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A new genus of tiny condor from the Pleistocene of Brazil
(Aves: Vulturidae)

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Abstract.—A new genus and species of Vulturidae (Cathartidae auct.), *Wingegyps cartellei*, is described from Pleistocene cave deposits in the states of Bahia and Minas Gerais, Brazil. This species is closely related to condors *Gymnogyps* and *Vultur*, particularly the former, as opposed to the smaller cathartid vultures, but is much smaller, being slightly smaller than the smallest living member of the family, the Lesser Yellow-headed Vulture *Cathartes burrovianus*. The Vulturidae appears to consist of two basic divisions (condors vs. other vultures) that differ profoundly in the morphology of the skull. Each appears to have been more diverse in the past and to contain larger or smaller species than survived to the present.

Resumo.—Um novo gênero e nova espécie de Vulturidae (Cathartidae auct.), *Wingegyps cartellei*, é descrito dos depósitos pleistocênicos de cavernas da Bahia e Minas Gerais, Brasil. Este é mais relacionado aos condores *Gymnogyps* e *Vultur*, principalmente com o primeiro, do que com os verdadeiros urubus, embora seja de tamanho reduzido, menor ainda que *Cathartes burrovianus*, o menor membro vivente da família. Os Vulturidae se constituem de dois grupos basais, condores e urubus, que diferem entre si basicamente pela morfologia do crânio (o tamanho não é fundamental), sendo que ambos parecem ter sido bastante diversificados no passado.

Peter Wilhelm Lund was a Danish naturalist who resided in Brazil from 1832 until his death in 1880. Between 1835 and 1849 he shipped masses of Quaternary fossils from the state of Minas Gerais back to Denmark for study (Voss and Myers 1991). The great majority of these fossils were of mammals, including extinct megafauna, but also rodents and bats (Voss and Myers 1991, Czaplewski and Cartelle 1998, Cartelle 1999).

The mammals were originally studied by Herluf Winge, who published his exceptionally perceptive findings in a series of volumes entitled *E Museo Lundii* from 1887 to 1915. The study of fossil birds from these deposits fell to his brother Oluf

Winge (1888) who produced a list of some 126 species. Only one of these, the anatid *Chenalopex* (now *Neochen*) *pugil*, was named as new, and many were referred to modern taxa. Others could not be assigned either for lack of comparative material or because Winge considered them probably to represent unknown species that he left unnamed.

Among the last was a vulture that Winge (1888: 33) regarded as probably belonging to a new genus and species ("G. sp. indet. magnitudine *Catharistae atrati*" [= *Cora-gyps atratus*]). This was represented by the distal end of a humerus and an ulna lacking the distal end. He described these specimens in considerable detail and illustrated

the humerus in comparison with a fossil of the Black Vulture *Coragyps atratus*. Nothing further was ever made of this discovery during the succeeding 115 years.

In identifying fossil bird remains from a cave in the state of Bahia, we puzzled over a peculiar ovoid cranium that defied placement to family until we happened to notice that fossil crania of *Gymnogyps* from Rancho La Brea, California, seemed to be similar in shape, although larger. We identified two humeri from Bahia as probably belonging to the same species as the cranium, and a well-preserved distal fragment appeared to be identical to that illustrated by Winge as his unidentified new genus. We were able to borrow Winge's original material and confirmed that he was quite correct that a new genus and species is indicated. This, however, turns out not to be closely related to the smaller genera of Vulturidae, *Cathartes* or *Coragyps*, but to the much larger condors, especially *Gymnogyps*.

Comparative material examined.—Preliminary comparisons were made with almost all families of non-passerine birds and all species of South American vultures in Museu de História Natural de Taubaté. The original material of Vulturidae collected by Lund in Minas Gerais was borrowed from the Zoological Museum University of Copenhagen (ZMUC) and restudied and compared. Modern skeletons examined in the Division of Birds, National Museum of Natural History, Smithsonian Institution (USNM) included: *Gymnogyps californianus* 3369, 492447; *Vultur gryphus* 345384, 429839; *Sarcoramphus papa* 345434, 559318; *Coragyps atratus* 613353; *Cathartes aura* 490864, 612254; *C. melambrotus* 621939, *C. burrovianus* 431336, 622341.

Systematics

Class Aves

Family Vulturidae

Within the family, there is marked osteological distinction, particularly in the neu-

rocranium, between the two living genera of condors (*Vultur* and *Gymnogyps*) on one hand, and all of the other genera (hereafter "vultures") on the other. The more salient of these were first noted by Miller and Howard (1938) and were further documented by Fisher (1944). The extinct genus and species *Breagyps clarki* was also shown to belong with the condors based on cranial characters (Miller and Howard 1938). Cranial differences were detailed and extended to additional fossil specimens by Emslie (1988). In the following comparisons, "condors" includes the new genus.

Neurocranium.—In dorsal view the neurocranium of condors is relatively longer and narrower, appearing almost ovoid in shape; the tranverse nuchal crest is visible because the attachments of the cervical musculature extend much farther dorsally than in the vultures, and the cerebellar prominence is much larger and more distinct.

In posterior view, the last two features are equally distinct. The foramen magnum is much larger and more elliptical in condors, as opposed to nearly circular in the vultures. The occipital condyle is more distinctly stalked (better seen in ventral view) and is rounded, lacking the notch in the dorso-posterior surface seen in vultures. In condors, the dorsolateral margins of the foramen magnum give rise to distinct crests that angle ventro-laterally to the extremely well developed paroccipital processes (supraoccipital processes of Suárez and Emslie 2003; opisthotic processes of Fisher 1944; postauditory processes of Miller & Howard 1938) that parallel the similarly well developed processes that angle out from the occipital condyle (occipital processes of Suárez and Emslie 2003; medial basitemporal processes of Bock 1960; exoccipital processes of Fisher 1944). In the vultures these processes were always much smaller and differently shaped.

In lateral view, the temporal fossa is much larger in condors, so that the postor-

bital and zygomatic processes are farther apart, and the orbit is relatively smaller than in the vulture.

Humerus.—Differs from *Cathartes* or *Coragyps* in having the distal end more expanded and the ectepicondylar prominence situated more distally on the shaft. *Sarcoramphus* differs in having a large pneumatic opening in the depression between the entepicondylar prominence and the ulnar condyle. The entepicondylar prominence is less developed than in *Vultur*. In almost every respect, down to the slightest detail of pneumatization, the distal end of the humerus of the new genus is a perfect duplicate in miniature of that of *Gymnogyps*. The complete humerus of the new genus is so worn as to preserve few useful characters, but it does have on the palmar surface a slightly pneumatized depression just distal to the head as in *Gymnogyps*. This depression is absent in *Cathartes*, only slightly indicated in *Vultur*, and bears a very large pneumatic foramen in *Coragyps* and *Sarcoramphus*.

Wingegyps, new genus

Type species.—*Wingegyps cartellei*, new species.

Diagnosis.—A tiny condor most similar to *Gymnogyps* in the narrowness and elongation of the neurocranium, but even narrower, with the braincase in dorsal view being of nearly uniform width, rather than expanding posteriorly. Muscle scars on either side of the cerebellar prominence are correspondingly narrower. The foramen magnum opens directly posteriorly rather than partly ventrally. The paroccipital processes and their associated crests are angled more ventrally than in *Gymnogyps* or *Vultur*. Differs from other condors in having the entire occipital condyle and its stalk visible in lateral view (not visible in *Breagyps*, only partially visible in *Gymnogyps* and *Vultur*).

The ulna is like that of condors and *Sarcoramphus* in having very little pneumati-

zation in the brachial depression (well developed in *Cathartes* and *Coragyps*) but differs from all but *Vultur* in having the olecranon more distinctly set off from the margin of the internal cotyla. The olecranon is narrower, however, than in *Vultur*.

Etymology.—Winge + Greek *gyps*, vulture, in commemoration of the perspicacity of Oluf Winge for recognizing the distinctiveness of this remarkable new genus.

Wingegyps cartellei, new species

Figs. 1–4

Holotype.—Neurocranium lacking the parasphenoid rostrum and ethmoid region, with damage to the anterior margin of the frontals and left otic area, MCL CLA782 (Fig. 1B, 2B).

Type-locality.—Brazil, Bahia State, Município de Morro do Chapeu, Gruta dos Brejões (11°00'30"S, 41°26'07"W), elevation ca. 600 m.

Horizon and age.—Probably late Pleistocene or early Holocene. A radiocarbon date of 12,200 ± 120 radiocarbon years before present was obtained from a coprolite of a ground sloth from the type-locality (Czaplewski and Cartelle 1998). Associated mammals from caves in Bahia and Minas Gerais are considered to be of Pleistocene age (Cartelle 1999).

Measurements (mm) of holotype.—Total length as preserved 48.6; width at level of postorbital processes 27.5; width at level of base of zygomatic processes 29.4; greatest depth at midline 27.2; width and depth of foramen magnum; 8.9 × 8.1; width of occipital condyle 4.1

Paratypes.—Topotypes: Complete but very worn left humerus MCL CLA670 (Fig. 4C); distal third of left humerus MCL CLA1678 (Fig. 3B).

Lapa do Tiú, Minas Gerais, Brazil: distal half of right humerus ZMUC 1116 (Fig. 3A); right ulna lacking distal end ZMUC 1118 (Fig. 4A).

Measurements (mm) of paratypes.—Humeri (in the same sequence as above): total

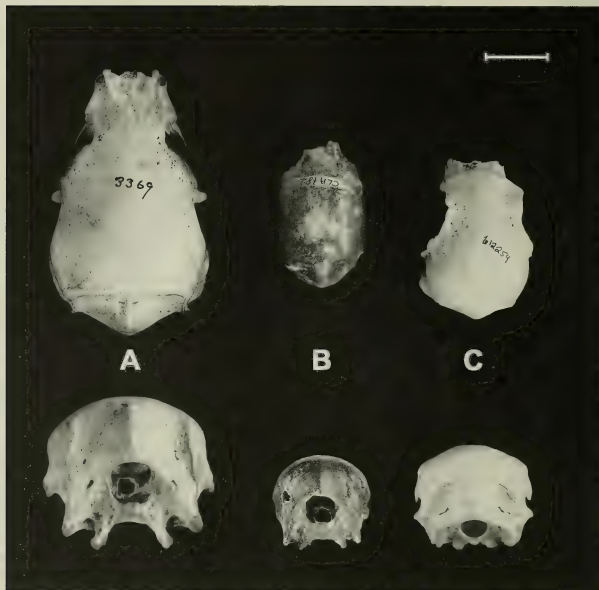


Fig. 1. Neurocrania in dorsal (top) and posterior (bottom) views: A, *Gymnogyps californianus* USNM 3369; B, *Wingegyps cartellei*, new species, holotype MCL CLA782; C, *Cathartes aura* USNM 612254. Scale = 2 cm.

length 129.5, —, —; length from head to distal end of pectoral crest 54.4, —, —; shaft width and depth at midpoint 10.0×8.5 , —, 9.7×7.6 ; distal width —, 24.8, 23.2; greatest dimension of brachial depression 13.4; 11.7, 13.0; greatest dimension of radial condyle —, 10.8 11.1. Ulna: proximal width 12.5; proximal depth 15.8; length of brachial depression 23.4.

Etymology. Dedicated to paleontologist Cástor Cartelle of the Universidade Federal de Minas Gerais in recognition of his ex-

cavations at Gruta dos Brejoes (Cartelle 1983) and his contributions to the paleontology of Brazil.

Diagnosis.—Much smaller than any known condor; slightly smaller than the smallest living cathartid vulture (Lesser Yellow-headed Vulture *Cathartes burrovi-anus*).

Discussion.—*Wingegyps* is indisputably a condor based on the very distinct features of the neurocranium and on similarities of the distal end of the humerus. Its extraor-

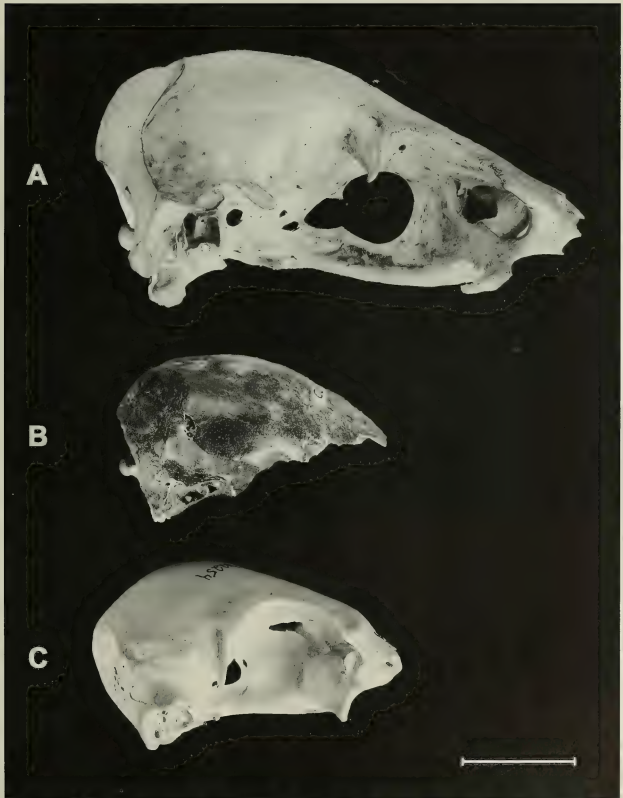


Fig. 2. Neurocrania in lateral view: A, *Gymnogyps californianus* USNM 3369; B, *Wingegyps cartellei*, new species, holotype MCL CLA782; C, *Cathartes aura* USNM 612254. Scale = 2 cm.

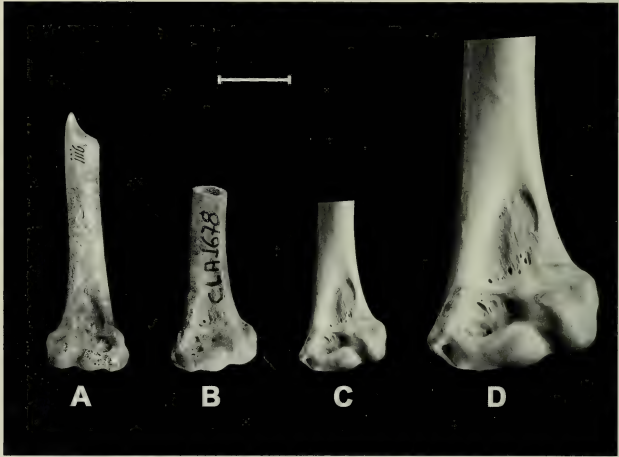


Fig. 3. Humeri in anconal view: A, *Wingegyps cartellei*, new species, paratype ZMUC 1116; B, *Wingegyps cartellei*, new species, paratype MCL CLA1678; C, *Gymnogyps californianus* USNM 492447, reduced to the same size as B; D, same natural size. Scale = 2 cm except for C.

dinarily small size is quite unanticipated, being somewhat smaller than the smallest living species of the family (*Cathartes burrovianus*). The humerus is only slightly shorter than in females of the Black Vulture *Coragyps atratus* from the tropics, which are smaller than individuals at the temperate ends of the species' range (Brodkorb 1944). But the humerus is proportionately much shorter in *Coragyps atratus* than in *Cathartes*, so that this species is otherwise much larger than *Cathartes burrovianus* (1875 g in a female *Coragyps* from Panama vs 960 g in a male *C. burrovianus* from Guyana).

