distinction of these small taxa is difficult because the differences between them are mostly of degree rather than absolute (see text and Tables 1–5 for comparisons). The baculum of *P. kulinae,* however, is quite different from those of both *P. pattoni* and *P. gardneri.* The three are also known only from allopatric populations where they co-occur with as many as three other congeneric taxa, such as *P. steerei, P. simonsi, P. cuvieri,* and *P. brevicauda* (*P. gardneri* is sympatric with the first two, *P. kulinae* with the first three, and *P. pattoni* with the last three).

While *P. brevicauda* and *P. cuvieri* are of medium size (see below), *P. steerei, P. simonsi,* and *P. echinothrix* are among the largest known species of *Proechimys,* with maxillary toothrow length ranging from 8 to 9 mm. Of those, the largest mean total length is 379 mm of *P. simonsi.* The tail of these species is approximately two-thirds of body length, but in average size tails range from 137 mm in *P. brevicauda* to 172 mm in *P. simonsi.* Together, *P. simonsi* and *P. echinothrix* have relatively and absolutely longer tails, as well as, on average, the same hind-foot and ear sizes (48 and 24 mm, respectively, for both species). However, despite the similarities in size between *P. simonsi* and *P. echinothrix,* they are readily distinguished by qualitative features such as the much heavier dorsal aristiform hair and by the markedly bicolored and furry tail of *P. echinothrix. Proechimys simonsi* also has a more slender body than *P. echinothrix* and a much longer and narrower baculum, as oppose to the shorter and broader baculum of *P. echinothrix.* Both species were collected in the same trap lines in the central and mouth areas of the Rio Juruá, and are presumably sympatric throughout the known range of *P. echinothrix.* The third large species is *P. steerei,* for which individuals can reach weights of almost a kilogram. This species is readily distinguished from all others by its large body size; relatively short tail; very soft body hair and dense, pure white hair on the underside. The hind-foot is usually bicolored, with a well-defined dark-brownish stripe along its length. *Proechimys steerei* is found along the entire length of Rio Juruá, but is the only species of spiny rat found in true várzea (seasonally flooded) forest. It may co-occur with, but be segregated by habitat from to as many as four congeners (including *P. simonsi, P. echinothrix, P. kulinae, P. gardneri, P. brevicauda,* and *P. cuvieri*) which inhabit upland forests.

Relative to the other species of *Proechimys, P. brevicauda* and *P. cuvieri* are both characterized by medium-sized body, ears, hind-feet and tail (mean total length 348 and 360 mm; tail 137 and 144 mm; ear 21 and 22 mm; hind-feet 46 and 48 mm). *Proechimys brevicauda* can be distinguished by darker body, tail (which sometimes is almost unicolored), and hind-feet (which vary from cream to dark-brown among specimens). It is the only species of spiny rat on the Rio Juruá characterized by a fulvous lateral stripe that often extends onto the venter, chin, throat, and abdominal region. In some individuals the entire venter is washed with fulvous. This range of ventral coloration was also observed in five younger-aged individuals (age classes 3 through 7). In contrast to *P. brevicauda,* the tail coloration of *P. cuvieri* tends to be darker towards the tip on the ventral surface, and is relatively well covered by hair. Examination of the entire series of *P. cuvieri* gives the impression that it is brighter and more reddish than *P. brevicauda,* which tends to be duller and more brownish. However, this distinction is difficult to apply when contrasting single specimens of either species. The aristiform hairs of *P. cuvieri* are stiffer to the touch, being much larger and wider (mean length 22.6 mm and width 0.9 mm) than those of *P. brevicauda* (mean length 17.6 mm and width 0.6 mm; see Fig. 3), with a whip-like tip. The dorsal surface of the hind-foot is mostly brown, and in most specimens the paler color of the undersurface of the hind limbs extends

Table 5.—Selected characters of the new species *Proechimys echinothrix, P. kulinae, P. gardneri,* and *P. pattoni.*