Wingegyps shows that condors were much more diverse in size in the past. The family Vulturidae may be viewed as being divisible into two basic groups: the condors (*Vultur*, *Gymnogyps*, *Breagyps*, *Winge-*

gyps), which appear to be derived (Emslie 1988) and the remaining living genera (*Cathartes*, *Coragyps*, *Sarcoramphus*), which may be paraphyletic. Both may have been more diverse at one time and perhaps some of the larger fossil taxa (*Geronogyps*, *Pliogyps*, "*Sarcoramphus*" *kernense*—see Emslie 1988), for which cranial material is unknown, may prove to be more closely related to the assemblage of smaller vultures than to condors.

Known only from a rather limited area in eastern Brazil, *Wingegyps* doubtless had a greater range than indicated at present, possibly much greater. If it has been collected in fossil deposits elsewhere the material might easily be overlooked as belonging to *Cathartes* or *Coragyps* because of its small size.



Fig. 4. Right ulnae (A, B) and left humeri (C, D) in palmar view: A, *Wingegyps cartellei*, new species, paratype ZMUC 1118; B, *Cathartes burrovianus* USNM 431336; C, *Wingegyps cartellei*, new species, paratype MCL CLA670; D, *Cathartes burrovianus* USNM 431336. Scale = 2 cm.

What sort of feeding niche might such a tiny condor have occupied? The habits of living species of the family are briefly summarized from Olson et al. (1967), Sick (1993), and Hertel (1994). The living condors *Vultur* and *Gymnogyps* forage by sight and prefer soft viscera from large carcasses. *Sarcoramphus* and *Coragyps* forage by sight and are very aggressive at carcasses. *Coragyps* takes food in small bits, tearing even small carcasses such as a frog or mouse to pieces before eating. The species of *Cathartes* are very different in finding food with their keen sense of smell. Thus, they specialize in finding carcasses of

small animals either before they are located by sight foragers or detecting food that cannot be seen at all from above. They are also very docile and not at all competitive with other vultures at carcasses.

The small size of *Wingegyps* would have placed severe limitations on its ability to process the majority of carcasses or to compete at carcasses with other species of vultures. If we assume that it was like its closest relatives in lacking the olfactory capabilities of *Cathartes*, *Wingegyps* would have had little success competing with any of the species of *Cathartes* for small carcasses. There does seem to be a potential

niche in the New World, however, that is not as fully exploited as it is in the Old World, viz. palm fruits.

In Africa, the Palm-nut Vulture (*Gypshierax*, Accipitridae) feeds mainly on the soft mesocarp of the African oil palm *Eleis guineensis*. This palm has been introduced to Brazil and Sick (1993:149) describes Turkey Vultures *Cathartes aura* as being a "nuisance" in palm plantations in Amazonia, where they consume the fruits. He also records them as feeding on the native palm *Acrocomia sclerocarpa* (= *A. aculeata*), a very widespread species occurring through the West Indies and from Mexico south to southern Brazil and Paraguay (Henderson et al. 1995), and overlapping the small known range of *Wingegyps*. Although *Wingegyps* may possibly have been the New World ecological equivalent of the unrelated Old World Palm-nut Vulture, its habits might also have been like that of the Egyptian Vulture *Neophron percnopterus* in subsisting on scraps thrown off of carcasses by larger vultures. Such habits might better explain the extinction of *Wingegyps*, as many of the larger avian scavengers in the New World also went extinct at the time of disappearance of much of the mammalian megafauna (Steadman and Martin 1984).

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Diagnoses of hybrid hummingbirds (Aves: Trochilidae).
13. An undescribed intrageneric combination,
Heliodoxa imperatrix* × *Heliodoxa jacula

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Abstract.—An enigmatic specimen collected by Perry O. Simons, presumably on the Pacific slope of the Ecuadorian Andes, is demonstrated to be a hybrid between *Heliodoxa imperatrix* and *Heliodoxa jacula jamesoni*. This represents the only known instance of intrageneric hybridization in *Heliodoxa*. External measurements of the hybrid are consistent with the proposed parental hypothesis.

At the monthly meeting of the British Ornithologists' Club on the 17 January 1900, Ernst Hartert (1900:39) exhibited a specimen of hummingbird, "obtained in Ecuador by Mr. Simons, combin[ing] in a striking way the shape and colours of *Eugenia [Heliodoxa] imperatrix* and *Heliodoxa jacula jamesoni* . . . to be described in detail in the 'Novitates Zoologicae'." Although Hartert never published a description or reported a museum registration number, this brief exhibition notice has been cited in catalogs of avian hybrids (Gray 1956, Panov 1989). Here I provide a taxonomic assessment of the specimen employing the methods and assumptions outlined in Graves (1990) and Graves & Zusi (1990), as modified by the findings of Graves (1998, 1999).

Methods

The specimen, now deposited in the Natural History Museum (registration number, 1902.3.13.2211), bears two labels, one from the British Museum marked "P. O. Simons," and an older one from the Rothschild Museum. Perry O. Simons collected mammals and birds for Oldfield Thomas (British Museum) from 1898 until his murder near Cuervas, Argentina, in 1901 (Allen 1903, Chubb 1919). Both specimen labels

are marked with Hartert's taxonomic determination. Curiously, neither the specimen labels nor the Natural History Museum catalog indicate when or where the specimen was collected.

I compared the specimen (Figs. 1, 2) with all species in the subfamily Trochilinae, the typical hummingbirds (Zusi & Bentz 1982, Sibley & Monroe 1990, Bleweiss et al. 1997), deposited in the Natural History Museum, Tring, and the National Museum of Natural History, Smithsonian Institution. The specimen appears to be a male in definitive plumage as judged by the absence of striations on the maxillary ramphotheca and the presence of a well-defined, strongly iridescent gorget and coronal stripe. Descriptions in this paper refer to definitive male plumage. Simons' specimen is clearly assignable to the genus *Heliodoxa* in possessing a unique combination of characters: (a) robust, moderately long (22.7 mm), nearly straight bill (Fig. 1); (b) feathers extend forward on the bill obscuring the nostrils; (c) unmodified regimens; (d) tarsal feathers extend to the base of toes; (e) moderately forked tail (fork depth = 35.3 mm; Fig. 2), (f) unspotted rectrices; (g) small brilliant gorget; and (h) brilliant coronal stripe.

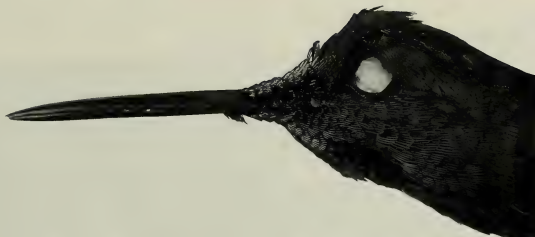


Fig. 1. A probable hybrid, *Heliodoxa imperatrix* × *H. jacula jamesoni* (BMNH 1902.3.13.2211).

According to Chubb (1919), Stephens & Traylor (1983), and Paynter (1993), Simons' collecting itinerary overlapped the known range of the genus *Heliodoxa* on the Pacific slope of the Ecuadorian Andes (prov. Azuay, Cañar, Chimborazo, Guayas, and El Oro), and on the Amazonian slope of the Andes in Peru (depto. Junín and Puno) and Bolivia (depto. La Paz). For the purposes of the hybrid diagnosis, I restricted the pool of potential parental species (Graves 1990, Graves & Zusi 1990) to *Heliodoxa aurescens*, *H. rubinoides*, *H. leadbeateri*, *H. schreibersii*, *H. branickii*, *H. imperatrix*, and *H. jacula jamesoni* (taxonomy

of Schuchmann 1999). I measured selected specimens with digital calipers (rounded to the nearest 0.1 mm): wing chord; bill length (from anterior extension of feathers); and rectrix length (from point to insertion of the central rectrices to the tip of each rectrix) (Table 1). Pairs of rectrices are numbered from the innermost (R1) to the outermost (R5).

I evaluated the color of the breast at the ventral midline and of the medial vane of the dorsal surface of R4 (7 mm from tip) with a calibrated colorimeter (CR-221 Chroma Meter, Minolta Corporation) equipped with a 3.0 mm aperture. The mea-

Table 1.—Ranges (mean ± standard deviation) of measurements (mm) of adult males of *Heliodoxa imperatrix*, *H. jacula jamesoni*, and a probable hybrid, *Heliodoxa imperatrix* × *H. jacula jamesoni* (BMNH 1902.3.13.2211).

	<i>Heliodoxa imperatrix</i> (n = 10)	<i>Heliodoxa jacula jamesoni</i> (n = 12)	BMNH 1902.3.13.2211
Wing chord	70.4–75.8 (73.2 ± 1.7)	73.3–79.0 (75.9 ± 1.8)	75.5
Bill length	23.3–24.9 (23.4 ± 0.8)	21.8–24.4 (23.2 ± 0.7)	22.7
Rectrix 1	22.6–26.6 (24.5 ± 1.2)	32.7–35.5 (33.7 ± 1.0)	28.7
Rectrix 2	27.9–32.9 (29.7 ± 1.4)	36.7–40.0 (38.5 ± 1.0)	34.3
Rectrix 3	38.7–46.5 (41.3 ± 2.3)	42.3–46.5 (44.4 ± 1.1)	43.7
Rectrix 4	51.0–60.3 (54.8 ± 2.8)	47.7–51.3 (49.7 ± 1.3)	55.6
Rectrix 5	62.2–76.2 (68.4 ± 5.7)	48.5–54.3 (51.7 ± 2.1)	64.0

suring head of the CR-221 uses 45° circumferential illumination. Light from the pulsed xenon arc lamp is projected onto the specimen surface by optical fibers arranged in a circle around the measurement axis to provide diffuse, even lighting over the measuring area. Only light reflected perpendicular to the specimen surface is collected for color analysis. Colorimetric data from iridescent feathers are acutely dependent on the angle of measurement, the curvature of plumage surfaces in museum skins, and the degree of pressure applied to the plumage surface by the Chroma Meter aperture. In order to reduce measurement variation, I held the aperture flush with the surface of the breast plumage or rectrix without depressing it. The default setting for the CR-221 Chroma Meter displays mean values derived from three sequential, in situ measurements. I repeated this procedure twice, removing the aperture between trials. Thus, each datum summarized in Table 2 represents the mean of six independent colorimetric measurements.

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

ors perceived by hummingbirds is unknown.

Results and Discussion

I considered hypotheses that the specimen represents (i) an undescribed geographic variant or genetic color morph of one of the aforementioned species of *Heliodoxa*; (ii) a hybrid; or (iii) an undescribed species of *Heliodoxa*. Simons' specimen does not appear to represent an unknown color morph or geographic variant of any described species because of its unique tail morphology (Table 1). As noted by Hartert (1900), the specimen combines characters of *Heliodoxa imperatrix* and *Heliodoxa jacula* (Figs. 1–3; Tables 1, 2).

The hybrid diagnosis focuses on the identification of apomorphic character states of possible parental species in putative hybrids (Graves 1990). Complete dominance and polygenic inheritance of plumage characters, however, may preclude or obscure the expression of parental apomorphies in hybrids. When parental apomorphies are not identifiable, the parentage of a hybrid may be indicated, although less conclusively, by the presence or absence of a suite of plesiomorphic characters.

The pool of potential parental species may first be narrowed by focusing on the absence of rufous or buff pigmentation in the hybrid's plumage. Because brown and reddish-brown pigments appear to exhibit consistent penetrance in hummingbird hybrids (Banks & Johnson 1961, Graves & Newfield 1996), *Heliodoxa rubinoides* (rufous on inner vanes of secondaries and primaries; cinnamon-buff margins of breast and abdominal feathers), *H. aurescens* (rufous pectoral band), and *H. branickii* (rufous inner vanes of rectrices) can be eliminated from further consideration as parental species. In a similar fashion, *H. schreibersi* (black throat, breast, and abdomen) and *H. leadbeateri* (brilliant violet coronal stripe; coppery-bronze hindcrown and neck) are exceedingly unlikely to be paren-

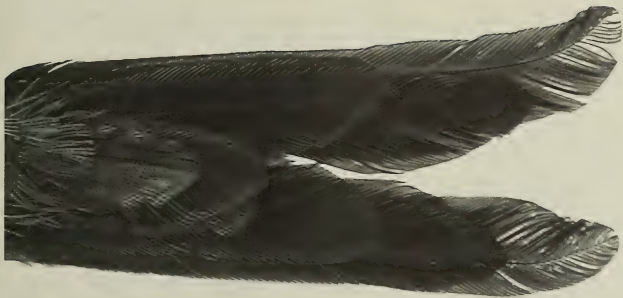


Fig. 2. Dorsal surface of the rectrices of a probable hybrid, *Heliodoxa imperatrix* \times *H. jacula jamesoni* (BMNH 1902.3.13.2211).

tal species because they possess characters not observed in the hybrid. Based on plumage characters, the hybrid is most likely the product of the species, *H. imperatrix* \times *H. jacula jamesoni*. Below, I present a synopsis of the essential evidence.

The visual display of iridescence in *Heliodoxa imperatrix* and *H. jacula* has evolved to be viewed head-on. Both parental species possess brilliant gorgets and coronal stripes that exhibit metallic iridescence. In *H. imperatrix*, the green coronal stripe is bluntly triangular in shape, extending from the base of the bill and narrowing to a point along the midline of the crown (even with the anterior edge of the eye). The bluish-green coronal stripe in *H. jacula* extends from the bill to the hindcrown forming a coronal stripe. The coronal stripe of the hybrid is intermediate in appearance between those of *H. imperatrix* and *H. jacula*. *Heliodoxa imperatrix* possesses a small purplish-pink gorget that appears to be surrounded by a field of dimly glowing, greenish-black plumage when viewed head-on. The blue gorget of *H. jacula* is surrounded by a field of green plumage, which is spangled with glowing iridescence when viewed head-on. In the hybrid, the color

and quality of iridescence exhibited by the gorget (purple exhibiting pinkish tones at certain angles) and the surrounding plumage are intermediate in appearance between those of *H. imperatrix* and *H. jacula*.

The ventral plumage of *Heliodoxa imperatrix* exhibits brilliant golden-green iridescence on the lower breast, flanks, and abdomen when viewed head-on. The breast and abdominal plumage is significantly darker in *H. jacula* and exhibits far less iridescence than in *H. imperatrix*. The color and quality of iridescence in the hybrid is intermediate between those of the postulated parental species (Table 2). The rectrices of *H. imperatrix* are dark bronzy-olive becoming progressively darker from R1 to R5, whereas those of *H. jacula* are bluish-black (the lateral webs of R1 are tinted with olive in some individuals). Rectrix color in the hybrid is roughly intermediate between that of the postulated parental species (Table 2).

As a second step, the parental hypothesis was tested with an analysis of size and external proportions (Table 1, Fig. 3). Measurements of avian hybrids fall within the mensural ranges exhibited by their parental species as a consequence of a polygenic

Table 2.—Maxima, minima, and means (\pm standard deviation) of opponent color coordinates (L , a , b) of breast and rectrix 4 (R4) for males in definitive plumage of *Heliodoxa imperatrix*, *H. jacula jamesoni*, and a hybrid, *Heliodoxa imperatrix* \times *H. jacula jamesoni* (BMNH 1902.3.13.2211).

	<i>Heliodoxa imperatrix</i> ($n = 10$)					<i>H. jacula jamesoni</i> ($n = 12$)					BMNH 1902.3.13.2211
	Min.	Max.	Mean	(\pm S.D.)	Min.	Max.	Mean	(\pm S.D.)			
Breast	L	17.3	28.8	21.4	(± 3.2)	26.5	33.5	29.3	(± 1.8)	24.4	
	a	-18.6	-8.6	-12.5	(± 3.0)	-20.1	-6.7	-13.9	(± 3.9)	-10.9	
	b	10.9	18.8	13.8	(± 2.7)	10.8	20.9	15.1	(± 3.4)	19.5	
R4	L	11.3	19.3	15.7	(± 2.3)	10.3	15.4	13.3	(± 1.7)	11.5	
	a	-1.5	2.3	0.9	(± 1.2)	0.5	2.3	1.2	(± 0.6)	2.6	
	b	4.8	11.3	7.9	(± 2.0)	-2.5	1.1	-0.8	(± 1.0)	1.6	

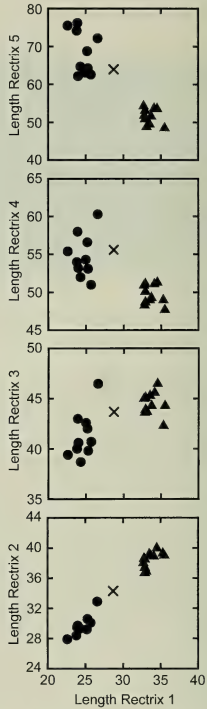


Fig. 3. Bivariate plots of measurements (see Table 1) of males in definitive plumage: *Heliodoxa imperatrix* (●), *H. jacula jamesoni* (▲), and a hybrid (X), *Heliodoxa imperatrix* \times *H. jacula jamesoni* (BMNH 1902.3.13.2211).

mode of inheritance (see Buckley 1982). Measurements of *H. imperatrix* and *H. jacula* overlap for four of seven characters. The percent difference in character means (larger species divided by smaller) varies

from negligible to moderate: wing chord (3.7%), bill length (0.9%), R1 (37.6%), R2 (29.6%), R3 (7.5%), R4 (10.3%), and R5 (32.3%). Measurements of the hybrid fall within the cumulative range of parental measurements for all seven characters and within the parental means for five characters (wing chord, R1, R2, R3, R5). In summary, evidence obtained from plumage color and pattern, as well as from external size and shape, is consistent with the hypothesis that Simons' specimen is an intrageneric hybrid between *Heliodoxa imperatrix* and *H. jacula jamesoni*.

Simons collected avian specimens on the Pacific slope of the Ecuadorian Andes in the provinces of Azuay, Chimborazo, Guayas, El Oro, and Pichincha from 1 November 1898 to 12 July 1899 (Chubb 1919, Paynter 1993). His northernmost collecting locality, Guailabamba, Pichincha (0°04'S, 78°21'W), lies in a semi-arid intermontane valley some 30 km southeast of the zone of sympatry for *Heliodoxa imperatrix* and *H. jacula jamesoni* in humid cloud forest on the Pacific slope (see Ridgely & Greenfield 2001). This suggests one of three possibilities: (1) Simons collected the specimen along the Quito-Guailabamba-Gualea road, but on the Pacific slope; (2) he purchased the specimen from a third party, possibly a native collector; or (3) he obtained the specimen at an unknown area of sympatry between the parental species on the Pacific slope in west-central or southwestern Ecuador. Whatever the source, Simons' specimen represents the only known instance of intrageneric hybridization in *Heliodoxa*.

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***Pholidochromis cerasina*, a new species of pseudochromine dottyback fish from the west Pacific (Perciformes: Pseudochromidae)**

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Abstract.—*Pholidochromis cerasina* is described from the 43.9-mm SL holotype from Talisei Island, off the northern tip of Sulawesi, Indonesia. It is distinguished from its congener *P. marginata* (Lubbock) from Papua New Guinea and the northern Solomon Islands in lacking both dark submarginal markings on the median fins and prominent dark grey to black spots surrounding sensory pores on the head.

Fishes of the Indo-Pacific subfamily Pseudochrominae were recently revised by Gill (2003), who recognised 80 species in 10 genera, four of which were newly described. One of the newly described genera, *Pholidochromis*, was erected to accommodate a single species, *Pseudochromis marginatus* Lubbock, 1980, and distinguished from other pseudochromine genera in having the following combination of external characters: lower lip complete (uninterrupted at symphysis); dorsal-fin rays III, 22; anal-fin rays III, 13; scales in lateral series 28–32; dorsal and anal fins with well-developed scale sheaths; and predorsal scales extending anteriorly to or forward of posterior nostrils. It is also unique among pseudochromid genera in having the following combination of osteological characters: three equal-sized supraneural bones; first dorsal pterygiophore posterior lamina running most of the length of the bone; and 11–12 consecutive dorsal pterygiophores inserting in a 1:1 relationship with interneural spaces directly behind neural spine 4.

Gill (2003) recorded *Pholidochromis marginata* from the east coast of Papua New Guinea, Bougainville Island, and off the northern tip of Sulawesi, Indonesia. The latter record was based on a single speci-

men (USNM 136954) collected at Talisei Island in 1909 by the United States Bureau of Fisheries Steamer *Albatross*; it bears a silk tag with the number “2038.” The specimen differs from other examined specimens (all of which were collected 50 or more years after the Sulawesi specimen) in lacking conspicuous dark spots on the head and dark submarginal stripes on the median fins. Although no comments on the condition of these markings were made in his revision, the first author attributed their absence to the age of the specimen, with the assumption that it was badly faded.

In 1995, the first author received a colour illustration of an aquarium individual of a pseudochromid from W. E. Burgess (formerly of Tropical Fish Hobbyist Publications Inc.). It was a pale pink, deep-bodied fish with orange to red spots on the body and median fins, and a yellow ring around the eye. The first author was unable to identify it confidently with any known species, but suggested that it was perhaps an unusually coloured individual of either *Pseudochromis fuscus* Müller & Troschel, 1849 (which is often yellow with blue to grey spots and a similar body shape) or a poor illustration of *P. marshallensis* Schultz, 1953 (which, though usually more slender

with a darker ground coloration, has yellow to orange or red spots on the body).

In May 2000, the second author sent the first author a photograph of a pseudochromid from a recent article in the Japanese aquarium journal *Aqualife*, as well as additional aquarium photographs of the specimen. The fish depicted was very similar in coloration and shape to the one in Burgess's illustration, thus rekindling interest in its identity. A search of the first author's collection of pseudochromid photographs revealed an illustration of a similar specimen collected on the *Albatross* expedition (original housed in the National Museum of Natural History, Smithsonian Institution). The number "2038" was written in pencil next to the illustrated fish.

As Fowler (1931) had reported on pseudochromids collected by the *Albatross*, his paper was searched in attempt to locate a reference to the number "2038." No such reference was found, but a colour description closely matching the illustration was found for a specimen numbered "22731" from Talisse Island, which Fowler had identified as *Pseudochromis xanthochir* Bleeker, 1855 (a junior subjective synonym of *P. fuscus*). The number "22731" refers to a linen tag attached to a 45.0-mm-SL specimen of the pseudoplesiopine *Pseudoplesiops typus* Bleeker, 1858 (now registered USNM 146624). However, the *Albatross* illustration (and Fowler's description) is obviously not based on the specimen of *P. typus*. Although *P. typus* may be pale pink to pale grey with a ring around the eye (which is red to black in life), it does not possess red spots on the body. Moreover, the illustration depicts a fish with relatively short, broad pelvic fins, whereas they are long and slender in specimens *P. typus* (including the specimen in USNM 146624). The other illustration and photographs of aquarium specimens are also not referable to *P. typus*.

However, the *P. typus* specimen was collected from Talisse (=Talisei) Island on the same date as the *Albatross Pholidochromis*

specimen (presumably from the same station), and this, coupled with the close similarity in body form and pelvic-fin shape, led us to question whether the illustration was of the *Pholidochromis* specimen, and whether the "2038" may refer to the silk tag number on that specimen. We therefore asked S. L. Jewett and J. T. Williams of the National Museum of Natural History to check whether there were further details that might corroborate this. Jewett consulted the original illustration and responded (pers. comm., 4 Aug 2000): "It not only says 2038 in pencil, but Leonard Schultz [former Curator of Fishes at USNM, and author of a paper on the pseudochromid genus *Labracinus*, based mostly on *Albatross* specimens] wrote a note in the margin that says "see USNM 136954." She also noted that there is a small tag in the jar containing USNM 136954 indicating that the specimen was drawn.

We therefore conclude that the illustration is based on the *Pholidochromis* specimen. Clearly, then, the absence of dark markings in the specimen are not due to fading, as such markings are not indicated in the *Albatross* illustration, nor are they evident in the illustrations or photographs of live aquarium specimens. Thus, we conclude that the specimens represent a species distinct from *P. marginata*, and therefore describe it as new.

Materials and Methods

Methods of counting, measuring and presentation follow Gill (2003). Institutional codes follow Leviton et al. (1985).

Pholidochromis cerasina, new species Cherry Dottyback Fig. 1

Pseudochromis xanthochir [non Bleeker, 1855]; Fowler, 1931: 32 (color description).

Pholidochromis marginata [non *Pseudochromis marginatus* Lubbock, 1980]; Gill,

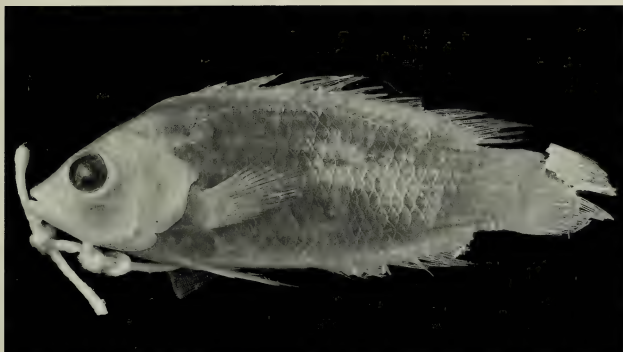


Fig. 1. *Pholidochromis cerasina*, USNM 136954, 43.9 mm SL, holotype, Talisei Island, Sulawesi, Indonesia. (Photo by P. Hurst.)

2003:000, fig. 5 (description and distribution in part).

Holotype.—USNM 136954, 43.9 mm SL, Indonesia, Sulawesi, Talisei (=Talissee) Island, R/V *Albatross*, 9 November 1909.

Diagnosis.—*Pholidochromis cerasinus* is distinguished from other pseudochromines in having the following combination of characters: dorsal-fin rays III, 22; anal-fin rays III, 13; scales in lateral series 29–30; dorsal and anal fins with well-developed scale sheaths; predorsal scales extending anteriorly to just behind anterior nostrils; and no prominent dark grey to black spots surrounding sensory pores on head.

Description.—Dorsal-fin rays III, 22, at least last 18 segmented rays branched (ray preceding first apparent branched ray damaged); anal-fin rays III, 13, at least last 12 segmented rays branched (anteriormost ray damaged); pectoral-fin rays 19/19; upper procurrent caudal-fin rays 6; lower procurrent caudal-fin rays 5; total caudal-fin rays 28; scales in lateral series 29/30; anterior lateral-line scales 23/24; anterior lateral line terminating beneath segmented dorsal-fin

ray 17/17; posterior lateral-line scales 10 + 0/9 + 0; scales between lateral lines 3/3; horizontal scale rows above anal-fin origin 12 + 1 + 3/13 + 1 + 3; circumpeduncular scales 16; predorsal scales 21; scales behind eye 3; scales to preopercular angle 4; gill rakers 5 + 10; pseudobranch filaments 9; circumorbital pores 17/18; preopercular pores 9/8; dentary pores 4/4; posterior interorbital pores 0.

Lower lip complete; dorsal and anal fins with well-developed scale sheaths; predorsal scales extending anteriorly to just behind anterior nostrils; posterior margin of opercle with 4 inconspicuous serrations; outer gill rakers of ceratobranchial-1 with teeth mostly confined to raker tips; anterior dorsal-fin pterygiophore formula S/S/S + 3/1 + 1/1/1/1/1/1/1/1/1/1/1 + 1; dorsal-fin spines pungent and moderately slender; anterior anal-fin pterygiophore formula 3/1/1 + 1/1/1/1 + 1; anal-fin spines pungent and moderately slender to stout, second spine stouter than third; pelvic-fin spine slender, tip weakly pungent; second segmented pelvic-fin ray longest; caudal fin

rounded (inferred for holotype from *Albatross* illustration); vertebrae 10 + 16; epineurals 13; epurals 3.

Upper jaw with 2 pairs of curved, enlarged caniniform teeth anteriorly, medial pair smallest, and about 6 (at symphysis) to 2–3 (on sides of jaw) irregular rows of small conical teeth, outermost of rows of teeth much larger and more curved than those of inner rows; lower jaw with 2 pairs of curved, enlarged caniniform teeth anteriorly, medial pair smallest, and about 5 (at symphysis) to 1 (on sides of jaw) inner rows of small conical to caniniform teeth, those on middle of jaw large and caniniform; vomer with 1–2 rows of small conical teeth arranged in chevron; palatine with 2–3 rows of small conical teeth arranged in elongate ovoid patch, anterior part of tooth patch more-or-less contiguous with posterolateral arm of vomerine tooth patch; ectopterygoid edentate; tongue moderately pointed and edentate.

As percentage of SL: head length 28.0; orbit diameter 9.1; snout length 7.7; fleshy interorbital width 6.2; bony interorbital width 3.9; body width 13.9; snout tip to posterior tip of retroarticular bone 15.9; predorsal length 35.3; prepelvic length 35.3; posterior tip of retroarticular bone to pelvic-fin origin 21.0; dorsal-fin origin to pelvic-fin origin 34.9; dorsal-fin origin to middle dorsal-fin ray 34.4; dorsal-fin origin to anal-fin origin 46.2; pelvic-fin origin to anal-fin origin 27.6; middle dorsal-fin ray to dorsal-fin termination 26.2; middle dorsal-fin ray to anal-fin origin 33.5; anal-fin origin to dorsal-fin termination 39.0; anal-fin base length 29.6; dorsal-fin termination to anal-fin termination 17.1; dorsal-fin termination to caudal peduncle dorsal edge 10.9; dorsal-fin termination to caudal peduncle ventral edge 19.6; anal-fin termination to caudal peduncle dorsal edge 19.8; anal-fin termination to caudal peduncle ventral edge 10.7; first dorsal-fin spine 2.7; second dorsal-fin spine 5.2; third dorsal-fin spine 7.1; first segmented dorsal-fin ray 13.7; fourth from last segmented dorsal-fin

ray broken; first anal-fin spine 3.0; second anal-fin spine 5.7; third anal-fin spine 7.1; first segmented anal-fin ray broken; fourth from last segmented anal-fin ray broken; third pectoral-fin ray broken (both sides); pelvic-fin spine 9.8; second segmented pelvic-fin ray 22.6; caudal-fin length not determined (ray tips broken).