Character	*P. echinothrix*	*P. kulinae*	*P. gardneri*	*P. pattoni*
External				
size of body	medium to large, total length range from 317 to 440 mm	small; total length not larger than 328 mm	small; total length not larger than 353 mm	smaller than *P. gardneri*; total length not larger than 328
aristform hair	extremely heavy, very broad and long with blunt tip	wider and longer than in *P. gardneri* and *P. pattoni,* with blunt tip at the mid-back	narrow and short	narrower and stiffer to the touch relative to *P. gardneri*
ear size	large (19 to 28 mm)	small (17 to 23 mm)	small (18 to 24 mm)	small (18 to 23 mm)
tail size and color	long (on average 79%–95% of body length); bicolored, sharply defined white venter and dark dorsum; hair almost completely covering scales	relatively short (on average 69% of body length; similar to *P. gardneri* and *P. pattoni*); bicolored, with white venter and dark dorsum	relatively short (on average 70% of body length); bicolored with sharper contrast than in *P. pattoni*; tail seems hairier than in *P. pattoni*	relatively short (on average 70% of body length); dark brown above, pale brown to white below
hind-foot and ankle	large hind-foot (41–54 mm); nearly unicolored pure white on dorsum without dark ring at tarsal joint	small and narrow hind-foot (38–44 mm); mostly white on dorsum; tarsal joint either covered by dark and rusty hair or with white hair confluent with undersurface of the hind limbs	small and narrow hind-foot (32–45 mm); mostly white on dorsum; tarsal joint either covered by dark and rusty hair or with white hair confluent with undersurface of the hind limbs	small and narrow hind-foot (37–43 mm); mostly white on dorsum but also golden or brownish, with a dark band around the ankle
foot pads	six tubercules; lmt weakly to moderately developed, and short when compared to mmt	mostly five tubercules (lmt absent in 12 out of 16 specimens)	six tubercules	six tubercules in 11 out of 14 individuals; mmt very long
Cranial				
skull	large (50–61 mm)	small (42–51 mm)	small (42–55 mm)	small & delicate (43–50 mm)
maxillary toothrow	long (7.6–9.2 mm); relatively large teeth	short (6.3–8.6 mm); small teeth	short (6.9–8.2 mm); small teeth; pm4 has 4 folds in most specimens	very short (6.7–7.5 mm); tiny teeth; pm4 has 3 folds in most specimens
incisive foramen	ovate to lyrate, posterolateral margins mostly flat; premaxillary long and narrow; maxillary attenuate to expanded anteriorly in very weak or no contact with premaxillary	squarish to slightly ovate or moderately lyrate, weakly developed posterolateral margins; premaxillary short; maxillary attenuate to expanded anteriorly, usually in contact with premaxillary	ovate to slightly lyrate, posterolateral margins flat to slightly flanged; premaxillary rather broad, in contact with maxillary, both equal to or less than half the length of the opening of foramen	ovate to slightly squarish, weakly developed to almost flat posterolateral margins; maxillary and premaxillary either not touching or connected by very attenuate keel

Table 5.—Continued.

Character	*P. echinothrix*	*P. kulinae*	*P. gardneri*	*P. pattoni*
mesopterigoid fossa	extends either to anterior or to posterior one-half of M3	extends to anterior one-half of M3	extends to anterior one-half of M3 to near middle of M2	extends to near middle of M2
postorbital process at the zygomatic arch	little developed and rounded	more spinose and developed	tends to be rounded and weakly developed or basically absent	always present, relatively developed and more spinose than in *P. gardneri*
ventral canal on the floor of the infraorbital foramen	moderate to strongly developed	not well developed	not well developed	not well developed
Glans penis	long, sub-cylindrical, almost straight dorsal and lateral margins	moderately large, elongate, tubular with fairly straight dorsal and lateral margins	moderately large, and sub-cylindrical; meatus urinarius opens at the level of the rim of the glans and is involved by the urethral processes	small and thick, slightly barrel-like shape; opening of meatus urinarius guarded ventrally by flap-like urethral process
Baculum	broad and short, thick and expanded base	elongate and relatively narrow, moderately developed apical wings	similar to *P. pattoni,* except that apical extensions are much shorter	distal end with relatively long pair of divergent apical extensions
Karyotype	2n = 32 and FN = 60	2n = 34 and FN = 52	2n = 40 and FN = 56	2n = 40 and FN = 56

across the tarsal joint, where it tends toward fulvous. As the other species of spiny rats, except *P. brevicauda,* there is no lateral stripe and the reddish color of the sides contrasts sharply with the mostly pure white ventral coloration. In general shape, the baculum of *P. cuvieri* is most similar to *P. echinothrix*; it is a short, massive baculum, with broad shaft and expanded base, as opposed to the elongate and moderately broad baculum of *P. brevicauda* (see illustrations in Patton 1987). These two species are sympatric in the upper Juruá, with *P. cuvieri* also being collected farther down along the central portion of this river.

The preceding discussion identifies some difficulties I found in assigning individuals to specific taxa. Only after the examination of hundreds of specimens, with associated karyotypes and DNA sequence data, did a better understanding of intra- and interspecific population morphological variation begin to emerge. Considering our current knowledge of the systematics of *Proechimys,* ecological studies involving these organisms in most areas of the Amazon Basin should be preceded by a reference collection in order to determine the species of spiny rats that occur at a given locality.

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Appendix 1.

Localities numbered according to maps in Figs. 2 & 9.

BRAZIL

Acre:

10 Sobral, left bank Rio Juruá, 72°49′W, 8°34′S
11 Porongaba, right bank Rio Juruá, 72°47′W, 8°40′S

Amazonas:

2 Condor, left bank Rio Juruá, 70°51′W, 6°45′S
3 Barro Vermelho, left bank Rio Juruá, 68°46′W, 6°28′S
4 Colocação Vira-volta, Ig. Arabidi, left bank Rio Juruá, 66°14′W, 3°17′S
5 Vai-quem-quer, right bank Rio Juruá, 66°01′W, 3°19′S
6 alto Rio Urucu, 65°16′W, 4°51′S
7 Altamira, right bank Rio Juruá, 68°54′W, 6°35′S

BOLIVIA

Pando:

8 Provincia General Federico Roman: Main camp on Rio Negro. About 9°52′S, 65°42′W (estimated from map)
9 Provincia Abuna. Centro 18 km. Approx. 18 km NNW of San Juan de Nuevo Mundo, 10°46.0′S, 66°44.0′W.

PERÚ

1 Depto. Loreto, Quebrada Blanco, just outside the Reserva Comunal Tamshiyacu-Tahuayo
12 Depto. Ucayali, Rio Curanja, Balta
13 Depto. Madre de Dios, Río Manu, Pakitza, 340 m
14 Depto. Puno, Puntina Punco

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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