Live coloration (based on a color illustration of holotype and photographs and an illustration of aquarium specimens).—Head and body pale pinkish grey to pinkish olive dorsally, becoming pale pink to pale yellow or white ventrally; posttemporal pore in dusky grey spot (not apparent in illustrations); orbital rim yellow to bright orange or bright red; pale blue to mauve stripe extending from anteroventral edge of eye to middle of upper lip (not apparent on illustration of holotype); iris silvery white, blue dorsally, with grey to blue suboval ring around pupil; body with small (about half pupil size) pale orange to bright orange or bright red spots, these best developed dorsally and posteriorly, and more or less arranged along horizontal scale rows; dorsal and anal fins pale pink to pale blue with blue distal margin, and 2–5 horizontal rows of pale orange to bright orange or crimson spots (crimson spots encircled with pale pink in photographed individuals); caudal fin pale pink to pale blue with blue distal margin and bright red to crimson spots (encircled with pale pink in photographed individuals), these irregularly arranged on basal part of fin, becoming arranged in convex columns on remainder of fin; pectoral fins hyaline with pinkish to yellowish hue; pelvic fins pale pink to pale blue.

Preserved coloration.—Head and body pale brown, paler ventrally; posttemporal pore in dusky grey spot; fins whitish hyaline to plain hyaline.

Habitat and Distribution.—No habitat data are known for the holotype. We also lack precise locality or habitat information for aquarium individuals of the species; however, K. Endoh (pers. comm.) informed



Fig. 2. *Pholidochromis marginata*, CAS 65783, 32.4 mm SL, southern side of Nagada Harbour, Madang Province, Papua New Guinea. (Photo by P. Crabb; after Gill, 2003:fig. 20.)

us that they were collected in the Philippine Islands.

Comparisons.—*Pholidochromis cerasina* agrees closely with its congener, *P. marginata* (Fig. 2), in most details, but differs in lacking conspicuous dark spots around the sensory pores on the head (only the post-temporal pore of *P. cerasina* has an inconspicuous dusky grey spot whereas *P. marginata* has conspicuous dark grey to black spots on at least the posterior suborbital, upper preopercular, anterior interorbital, posttemporal and parietal pores) and in lacking dark submarginal markings on the median fins (present as dark grey to black convex marking on the caudal fin, and short dark grey to black stripe on the posterior part of the dorsal and anal fins in *P. marginata*).

Values for 13 morphometric characters of the holotype of *P. cerasina* lay at the extreme or outside ranges observed in *P. marginata* (15 specimens, 27.2–45.6 mm SL). Although more specimens are needed to determine whether these are truly diagnostic, they are at least suggestive. We also document these in order to correct Gill's (2003)

description of *P. marginata*, as this included data from the holotype of *P. cerasina*. The characters are as follows (values expressed as % SL, and given first for *P. cerasina*, followed by *P. marginata*): fleshy interorbital width (6.2; 5.0–6.1); predorsal length (35.3; 36.0–39.0); middle dorsal-fin ray to dorsal-fin termination (26.2; 20.5–25.2); anal-fin termination to caudal peduncle ventral edge (10.7; 10.8–12.4); first dorsal-fin spine (2.7; 2.7–5.1); second dorsal-fin spine (5.2; 5.1–7.9); third dorsal-fin spine (7.1; 7.0–10.3); first segmented dorsal-fin ray (13.7; 11.0–13.9); first anal-fin spine (3.0; 3.7–5.7); second anal-fin spine (5.7; 6.8–9.6); third anal-fin spine (7.1; 7.0–11.1); pelvic-fin spine (9.8; 9.6–13.2); and second segmented pelvic-fin ray (22.6; 22.6–26.3).

Pholidochromis cerasina might also be confused with *Pseudochromis fowleri* Herre, 1934, from Sabah and the Philippine Islands, and *Pseudochromis fuscus*, from throughout the West Pacific, which it resembles in general body shape. These species differ from *Pholidochromis cerasina* in having an incomplete lower lip (interrupted

at symphysis) and more segmented dorsal-fin rays (23–25, usually 24 in *fowleri* and 25–29 in *fuscus* versus 22 in *cerasina*).

Remarks.—The live coloration of *P. marginata* is unknown, but, accepting the dark pigmentation on the head and median fins, is likely to be similar to *P. cerasina*. Moreover, as noted by Gill (2003), some specimens of *P. marginata* have pale spots on the body and median fins, and these possibly correspond with the red to orange spots shown by *P. cerasina*.

Etymology.—The specific epithet is from the Latin *cerasinus*, meaning “of cherry.” It alludes to the cherry-like bright orange to red spots on the body and median fins.

Material examined.—See above.

Acknowledgments

We thank S. L. Jewett and J. T. Williams for lending the holotype for study, and for their help in checking the history of the *Albatross* specimen and its illustration. We thank W. E. Burgess and K. Endoh for sending an illustration and photographs, respectively, of the species. S. E. Reader assisted with radiographing the holotype.

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**Redescription of *Cambaroides japonicus* (De Haan, 1841)
(Crustacea: Decapoda: Cambaridae) with allocation of a type locality
and month of collection of types**

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Abstract.—The Japanese crayfish, *Cambaroides japonicus* (De Haan), is re-described and illustrated, and details of its distribution and morphological variation are provided. Notable character differences between the populations of Honshu Island and Hokkaido Island indicate that gene flow between them is precluded. Analysis of geographical variation demonstrates that the undesignated type locality of the species is in central-western Aomori Prefecture, Honshu. The analysis of the gastrolith weights of the lectotype and possible topotypes indicates that the lectotype was collected in June.

The German medical doctor, Philip Franz von Siebold, was the first to introduce the natural history of Japan to European academics (Siebold 1897). He also taught European medicine to traditional Japanese practitioners, and on 23 February 1826, at Shimonoseki City, Yamaguchi Prefecture, received specimens of a crayfish used as a Japanese drug from his student, Kosai Yamaguchi (Siebold 1897). These were sent to the Netherlands and were described as *Cambaroides japonicus* by De Haan (1841). The brief description of the species included no locality or other collection data. Heretofore, taxonomic studies of *C. japonicus* have been limited to examining cyclic dimorphism (Kawai & Saito 1999), and the genus *Cambaroides* has yet to be the subject of modern morphological studies.

This paper provides a redescription of *C. japonicus*, allocates a type locality based on an analysis of geographic variation, and suggests a probable month of collection of

the types based on an analysis of monthly changes in gastrolith weight.

Abbreviations used in the text are: GVM, geographical variation in morphology; POCL, postorbital carapace length; RMNH, Nationaal Natuurhistorisch Museum, Leiden; and TCL, total carapace length.

Calculation of GVM: The geographical variation of each specimen was divided into three different levels (see Fig. 1), and the mean of the levels among specimens was calculated in each collection (Appendix I). The mean in each collection was classified into three degrees; 1.0–1.6, 1.7–2.3, 2.4–3.0.

Cambaroides japonicus (De Haan, 1841)
Fig. 2, Table 1

Diagnosis.—Body pigmented; eyes well developed, pigmented. Carapace subcylindrical, dorsal and lateral surfaces with large punctations, without tubercles; cervical spines absent. Rostrum acuminate, broadest at base; margins thickened, strongly convergent, lacking spines or tubercles; median carina present, often very weak;

* Deceased 11 July 2002.

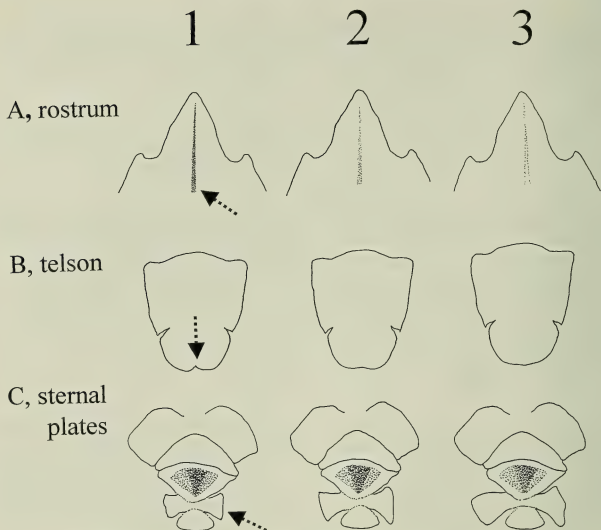


Fig. 1. Definition of morphological variations. A-1, median carina present on rostrum; A-2, carina intermediate between A-1 and A-3; A-3, carina almost absent. B-1, caudomedian excavation present on telson; B-2, excavation intermediate between B-1 and B-3; B-3, excavation absent; C-1, sternal plates closed; C-2, sternal plates intermediate between C-1 and C-3; C-3, sternal plates open.

acumen comprising 27.5–59.5% (\bar{X} = 47.8%, SD = 4.6, n = 200) of rostrum length, latter consisting 14.7–26.7% (\bar{X} = 17.3%, SD = 2.5, n = 200) of TCL. Areola 1.1–2.8 (\bar{X} = 1.9%, SD = 0.2, n = 200) times as long as broad, constituting 26.3–41.1% (\bar{X} = 29.5%, SD = 3.1, n = 200) of TCL and 30.9–46.9% (\bar{X} = 35.5%, SD = 3.3, n = 200) of POCL. Antennal scale 1.6–2.8 (\bar{X} = 2.2%, SD = 0.3, n = 100) times as long as broad, widest at midlength, lateral margin thickened, terminating in large, stout spine. Pleura of somites 2 and 3 with rounded to subtruncate ventral margins.

Palm of chela of cheliped with scattered

large punctations on dorsal, lateral, and ventral surfaces, without setae; palm inflated, width 1.2–1.6 (\bar{X} = 1.4%, SD = 0.1, n = 100) times length of mesial margin. Large punctations on dorsal, lateral and ventral surface of fixed finger and dactyl.

Hooks present on ischia of second and third pereopods in males, hooks simple and not reaching basioischial articulation. In situ gonopods (first pleopods) of adult male symmetrical, bases not contiguous. In mesial aspect (Fig. 2A), apex directed cephalodistally nearly 45° to axis of shaft, with strong endopodite and protopodite; apex (Fig. 2B) sclerotized, at least distally, ce-

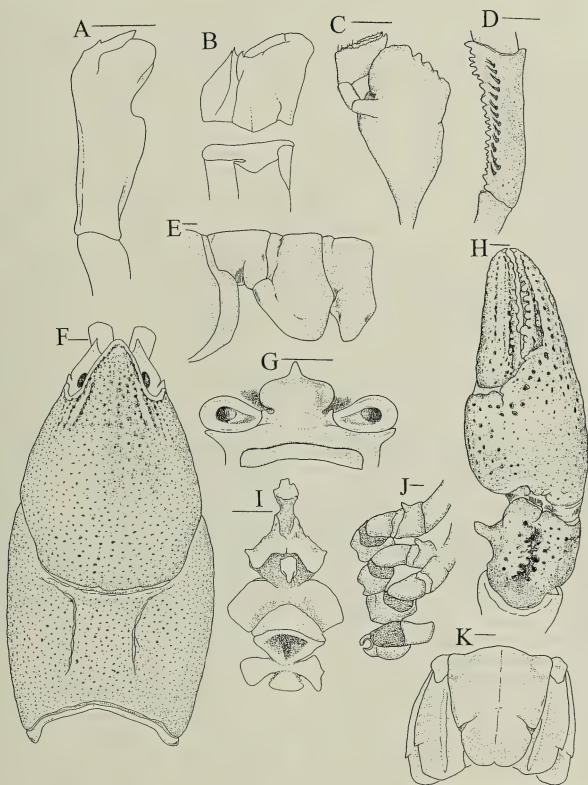


Fig. 2. *Cambaroides japonicus* (De Haan, 1841), all figures from lectotype (RMNH 5602, RMNH 5603), except B (redrawn from Hart 1953), I from paralectotype female (RMNH 2912), and j from paralectotype male#1: A, mesial view of first pleopod; B, mesial view of distal portion of first pleopod; C, lateral view of mandible; D, ventral view of ischium of third maxilliped; E, lateral view of first three abdominal segments; F, dorsal view of carapace; G, epistome; H, dorsal view of distal podomeres of right cheliped; I, annulus ventralis; J, proximal podomeres of pereopods; K, dorsal view of telson and uropods. Line = 2 mm.

Table 1.—Measurements of type series of *Cambaroides japonicus*.

	Lectotype	Paralectotype male #1	Paralectotype male #2	Paralectotype female
Carapace				
Total length	31.6	22.1	21.7	30.4
Postorbital length	25.4	18.6	17.6	25.1
Width	16.4	11.1	11.7	15.1
Height	11.1	8.7	9.4	11.1
Areola				
Length	9.8	7.3	7.0	9.4
Width	4.9	3.7	2.6	4.2
Rostrum				
Length	6.6	4.7	4.3	7.1
Width	7.3	4.9	4.5	7.3
Chela				
Length of mesial margin of palm	10.9	6.9	5.6	8.9
Width of palm	11.4	7.6	7.3	8.9
Length of lateral margin	24.5	16.4	15.8	20.4
Length of dactyl	14.2	8.3	8.0	10.8
Abdomen width	14.7	10.6	10.2	17.3

phalolaterally swollen into straight, subacute, stout, cephalodistally directed mesial process, cephalic process, and central projection with blade-like caudal process; 3 subequal spines near mid-width of apex, length about one-tenth of width of apex. Proximal part of gonopod subcylindrical in cross section, becoming subtriangular distally. Sperm groove along caudomesial face of gonopod shallow, open between mesial process and central projection, ending in relatively blunt tip. Adult male gonopod with "juvenile suture".

Annulus ventralis (Fig. 2I) immovable, symmetrical, rounded in outline, about 1.2 times as long as wide. Preannular plate transversely subdivided into 2 subtriangular plates, cephalic margin of anterior part broadly attached to preceding sternite, middle section of posterior part with shallow depression as fossa without sinus. Postannular sclerite subcircular, about 1.7 times as broad as long, and 0.5 times as wide as annular plate.

Measurements of type specimens provided in Table 1.

Description of lectotype.—Cephalotho-

rax (Fig. 2F) subcylindrical, slightly compressed laterally; dorsoventrally depressed (greatest width of thoracic section 1.5 times depth); POCL 80.4% of TCL. Areola 2.0 times longer than wide, dense punctate, length 31.0% of TCL (38.6% of POCL). Rostrum acuminate, tip barely reaching distal margin of antennal scale and midlength of ultimate podomere of antennal peduncle; acumen comprising 48.4% of rostrum length, latter consisting 20.9% of TCL; floor (dorsal surface) of rostrum dense punctate; median carina nearly absent.

Postorbital ridges poorly defined. Suborbital angle obtuse, without tubercle or spine. Antennal scale with strong distolateral spine, tip reaching tip of rostrum and midlength of ultimate podomere of antennal peduncle.

Greatest width of abdomen 89.6% greatest width of carapace. Proximal podomere of uropod lacking spine or tubercle on lateral lobe, mesial lobe broadly rounded; mesial ramus of uropoda with caudolateral spine, and submedian dorsal ridge terminating in small caudomedian spine, tip of which not reaching caudal margin; lateral

ramus with stout caudolateral spine; lateral ramus divided into cephalic and caudal sections, separated by transverse flexure bearing spines. Telson divided into cephalic and caudal sections, each caudolateral corner with pair of stout, fixed spines. Caudal margin of telson with deep median excavation.

Epistome (Fig. 2G) with subovate cephalic lobe bearing prominent cephalomedian projection, margins of lobe markedly elevated; fovea of epistome scarcely visible; central portion of epistome with pair of transverse grooves, and deep transverse grooves along cephalic margin of weakly arched zygoma. Third maxilliped (Fig. 2D) with mesial margin bearing 21 denticles; mesial half of ischium with row of clusters of long, stiff setae. Incisor ridge of right margin (Fig. 2C) with 5 corneous denticles.

Palm of right chela (Fig. 2H) subovate in cross section, moderately depressed dorsoventrally. Total chela length 77.5% of TCL. Palm 2.1 times as long as wide, length of mesial margin 44.5% of total chela length; dorsal surface with deep, widely scattered punctations, which become scarce laterally and caudolaterally; ventral surface less punctate. Dorsal surface of both fingers with poorly defined, longitudinal submedian ridge, and rows of deep punctations; tip of fingers corneous, subacute. Opposable surface of fixed finger with row of 9 tubercles, third from base largest. Opposable surface of dactyl with row of 5 tubercles; length of dactyl 1.3 times length of mesial margin of palm. Carpus (Fig. 2H) longer than broad, dorsal surface with prominent longitudinal furrow, lateral and mesial surface with large, crowded punctations; mesial surface with large, blunt subdistal spine, lateral surface with proximal spine; ventral surface with oblique furrow, short longitudinal furrow, and deep punctations. Merus with row of prominent tubercles on ventromesial margin, punctuate dorsally and ventrally.

Gonopods as described in "Diagnosis". In addition, tips of gonopods extending be-

yond cephalic margin of coxae of fourth pereopods.

Description of paralectotype male#1.—Differing from lectotype as follows: greatest width of thoracic section 1.3 times depth. POCL 84.2% of TCL. Areola length 33.0% of TCL (39.2% of POCL). Acumen comprising 46.1% of rostrum length, latter consisting 21.3% of TCL. Greatest width of abdomen 95.5% greatest width of carapace. Total chela length 74.2% of TCL; palm of right chela 2.2 times as long as wide; length of mesial margin 42.1% of total chela length. Dactyl length 1.2 times length of mesial margin of palm; opposable surface of fixed finger with 10 tubercles; opposable surface of dactyl with 6 tubercles.

Description of paralectotype—female.—Differing from lectotype, except in secondary sexual characteristics, as follows: greatest width of thoracic section 1.4 times depth. POCL 82.6% of TCL. Areola 2.2 times as long as broad. Areola length 30.9% of TCL (37.5% of POCL). Acumen comprising 50.0% of rostrum length, latter consisting 23.4% of TCL. Opposable surface of fixed finger with 6 tubercles, proximal largest; opposable surface of dactyl with 6 tubercles, length of finger 1.2 times length of mesial margin of palm.

Disposition of types.—All dry and lacking most appendages. Lectotype: 1 male, RMNH 5602, RMNH 5603. Paralectotypes: 2 males and 1 female, RMNH 2912. The lectotype has the mark "♀" written on the areola, but is a male. A milky-white gastrolith is included with the lectotype. Its dry weight (dried at 80°, 48 hr) is 0.0305 g, and its shape is semi-globular, with the greatest diameter 4.5 mm, the least diameter 4.2 mm, and the greatest height 1.8 mm.

Type locality.—No type locality for *C. japonicus* has ever been designated. In order to establish a type locality, we examined geographic variation in morphology (GVM) to identify any unique characters that might be displayed by the type specimens. Earlier, Fitzpatrick (1995) detected possible geographically defined races based

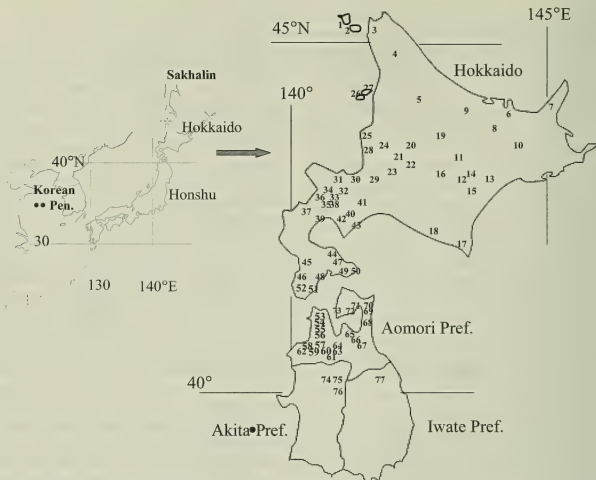


Fig. 3. Known geographical range of *Cambaroides japonicus* (De Haan, 1841). Numbers correspond to sampling sites listed in Appendix I.

on a distinct rostral carina and pleural margin shape of the abdominal segment. Samples, however, were too small and too widely scattered for definite conclusions. In our larger series from far more localities, we examined the presence or absence of a median carina on the rostrum, median excavation in the caudal margin of the telson, and open or closed sternal plates. The GVM was classified into three levels (Fig. 1), and mean GVM in each collection was summarized according to three categories by previously mentioned calculation (Fig. 4). Three GVM characters were found to be common in all the type series specimens, and similar to characters found only in specimens from central-western Aomori Prefecture, Honshu (Figs. 1–4, Appendix I, 55–62). This strongly suggests that the type

specimens were collected in that area. The central western Aomori Prefecture was designed as a probable locality of the type series. Kurimi (1811) and Ohtsuki (1817), in a paper published at the time Siebold received specimens of *C. japonicus*, remarked that the species commonly inhabited central-western Aomori Prefecture. This lends support to our assumption about the type locality.

Date of type collection.—Monthly samplings of *C. japonicus* were made from April to November 1989 in Iwaki City (Fig. 3, Appendix I, 59), in the central-western part of Aomori. For each sampling, gastroliths were removed from the stomachs of 30 individuals, ranging in size from 17.7 mm to 25.4 mm POCL, which corresponds to size range of the types. The result indi-

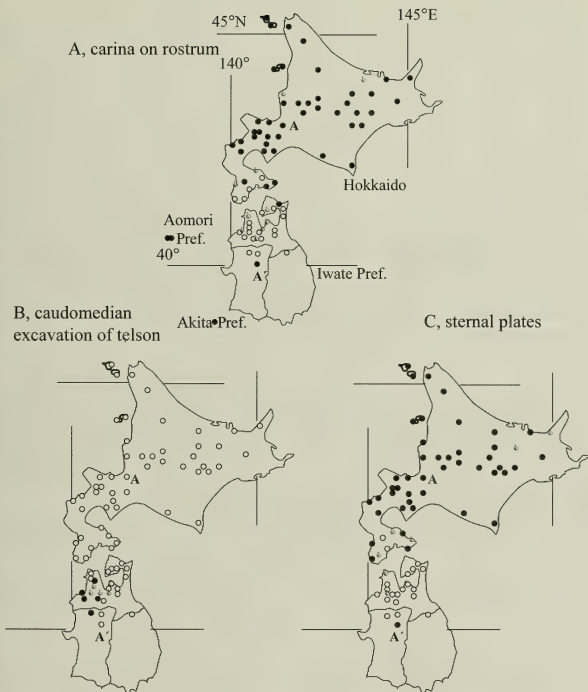


Fig. 4. Geographical variation of (A) carina on rostrum, (B) caudomedian excavation of telson, and (C) sternal plates. Solid circle, 1.0–1.6 level of mean GVM in collection; semi-open circle, 1.7–2.3; open circle, 2.4–3.0. A, Sapporo City; A', Kazuno City.

cates that the dry weight (dried at 80°, 48 hr) of the gastrolith from lectotype (0.0305 g) is similar to that of the June sample (Fig. 5). Thus, it is believed the type series was likely collected in June.

Range and specimens examined.—We examined a total of 405 specimens from Hokkaido Islands and four of its larger

nearby islands (Rebun, Rishiri, Teuri, and Yagishiri), as well as the northern part of Honshu Island (major parts of Aomori Prefecture, and northern part of Akita and Iwate Prefecture). Information on sampling sites is provided in Fig. 3 and Appendix I.

As far as known, *C. japonicus* is endemic to the entire Japanese Archipelago. How-

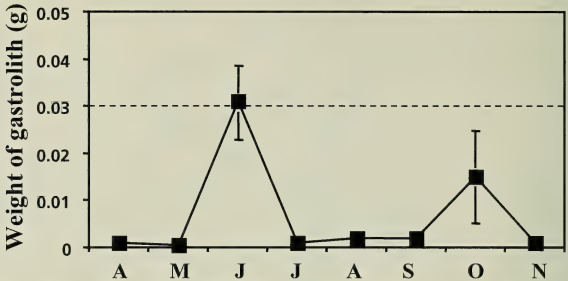


Fig. 5. Monthly change of dry gastrolith weight in *Cambaroides japonicus* (De Haan, 1841) from Iwaki City, Aomori Prefecture (see Fig. 3, 59). Vertical bar indicates *SD*. Dotted horizontal line shows the dry gastrolith weight of the lectotype (0.0305 g).

ever, Okada (1933:155–156) mentioned that “Mr. T. Urita, a director of the Girl’s High School at Maoka in south part of Sakhalin, U.S.S.R., informed me that *C. japonicus* seems not to occur in the stream and rivers, and that if it is found in anywhere in Sakhalin, it is very rare; however, I examined Outomari of Sakhalin specimens in the collection of Professor Iijima of Tokyo Imperial University, these are preserved in the Zoological Institute, Faculty of Sciences, Tokyo Imperial University”. And Urita (1942:39) said “I consequently spent considerable time and labour in search of this species, especially in Outomari and its neighbourhood, but unfortunately, without success; presumably, this species does not exist here in south Sakhalin, not, at any rate, at present”. On 11 November 2001, all specimens in the Tokyo Imperial University were transferred to the University Museum, the University of Tokyo, but no specimen from the Sakhalin could be found there.

Size.—The largest lake specimen is a male from Lake Akan, Hokkaido, measuring 39.2 mm POCL; the largest brook specimen is a male from Hamamasu with a

POCL of 34.3 mm. The smallest ovigerous female is 17.6 mm POCL.

Variation.—Most variations were noted in the number and comparative sizes of tubercular ornamentation, particularly on the cheliped. The caudolateral corner of the cephalic section of the telson bears one to three fixed spines. The lateral margin of the telson of most specimens gently tapers to a rounded caudal margin, but in some the lateral margins are subparallel and the caudal margin is flat. Some specimens have bosses between the sternal plates (Fig. 2I), but in most specimens these bosses are nearly absent.

Color.—Dorsal and lateral surfaces of cephalothorax, abdomen, chelae, and tail fan dark brown to chocolate, ventral surface light brown. Ventral surface of chela dark orange. Tips of pereopods dark orange. Caudal process and three spines of distal adult male gonopods amber. Background colors translucent to light brown in freshly molted individuals. The whitish-blue colorations or “blue color phase” (Fitzpatrick 1987) on the dorsal and lateral surfaces of thoracic carapace, abdomen, chelae, and tail fan, was found in specimens from Abashiri,

Obihiro, Iwamisawa, and Hamamasu, Hokkaido Prefecture, and in Shichinohe, Aomori Prefecture (see Appendix I).

Crayfish associates and conservation status.—During the past decade, local extinctions of *C. japonicus* have been reported from throughout its range. In eastern Hokkaido its numbers have been declining rapidly, while population numbers of the introduced crayfish, *Pacifastacus leniusculus* (Dana, 1852) in the same area have been increasing (Kawai et al. 2002). Also, Kawai et al. (2002) demonstrated that following the introduction of *P. leniusculus* into Lake Kussharo and Lake Shikaribetsu, *C. japonicus* disappeared. *Pacifastacus leniusculus* is known to be a vector of crayfish plague fungus, *Aphanomyces astaci* (Schikora), to which it is resistant, but to which *C. japonicus* is highly susceptible (Unestam 1969). It is possible that *Aphanomyces* may be a factor affecting displacement of *C. japonicus* at some localities, but there is as yet no investigation of infection to the natural populations in Hokkaido. The mechanisms underlying the negative impacts of *P. leniusculus* on *C. japonicus* required further investigation.

Cambaroides japonicus was designated an endangered species by the Japanese Fisheries Agency in 1995 and by the Japanese Environmental Agency in 2000.

Ecological notes.—*Cambaroides japonicus* appears to be restricted to lentic habitats, either lakes or small brooks in which current velocity is less than 10.0 cm/sec. In brooks, the species is found beneath boulders, or burrows in the banks. It appears to be a secondary burrower, and retreats underground to remain below the frost line in winter. Females enter burrows prior to ovulation, and remain in them to lay eggs. Most burrows are Y- or T-shaped, with two openings slightly above or below the water surface.

Reproduction.—Mating in *C. japonicus* is unique (Kawai & Saito 2001). The male moves beneath the female to deposit its spermatophore, and does not grasp the fe-

male with its chelae. In Hokkaido, mating pairs were encountered only in September and October, and ovigerous females during the subsequent May. Spermatozoa obviously are stored in the annulus ventralis for a six-month period during winter. Number of ova ranges from 50 to 100, and egg diameter is 2.3–2.7 mm.

Name in Japanese.—In Japan, it is usual for organisms to have one or more local names. To prevent possible ambiguity in this pragmatic system, and make it easier to incorporate taxonomic and distributional information, the common, Japanese name Zarigani, is proposed. This name, which refers to an animal that moves backward (Ohtsuki 1817), is also mentioned in older papers (e.g., Kurimi 1811). The names “Sarugani” which is the local name in Aomori Prefecture, and “Sarukani,” the local name in Akita Prefecture, means “the backward creeping crab.” Two local names are on the label attached to the specimens of *C. japonicus* at Saito Ho-Onkai Museum, Sendai, Japan (Nos. 1039, 1369). Also, the Ainu people, former occupants of Hokkaido and northern Honshu, know *C. japonicus* as “Tekinpekorupe,” alluding to an armed knight (Ohtsuki 1817).

Discussion

Cambaroides japonicus occurs in northern parts of Honshu and Hokkaido Islands (Fig. 3). It is likely that populations of the species inhabiting certain areas of Honshu were introduced from Hokkaido, but differences in the GVM (Fig. 4, Appendix I) indicate that the majority of populations on Honshu are native. An exception is seen in the GVM of specimens from Kazuno City (A'), Akita Prefecture, Honshu, which agrees with that of Sapporo City (A), Hokkaido. In 1943, a locality report in a small stream in Kazuno City originated from introduction of a population in Sapporo City (Mr. T. Komoriya, Japanese regional report 1978).

The distribution of Asian branchiobdel-

lidans, which are symbionts on crayfish, including *C. japonicus*, may shed some additional light on this issue, since there is a high degree of endemism in the various species. *Cirrodriulus aomorensis* and *C. tsugarensis* occur in Honshu (Gelder & Ohtaka 2000), while *C. inukaii* and *C. uchidai*, and others occur only in Hokkaido (Yamaguchi 1934). There is no overlap in the natural distributions of these two species. However, *C. inukaii* and *C. uchidai* have both been found in Kazuno City, Akita Prefecture, northern Honshu, an occurrence that might be explained by an introduction of *C. japonicus* from Hokkaido (Gelder & Ohtaka 2000).

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Appendix I.—Sampling data and geographic variation of morphology in *Cambaroides japonicus*.

	Sampling site (No. ref. to Fig. 3)	Date	Specimens	POCL \pm SD	Rostrum	Telson	Sternal plates
1	Rebun	04 Sep 1968	♂3 ♀2	21.3 \pm 2.9	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
2	Rishiri	17 Nov 1992	♂1 ♀1	22.3 \pm 4.8	1.5 \pm 0.7	3.0 \pm 0.0	1.0 \pm 0.0
3	Wakkanai	11 Aug 1998	♂4 ♀1	22.2 \pm 2.8	1.2 \pm 0.4	2.8 \pm 0.4	1.0 \pm 0.0
4	Nakagawa	16 Aug 1990	♂1 ♀0	20.2 \pm 0.0	1.0 \pm 0.0	3.0 \pm 0.0	—
5	Shibetsu	01 Sep 1957	♂1 ♀1	16.1 \pm 2.0	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
6	Abashiri	04 July 1982	♂0 ♀2	22.3 \pm 2.3	1.0 \pm 0.0	2.5 \pm 0.7	1.0 \pm 0.0
7	Utoro	18 Aug 1999	♂3 ♀1	19.2 \pm 1.5	1.3 \pm 0.5	2.5 \pm 1.0	2.0 \pm 0.0
8	Tsubetsu	25 Apr 1987	♂2 ♀0	23.1 \pm 6.2	1.0 \pm 0.0	3.0 \pm 0.0	2.0 \pm 0.0
9	Maruseppu	10 Aug 1998	♂2 ♀1	21.0 \pm 4.1	1.7 \pm 0.6	3.0 \pm 0.0	1.0 \pm 0.0
10	Akan	04 Aug 1933	♂1 ♀2	26.8 \pm 10.8	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
11	Shikaoi	14 May 1987	♂6 ♀1	26.9 \pm 8.4	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
12	Memuro	04 Aug 1986	♂0 ♀1	24.5 \pm 0.0	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
13	Ikeda	25 Sep 2000	♂0 ♀1	13.2 \pm 0.0	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
14	Otofuke	25 Sep 2000	♂1 ♀0	1.97 \pm 0.0	1.0 \pm 0.0	3.0 \pm 0.0	—
15	Obihiro	08 May 1986	♂1 ♀0	19.2 \pm 0.0	1.0 \pm 0.0	3.0 \pm 0.0	—
16	Shintoku	09 Aug 1998	♂0 ♀1	15.4 \pm 0.0	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
17	Erimo	19 Sep 2000	♂2 ♀1	18.8 \pm 0.5	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
18	Monbetsu	20 July 1990	♂4 ♀0	18.5 \pm 2.3	1.0 \pm 0.0	2.5 \pm 0.6	—
19	Kamikawa	20 Sep 2000	♂1 ♀1	21.4 \pm 4.9	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
20	Biei	07 Aug 1998	♂1 ♀1	25.3 \pm 3.3	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
21	Akabira	08 Aug 1999	♂1 ♀0	19.6 \pm 0.0	1.0 \pm 0.0	3.0 \pm 0.0	—
22	Furano	08 Aug 1999	♂2 ♀2	18.5 \pm 3.0	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
23	Iwamisawa	27 May 1959	♂2 ♀3	18.7 \pm 1.0	1.0 \pm 0.0	2.8 \pm 0.5	1.0 \pm 0.0
24	Takikawa	11 Aug 1992	♂1 ♀1	20.2 \pm 2.1	1.0 \pm 0.0	2.5 \pm 0.9	1.0 \pm 0.0
25	Ofuyu	23 Aug 1992	♂0 ♀1	20.0 \pm 0.0	2.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
26	Teuri	29 July 2002	♂5 ♀5	21.6 \pm 2.0	1.2 \pm 0.4	3.0 \pm 0.0	1.2 \pm 0.5
27	Yagishiri	29 July 2002	♂5 ♀5	20.4 \pm 1.6	1.5 \pm 0.5	3.0 \pm 0.0	1.0 \pm 0.0
28	Hamamasu	17 June 2000	♂5 ♀3	20.7 \pm 3.0	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
29	Sapporo	03 Nov 1990	♂4 ♀5	23.5 \pm 2.6	1.3 \pm 0.4	3.0 \pm 0.0	1.2 \pm 0.5
30	Otaru	03 June 1999	♂5 ♀6	20.9 \pm 2.7	1.0 \pm 0.0	3.0 \pm 0.0	1.1 \pm 0.4
31	Yoichi	28 Aug 2001	♂5 ♀5	18.8 \pm 1.3	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
32	Kucchan	07 Oct 2000	♂5 ♀5	21.3 \pm 2.8	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
33	Niseko	08 Oct 2000	♂5 ♀5	21.6 \pm 2.7	1.1 \pm 0.4	3.0 \pm 0.0	1.0 \pm 0.0
34	Kyowa	10 Oct 1998	♂4 ♀6	21.8 \pm 2.7	1.1 \pm 0.4	3.0 \pm 0.0	1.3 \pm 0.5
35	Rankoshi	21 July 2001	♂5 ♀5	19.0 \pm 2.7	1.6 \pm 0.5	3.0 \pm 0.0	1.0 \pm 0.0
36	Iwanai	01 July 2001	♂6 ♀4	19.2 \pm 1.8	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
37	Suttso	13 Sep 2001	♂5 ♀5	20.5 \pm 4.2	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
38	Kyogoku	28 Sep 2001	♂4 ♀6	22.3 \pm 1.9	1.4 \pm 0.5	3.0 \pm 0.0	1.0 \pm 0.0
39	Oshamanbe	19 Sep 2001	♂3 ♀5	19.7 \pm 2.2	1.4 \pm 0.5	3.0 \pm 0.0	1.2 \pm 0.4
40	Chitose	02 Aug 1999	♂2 ♀5	21.0 \pm 2.5	1.5 \pm 0.5	3.0 \pm 0.0	1.0 \pm 0.0
41	Eniwa	04 Nov 2001	♂2 ♀2	20.3 \pm 2.5	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
42	Soubetsu	02 Aug 1998	♂1 ♀0	20.7 \pm 0.0	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
43	Shiraoi	12 Aug 1990	♂0 ♀3	18.8 \pm 1.7	1.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
44	Sahara	01 Aug 1998	♂2 ♀1	21.5 \pm 2.0	2.3 \pm 0.6	3.0 \pm 0.0	2.0 \pm 0.0
45	Assabu	23 June 1997	♂4 ♀3	20.3 \pm 2.5	1.4 \pm 0.5	3.0 \pm 0.0	2.7 \pm 0.6
46	Kaminokuni	22 June 1997	♂1 ♀1	22.4 \pm 1.5	2.0 \pm 0.0	3.0 \pm 0.0	1.0 \pm 0.0
47	Shikabe	23 Aug 1998	♂1 ♀4	22.2 \pm 2.1	2.6 \pm 0.5	2.4 \pm 0.5	1.5 \pm 0.6
48	Kikonai	22 June 1997	♂2 ♀7	20.4 \pm 1.7	2.7 \pm 0.5	3.0 \pm 0.0	2.6 \pm 0.6
49	Toi	20 Aug 1992	♂2 ♀7	19.9 \pm 1.0	1.0 \pm 0.0	3.0 \pm 0.0	1.4 \pm 0.5
50	Todohokke	23 June 1997	♂5 ♀7	20.7 \pm 2.5	1.1 \pm 0.3	3.0 \pm 0.0	2.1 \pm 0.4
51	Fukushima	22 June 1997	♂3 ♀7	21.7 \pm 2.1	2.4 \pm 0.8	3.0 \pm 0.0	2.1 \pm 0.4
52	Matsumae	22 June 1997	♂7 ♀5	23.4 \pm 3.2	2.6 \pm 0.8	2.6 \pm 0.6	1.6 \pm 0.5
53	Imabetsu	05 Aug 1998	♂1 ♀4	22.0 \pm 1.4	2.2 \pm 0.8	2.8 \pm 0.4	2.0 \pm 0.0
54	Shiura	30 Aug 1997	♂2 ♀0	20.9 \pm 2.3	2.0 \pm 1.4	3.0 \pm 0.0	—

Appendix I.—Continued.

	Sampling site (No. ref. to Fig. 3)	Date	Specimens	POCL \pm SD	Rostrum	Telson	Sternal plates
55	Nakasato	21 Nov 1999	♂1 ♀1	22.5 \pm 2.5	2.5 \pm 0.7	1.5 \pm 0.7	3.0 \pm 0.0
56	Kanagi	07 Oct 2000	♂0 ♀2	20.3 \pm 0.4	3.0 \pm 0.0	2.0 \pm 1.4	2.5 \pm 0.7
57	Goshogawara	19 Sep 1998	♂7 ♀4	19.2 \pm 2.4	2.3 \pm 0.5	2.0 \pm 0.9	2.5 \pm 0.6
58	Kizukuri	22 Aug 1999	♂8 ♀2	23.7 \pm 2.2	2.7 \pm 0.5	2.7 \pm 0.7	2.0 \pm 0.0
59	Iwaki	26 July 1998	♂6 ♀0	21.3 \pm 2.6	2.7 \pm 0.6	1.5 \pm 0.8	—
60	Hirosaki	30 Sep 1997	♂2 ♀2	19.8 \pm 2.2	3.0 \pm 0.0	2.0 \pm 1.0	3.0 \pm 0.0
61	Ikarigaseki	04 Oct 1931	♂2 ♀5	17.6 \pm 2.2	2.7 \pm 2.2	2.6 \pm 0.5	3.0 \pm 0.0
62	Ajigasawa	12 Aug 1998	♂2 ♀2	20.1 \pm 2.3	2.8 \pm 0.5	1.5 \pm 1.0	3.0 \pm 0.0
63	Namioka	22 June 2000	♂4 ♀1	21.3 \pm 1.9	2.8 \pm 0.4	2.2 \pm 0.8	3.0 \pm 0.0
64	Aomori	03 May 1998	♂7 ♀3	20.7 \pm 3.4	1.9 \pm 0.6	2.8 \pm 0.4	2.7 \pm 0.6
65	Hiranai	10 Oct 2000	♂2 ♀3	19.4 \pm 2.1	2.4 \pm 0.5	3.0 \pm 0.0	3.0 \pm 0.0
66	Tenmabayashi	14 July 1994	♂0 ♀2	18.6 \pm 1.7	3.0 \pm 0.0	3.0 \pm 0.0	3.0 \pm 0.0
67	Shichinohe	22 June 1999	♂2 ♀1	15.2 \pm 1.6	2.7 \pm 0.6	3.0 \pm 0.0	3.0 \pm 0.0
68	Yokohama	23 May 1999	♂1 ♀0	19.4 \pm 0.0	3.0 \pm 0.0	3.0 \pm 0.0	—
69	Higashidouri	27 Aug 1999	♂2 ♀2	19.0 \pm 1.4	2.5 \pm 0.6	3.0 \pm 0.0	3.0 \pm 0.0
70	Mutsu	27 Aug 1999	♂1 ♀1	23.0 \pm 0.7	2.5 \pm 0.7	3.0 \pm 0.0	3.0 \pm 0.0
71	Ouhata	22 June 1999	♂1 ♀5	18.3 \pm 0.8	1.2 \pm 0.4	3.0 \pm 0.0	2.6 \pm 0.5
72	Kawauchi	05 June 1998	♂0 ♀2	21.4 \pm 1.7	2.0 \pm 1.4	3.0 \pm 0.0	2.5 \pm 0.7
73	Wakinosawa	17 May 1998	♂3 ♀0	18.3 \pm 0.9	3.0 \pm 0.0	3.0 \pm 0.0	—
74	Tashiro	21 June 1991	♂0 ♀2	7.5 \pm 0.3	3.0 \pm 0.0	1.5 \pm 0.0	3.0 \pm 0.0
75	Ohdate	24 Aug 2002	♂3 ♀7	21.9 \pm 3.9	3.0 \pm 0.0	3.0 \pm 0.0	3.0 \pm 0.0
76	Kazuno	23 June 1990	♂7 ♀2	18.9 \pm 1.1	1.3 \pm 0.5	3.0 \pm 0.0	1.0 \pm 0.0
77	Ninohe	22 June 1999	♂1 ♀2	18.3 \pm 1.2	2.7 \pm 0.6	2.7 \pm 0.6	3.0 \pm 0.0

—: not measured.

Two new species of freshwater crabs of the genus *Chaceus* Pretzmann, 1965 from the Serranía de Perijá of Colombia (Crustacea: Decapoda: Pseudothelphusidae)

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Abstract.—Two new species of the genus *Chaceus* Pretzmann, 1965, *C. curumanensis* and *C. ibiricensis*, are described and illustrated. The description of these two new species brings to nine the total number of species known in this genus, distributed in the Sierra de Santa Marta in Colombia, and Serranía de Perijá of Colombia and Venezuela. A key for the identification of the species based on the morphology of the first male gonopod is presented.

The genus *Chaceus* Pretzmann, 1965 comprises a group of freshwater crabs distributed in the Sierra de Santa Marta in Colombia and the Serranía de Perijá in Colombia and Venezuela. The systematics, cladistic and biogeography of the genus have been reviewed by Rodríguez (1982, 1992), Campos & Rodríguez (1984), Rodríguez & Campos (1989), Rodríguez & Bosque (1990), Rodríguez & Vilorio (1992) and Rodríguez & Herrera (1994). With the discovery of two new species, described herein, from the western slope of the Serranía de Perijá of Colombia, the genus now contains nine species.

Species of *Chaceus* are distinguished primarily by characteristics of the efferent branchial channel, the third maxilliped and the first male gonopod. The efferent branchial channel is partially closed by the spine of the jugal angle, and by the produced lateral lobe of the epistome. The exognath of the third maxilliped is 0.60 to 0.80 times as long as the ischium. The first male gonopod usually has the lateral process well developed, its shape varying according to the species, and is either subtriangular, elongated, or rounded. The apex is formed by mesial and caudal processes. A key for the

species of the genus is presented, based exclusively on the morphology of the first male gonopod. The terminology used for the different processes of the gonopod is that established by Smalley (1964), and Rodríguez (1982).

The shape of the efferent branchial channel, the length of the exognath of the third maxilliped, and the structure of the first male gonopod of the genus *Chaceus* suggest a close relationship with the genus *Strengeriana* Pretzmann, 1971. The first male gonopods in all species of *Chaceus* have the same basic elements as species of *Strengeriana*. Rodríguez (1982) has theorized on the possible derivation of the genus *Hypolobocera* Ortmann, 1897, from an ancestral *Chaceus* based on the homology of the finger-like mesial process in the latter, and the triangular caudal process with the two papillae found near the spermatocanal in the former. The morphology of the first gonopod in *C. davidi* Campos & Rodríguez, 1984, for example, supports this theory since the mesial and caudal processes are surrounded by a ridge that somewhat resembles the shape of the apex in species of *Hypolobocera*.

The material is deposited in Museo de

Historia Natural, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN-MHN). The abbreviations cb and cl, reported as $cl \times cb$, indicate carapace breadth and carapace length, respectively. Color nomenclature follows Smithe (1975).

Family Pseudothelphusidae Rathbun, 1893

Tribe Strengerianini Rodríguez, 1982

Genus *Chaceus* Pretzmann, 1965

Chaceus curumanensis, new species

Fig. 1

Holotype.—Quebrada San Sebastián, Municipio Curumaní, foothill of the Serranía de Perijá, Cesar Department, Colombia, 100 m alt., 8 Dec 1978, leg. M. Türkay, male, 14.7 × 24.5 mm, ICN-MHN-CR 1993.

Paratype.—Same locality data as holotype: 1 male, 13.2 × 23.4 mm, ICN-MHN-CR 1266.

Type locality.—Quebrada San Sebastián, Municipio Curumaní, foothill of the Serranía de Perijá, Cesar Department, Colombia, 100 m alt.

Diagnosis.—Third maxilliped with exognath 0.67 times length of ischium. First gonopod with lateral process elongated, with distal portion slightly rounded in caudal view, subtriangular in distal view; apex with needle-shaped mesial process, and triangular caudal process; disto-mesial margin curving below mesial and caudal processes.

Description of holotype.—Carapace (Fig. 1F) with cervical groove straight, narrow and shallow distally, wide and deep proximally, ending some distance from lateral margin. Anterolateral margin lacking depression behind external orbital angle, but with slight depression near middle followed by another near level of cervical groove. Lateral margin with series of tubercles. Postfrontal lobes small, oval, delimited anteriorly by 2 depressions. Median groove lacking. Front without distinct upper border, frontal area regularly sloping downward, slightly bilobed in dorsal view, lower mar-

gin sinuous in frontal view. Dorsal surface of carapace smooth, covered by small papillae, regions not well demarcated. Third maxilliped with slight depression on distal half of external margin of merus, exognath 0.67 times length of ischium (Fig. 1H). Orifice of efferent branchial channel partially closed by spine of jugal angle, and by produced lateral lobe of epistome (Fig. 1G). First pereopods heterochelous; chelae with palms swollen, and fingers slightly gaping when closed (Fig. 1I). Walking legs (pereopods 2–5) slender, but not unusually elongated (total length 1.14 times breath of carapace).

First male gonopod with lateral process elongated, with distal portion slightly rounded in caudal view (Fig. 1A), subtriangular in distal view (Fig. 1E); apex with needle-shaped mesial process, directed cephalically, and triangular caudal process, directed transversely to mesial process in caudal and cephalic views, both processes surrounded by lateral process in distal view; disto-mesial margin curving below mesial and caudal processes (Fig. 1C–E); lateral side of gonopod expanded with irregular rows of short setae, caudal surface with long setae proximally (Fig. 1A, B, D).

Color.—The holotype, preserved in alcohol, is light brown (near 37, Antique Brown) with dark specks on the dorsal side of the carapace. The dorsal and ventral surfaces of the chelae and walking legs are brown (near 139, True Cinnamon). The ventral surface of the carapace is brown (near 239, Ground Cinnamon).

Etymology.—The specific name refers to the type locality, the Municipio Curumaní.

Remarks.—Comparison of this new species with descriptions and specimens of other species of the genus revealed that this new species is most similar to *Chaceus pearsei* (Rathbun, 1915). The two can be distinguished by differences in the gonopods. The male first gonopod of *C. pearsei* has been described and illustrated by Rodríguez (1982:37, fig. 12). The lateral process in this new species is elongated, with

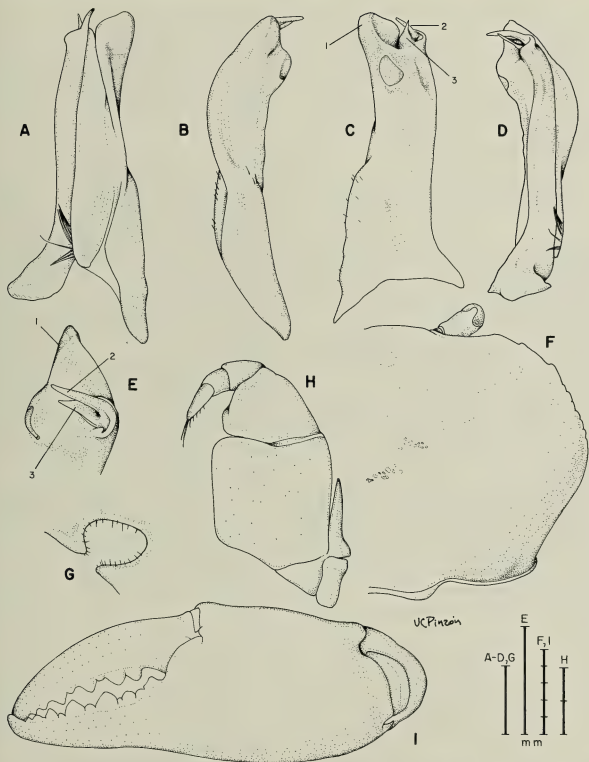


Fig. 1. *Chaceus curumanensis*, new species, male holotype, ICN-MHN-CR 1993: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, apex, distal view; F, right side of carapace with eye, dorsal view; G, left orifice of efferent branchial channel; H, left third maxilliped, external view; I, left cheliped, external view. 1, lateral process; 2, mesial process; 3, caudal process.

the distal portion slightly rounded in caudal view, whereas it is subtriangular in *C. pearsei*. The mesial process in *C. pearsei* is finger-like, blunt, whereas it is needle-shaped in *C. curumanensis*. The caudal process in this new species is slightly parallel to the mesial process in distal view, whereas it is recurved at its base in *C. pearsei*.

Chaceus ibiricensis, new species

Fig. 2

Holotype.—Los Laureles Farm, Vereda Alto del Tucuy, Corregimiento La Victoria de San Isidro, Municipio La Jagua de Ibirico, Serranía de Perijá, Cesar Department, Colombia, 1100 m alt., 9°34'35.8"N, 73°6'26.0"W, 7 Mar 1996, leg. M. R. Campos, male, 13.0 × 21.3 mm, ICN-MHN-CR 1992.

Paratypes.—Same locality data as holotype: 19 males, size range 8.6 × 13.7 mm to 13.7 × 22.7 mm, 16 females, size range 8.2 × 12.8 mm to 12.4 × 20.1 mm, ICN-MHN-CR 1549.

Additional non-paratypic material.—Between Veredas Alto de las Flores, and Nuevo Mundo, Corregimiento La Victoria de San Isidro, Municipio La Jagua de Ibirico, Serranía de Perijá, Cesar Department, Colombia, 1350–1400 m alt., 7, 8 Mar 1996, leg. M. R. Campos, 23 males, size range 7.3 × 11.4 mm to 13.0 × 21.4 mm, 15 females, size range 8.4 × 13.1 mm, to 14.4 × 24.8 mm, ICN-MHN-CR 1550, 1552.—Tucuy River, Vereda Alto de las Flores, Corregimiento La Victoria de San Isidro, Municipio La Jagua de Ibirico, Serranía de Perijá, Cesar Department, Colombia, 870 m alt., 11 Mar 1996, leg. M. R. Campos, 6 males, size range 9.9 × 15.9 mm to 10.9 × 17.6 mm, 3 females, size range 10.8 × 17.2 mm to 11.9 × 20.4 mm, 2 juveniles, ICN-MHN-CR 1559.—La Sorpresa Farm, Vereda Alto de las Flores, Corregimiento La Victoria de San Isidro, Municipio La Jagua de Ibirico, Serranía de Perijá, Cesar Department, Colombia, 1280 m alt., 12 Mar

1996, leg. J. V. Rueda, 1 male, 12.4 × 21.1 mm, ICN-MHN-CR 1560.

Type locality.—Los Laureles Farm, Vereda Alto del Tucuy, Corregimiento La Victoria de San Isidro, Municipio La Jagua de Ibirico, Serranía de Perijá, Cesar Department, Colombia, 1100 m alt., 9°34'35.8"N, 73°6'26.0"W.

Diagnosis.—Third maxilliped with exognath 0.72 times length of ischium. First male gonopod with lateral process hood-like; mesial process prominent, subcylindrical, semicircular caudally with median constriction and subdistal subtriangular papilla cephalically; caudal process subtriangular; disto-mesial margin forming semicircular projection in cephalo-lateral direction.

Description of holotype.—Carapace (Fig. 2F) with cervical groove straight, narrow, shallow, ending some distance from lateral margin. Anterolateral margin with shallow depression behind external orbital angle followed by approximately 5 papillae. Lateral margin with series of approximately 10 tubercles. Postfrontal lobes small, oval, delimited anteriorly by 2 depressions. Median groove shallow, and narrow. Front lacking distinct upper border, frontal area regularly sloping downward, bilobed in dorsal view, lower margin sinuous in frontal view. Dorsal surface of carapace smooth, covered by small papillae, regions not well demarcated. Third maxilliped with external margin of merus straight, exognath 0.72 times length of ischium (Fig. 2H). Orifice of efferent branchial channel partially closed by spine of jugal angle, and by produced lateral lobe of epistome (Fig. 2G). First pereopods heterochelous; palm of larger chela strongly swollen, fingers gaping when closed (Fig. 2I); palm of smaller chela moderately swollen, fingers not gaping when closed. Walking legs (pereopods 2–5) slender and elongated (total length 1.25 times the breadth of carapace).

First male gonopod with lateral process hood-like, lateral and cephalic outer surface covered with irregular papillae and spinules (Fig. 2A–C); apex with mesial and caudal

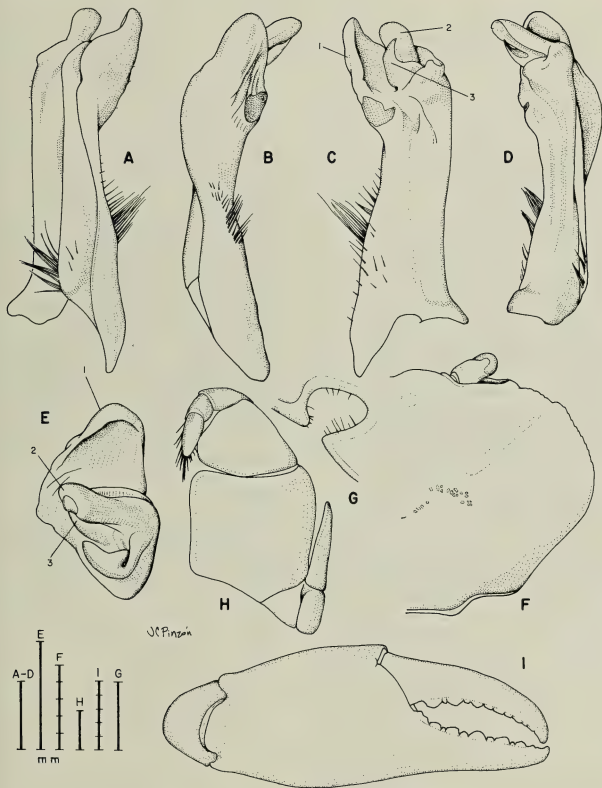


Fig. 2. *Chaceus ibiricensis*, new species, male holotype, ICN-MHN-CR 1992: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, apex, distal view; F, right side of carapace with eye, dorsal view; G, left orifice of efferent branchial channel; H, left third maxilliped, external view; I, right cheliped, external view. 1, lateral process; 2, mesial process; 3, caudal process.

processes; mesial process prominent, subcylindrical, semicircular caudally (Fig. 2A, B); with median constriction, and subdistal subtriangular papilla cephalically (Fig. 2C–E); caudal process subtriangular, both processes partially surrounded by lateral process in distal view; disto-mesial margin forming semicircular projection into cephalo-lateral direction (Fig. 2E); lateral expanded side of gonopod with rows of long, plumose setae, mesial side with row of spinules; caudal surface with conspicuous long setae proximally (Fig. 2A–D).

Color.—The holotype, preserved in alcohol, is brown (near 240, Kingfisher Rufous) on the dorsal side of the carapace. The dorsal and ventral surfaces of chelae and walking legs are brown (near 223B, Verona Brown). The ventral surface of the carapace is light brown (near 223C, Sayal Brown).

Habitat.—The vegetation of the collection areas is primary forest. The specimens were collected in shaded, moist banks of springs and streams, in soft mud under rocks.

Etymology.—The specific name refers to the type locality, the Municipio La Jagua de Ibirico.

Remarks.—Comparison of this new species with descriptions and specimens of other species of the genus revealed that it is most similar to *Chaceus turikensis* Rodríguez & Herrera, 1994. The two can be distinguished by differences in the size of the eyes, and in the gonopod. The male first gonopod of *C. turikensis* has been described and illustrated by Rodríguez & Herrera (1994:123, fig. 2). In *C. turikensis* the eyes do not fill the orbital cavity, whereas in this new species they do fill the orbital cavity. In *C. ibiricensis* the lateral process of the gonopod is hood-like with the distal portion directed distally in caudal view (Fig. 2A–E), whereas the lateral lobe is foliose and the distal portion is directed transversely to the main axis of the appendage in *C. turikensis*. The mesial process is ellipsoidal in *C. turikensis*, whereas it is subcylindrical with a median constriction and subdistal

subtriangular papilla cephalically in *C. ibiricensis*.

Key to Species of *Chaceus*

1. Lateral process of gonopod well developed 2
 - Lateral process of gonopod reduced *C. nasutus* Rodríguez, 1980
2. Lateral process of gonopod subtriangular or elongated 3
 - Lateral process of gonopod rounded ... 8
3. Lateral process of gonopod with semicircular notch on lateral surface
 - .. *C. cesarensis* Rodríguez & Vilorio, 1992
 - Lateral process of gonopod without semicircular notch on lateral surface .. 4
4. Mesial process of gonopod about same length as length of caudal process
 - *C. davidi* Campos & Rodríguez, 1984
 - Mesial process of gonopod longer than caudal process 5
5. Mesial process of gonopod with median constriction and subapical subtriangular papilla cephalically
 - *C. ibiricensis*, new species
 - Mesial process of gonopod without median constriction and subapical papilla cephalically 6
6. Mesial process of gonopod ellipsoidal ...
 - .. *C. turikensis* Rodríguez & Herrera, 1994
 - Mesial process of gonopod not ellipsoidal 7
7. Mesial process of gonopod finger-like, blunt *C. pearsei* (Rathbun, 1915)
 - Mesial process of gonopod needle-shaped *C. curumanensis*, new species
8. Mesial process of gonopod with rounded, elongated papilla basally
 - *C. caecus* Rodríguez & Bosque, 1990
 - Mesial process of gonopod lacking rounded, elongated papilla basally
 - *C. motiloni* Rodríguez, 1980

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Reevaluation of the hermit crab genus *Parapagurodes* McLaughlin & Haig, 1973 (Decapoda: Anomura: Paguroidea: Paguridae) and a new genus for *Parapagurodes doederleini* (Doflein, 1902)

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Abstract.—The question of polyphyly in the hermit crab genus, *Parapagurodes* McLaughlin & Haig, 1973, has been investigated by comparisons of a series of morphological characters among the eight species presently assigned to the genus. The results of the analysis have shown that the only mutually shared characters are an acutely developed rostrum and the presence, in males, of a short or very short right sexual tube. Consequently, the composition of *Parapagurodes* is herein restricted to the two species originally assigned, viz. *P. makarovi* McLaughlin & Haig, 1973, and *P. laurentae* McLaughlin & Haig, 1973. *Parapagurodes hartae* McLaughlin & Jensen, 1996, is transferred to the genus *Pagurus*, and four species subsequently transferred from *Pagurus* to *Parapagurodes*, viz. *P. gracilipes* (Stimpson, 1858), *P. nipponensis* (Yokoya, 1933), *P. constans* (Stimpson, 1858), and *P. imaii* (Yokoya, 1939) are returned to *Pagurus*. A new genus, *Dofleinia*, is proposed for the species, *Parapagurodes doederleini* (Doflein).

When first proposed, the genus *Parapagurodes* McLaughlin & Haig, 1973, was characterized, in part, as having 11 pairs of biserial gills; a moderately well developed, but not recurved external lobe of the maxillulary endopod; fifth pereopods with coxae symmetrical; males with a short right sexual tube, and biramous left pleopods absent or weakly developed on pleomeres (cf. Schram & Koenmann 2003) 3–5; females lacking paired first pleopods, with biramous left pleopods 2–4 weakly to moderately well developed, left fifth pleopod weakly developed or absent; and a telson with terminal margins straight, slightly concave or slightly oblique. Additionally, the authors noted that while a right sexual tube was always present in mature males, its length and orientation were variable, and in one specimen both right and left tubes were present. Variations also were observed in the

number and development of male and female pleopods in both *P. makarovi* McLaughlin & Haig, 1973, the type species of the genus, and the second described species, *P. laurentae* McLaughlin & Haig, 1973. In recent years, one new species, *P. hartae* McLaughlin & Jensen, 1996, has been described in the genus, and five Japanese species have been transferred to it viz.: *Pagurus gracilipes* (Stimpson, 1858), *P. nipponensis* (Yokoya, 1933), *P. constans* (Stimpson, 1858), and *P. imaii* (Yokoya, 1939) by Komai (1998, 1999) and *Catapagurus doederleini* Doflein, 1902 by Asakura (2001).

At the time of the establishment of *Parapagurodes* McLaughlin & Haig, 1973, male sexual tube development had been reported in less than two dozen genera. McLaughlin & Haig (1973) could relate *Parapagurodes* to only two of those genera,

Pagurodes Henderson, 1888 and *Acanthopagurus* de Saint Laurent, 1969, but cited several characters by which the three genera could be separated. In the subsequent 30 years the number of genera with documented sexual tube development has more than doubled (cf. McLaughlin 2003). Nonetheless, *Parapagurodes* still can be allied only to *Pagurodes* and *Acanthopagurus* and more remotely to *Catapagurus* A. Milne Edwards, 1880. However, recently the monophyly of *Parapagurodes* itself has come under question (Lemaitre & McLaughlin 2003b).

In their introductory remarks regarding *Parapagurodes hartae*, McLaughlin & Jensen (1996: 841) made the unfortunate statement that "... males have a small sexual tube on the coxa of the right fifth pereopod. This species, therefore, cannot be attributed to *Pagurus*, but must be assigned to *Parapagurodes*..." The comment was prompted by the fact that prior to their description of *P. hartae*, this taxon had been reported from California and Washington, USA, and British Columbia, Canada, as *Pagurus* sp. (McLaughlin & Haig 1973, Hart 1982, Jensen 1995). Regrettably, McLaughlin & Jensen's (1996) remark has been interpreted by some carcinologists to mean that species with papillae and/or very short sexual tubes are automatically excluded from the genus *Pagurus* (e.g., Komai 1998, 1999). According to the views of McLaughlin & Lemaitre (2001) and Lemaitre & McLaughlin (2003a, 2003b), the presence or absence of very short male sexual tubes and/or papillae should not be seen as the single cause to transfer species from genera to which they are otherwise morphologically attributable, or assign species to genera that they are not otherwise morphologically allied.

McLaughlin & Jensen (1996) justified their generic assignment on the basis of morphological and larval similarities among the three species then assigned to *Parapagurodes*. However, they also pointed out, as McLaughlin & Haig (1973) had for *P. laurentae*, that *P. hartae* had superficial

resemblances to a few northeastern Pacific species of *Pagurus*.

Upon the observation of very short sexual tubes in *Pagurus gracilipes* and *P. nipponensis*, Komai (1998) provisionally transferred these two species to *Parapagurodes*, while noting their close similarities to species of McLaughlin's (1974) *bernhardus* group of *Pagurus*. Komai (1998) also pointed out that while *Pagurus gracilipes* and *P. nipponensis* shared the presence of a small right male sexual tube, both species differed substantially from *Parapagurodes makarovi*, *P. laurentae*, and *P. hartae*.

In the subsequent, continuing study of Japanese species of *Pagurus*, Komai (1999) transferred *Pagurus constans* and *P. imaii* to *Parapagurodes* because he found very short male sexual tubes on both fifth coxae in the former species, and a single right tube in the latter. He also provided a minor emendation to the generic diagnosis by calling attention to the slight median indentation, cleft or concavity sometimes seen in the gill lamellae, and to the occurrence of the left sexual tube, although he acknowledged that McLaughlin & Haig (1973) similarly had reported the rare occurrence of a left tube in *P. makarovi*. Unfortunately, Komai's (1999) emendation, like McLaughlin & Jensen's (1996) brief generic diagnosis, failed to acknowledge the absence or reduction in number of male pleopods and the usual absence of the fifth left female pleopod in the type species.

In his review of the genus *Catapagurus* A. Milne-Edwards, 1880, Asakura (2001) redescribed *Catapagurus doederleini* and found it to be markedly divergent from all other species that had been assigned to *Catapagurus*. Asakura transferred Doflein's (1902) taxon to *Parapagurodes* stating that it agreed with all the diagnostic characters proposed by McLaughlin & Haig (1973) for their genus; however, it was primarily the presence of a very short right sexual tube that prompted his action. He quite correctly acknowledged the dimorphic second pereopods of *P. doederleini*, as well as the lack

of corneous spines on the ventral margins of the second right and both third pereopods.

As previously indicated, Lemaitre & McLaughlin (2003b) expressed the opinion that *Parapagurodes*, as presently constituted, represented a polyphyletic taxon. To evaluate the merits of their conclusion, we have critically reviewed the descriptions of each of the assigned taxa. We have supplemented these reviews by reexamining specimens of *Parapagurodes laurentae* and *P. hartae* in the first author's personal collections (PMcL). Additionally we have examined representatives of *P. constans*, *P. doederleini*, *P. gracilipes*, *P. imaii*, and *P. nipponensis* from the collections of the Natural History Museum and Institute, Chiba (CBM-ZC), the Hilgendorf collection from the Museum für Naturkunde, Berlin, Germany (ZMB), and specimens donated to one of the authors by Dr. M. Imafuku, Kyoto University. From our reviews and examinations, we present the comparative diagnoses of the eight species we have used to determine the validity of the current generic assignments.

Animal size is indicated by shield length (sl) as measured from the tip of the rostrum to the midpoint of the posterior margin of the shield. Reported sexual tube length corresponds to the criterion of McLaughlin (2003): very short (<1 coxal length), short (1–2 coxal lengths), moderate (>2–5 coxal lengths). The reference by McLaughlin & Haig (1973) to the fourth pereopod being subchelate or not subchelate is interpreted here according to McLaughlin (1997) who recognized three conditions in the propodal-dactyl articulation of this appendage. McLaughlin & Haig's (1973) "subchelate" is viewed by McLaughlin (1997) as being semichelate, whereas McLaughlin & Haig's (1973) "not subchelate" is now considered to actually be subchelate. The abbreviation ovig. indicates ovigerous female. Previously published illustrations used in this manuscript are of specimens in the collections of the Los Angeles Country Natural His-

tory Museum (LACM) [transferred to that Museum from the Allan Hancock Foundation (AHF)], Los Angeles, California; the Royal British Columbia Provincial Museum (RBCPM), Victoria, British Columbia; and Zoologische Staatssammlung München (ZSSM), Munich.

Review and Reexamination

Parapagurodes makarovi McLaughlin & Haig, 1973
Figs. 1A, 2A, 3A, 4A, B, 5A

Description by McLaughlin & Haig (1973:119–120, figs. 4a, 5–8). No supplemental material available.

Diagnosis.—Gill lamellae essentially biserial but with or without very weak distal indentation or concavity. Rostrum acutely triangular. Maxillule with somewhat produced endopodal external lobe, not recurved. Right cheliped elongate, more so in large individuals; dorsal surface of palm distinctly convex; dorsal surface of carpus with row of spines mesiad of midline. Left cheliped elongate dorsal surface of palm convex, elevated in midline proximally. Ambulatory legs similar, somewhat laterally compressed; dactyls as long or longer than propodi, slender, in dorsal view straight, each with row of corneous spines on ventral margin; carpi each with dorso-distal spine. Fourth pereopods usually subchelate, occasionally weakly semichelate; preungual process very small; propodal rasp with 1–3 irregular rows of corneous scales. Sternite of third pereopods (sixth thoracomere) semi- or subsemicircular. Sternite of fifth pereopods (eighth thoracomere) separated into two broad lobes by weak median depression; coxae of fifth pereopods symmetrical. Males with short sexual tube developed from coxa of right fifth pereopod; left gonopore sometimes with papilla, occasionally with short tube. No paired pleopods in either sex. Males usually without, occasionally with weakly biramous left pleopods on pleomeres 3 and 4. Females with weakly developed, biramous left

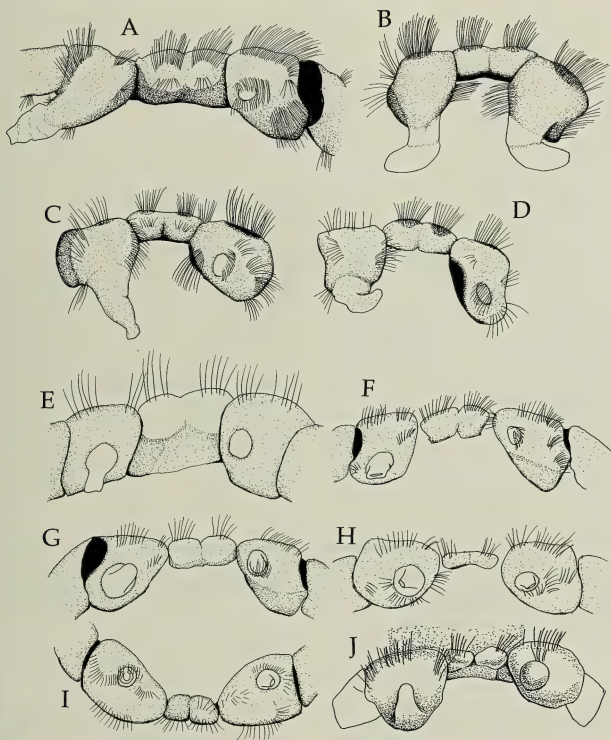


Fig. 1. Coxae and sternite of fifth pereopods. A, B, *Parapagurodes makarovi* McLaughlin & Haig, 1973, ♂ (sl = 3.5 mm), ♂ (sl = 3.6 mm), LACM; C, D, *P. laurentae* McLaughlin & Haig, 1973, ♂ (sl = 3.4 mm), ♂ (sl = 3.4 mm), LACM; E, *P. hartae* McLaughlin & Jensen, 1996, ♂ (sl = 3.2 mm), RBCPM 974-00368-22; F, *P. gracilipes* (Stimpson, 1858), ♂ (sl = 9.0 mm), CBM-ZC 2977; G, *P. nipponensis* (Yokoya, 1933), ♂ (sl = 7.3 mm), CBM-ZC 1162; H, *P. constans* (Stimpson, 1858), ♂ (sl = 8.7 mm), CBM-ZC 59; I, *P. imaii* (Yokoya, 1939), ♂ (sl = 2.5 mm), CBM-ZC 2699; J, *P. doederleini* (Doflein, 1902), ♂ (sl = 8.6 mm), ZSSM 274/1. A–D redrawn from McLaughlin & Haig (1973); E redrawn from McLaughlin & Jensen (1996); J from Asakura (2001).

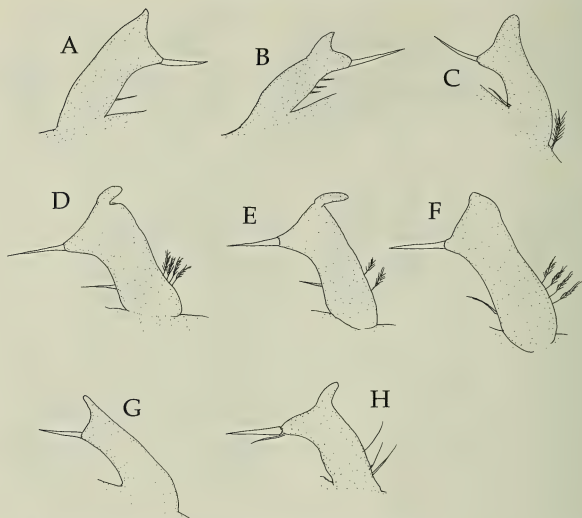


Fig. 2. Endopod of maxillule. A, *Parapagurodes makarovi* McLaughlin & Haig, 1973, ♂ (sl = 3.5 mm), LACM; B, *P. laurentae* McLaughlin & Haig, 1973, ♂ (sl = 3.4 mm), LACM; C, *P. hartae* McLaughlin & Jensen, 1996, ♂ (sl = 3.2 mm), RBCPM 974-00368-22; D, *P. gracilipes* (Stimpson, 1858), ♂ (sl = 9.0 mm), CBM-ZC 2977; E, *P. nipponensis* (Yokoya, 1933), ♂ (sl = 7.3 mm), CBM-ZC 1162; F, *P. constans* (Stimpson, 1858); ♂ (sl = 8.7 mm), CBM-ZC 59; G, *P. imaii* (Yokoya, 1939), ♂ (sl = 2.5 mm), CBM-ZC 2699; H, *P. doederleini* (Doflein, 1902), ♂ (sl = 8.6 mm), ZSSM 274/1. A, B redrawn from McLaughlin & Haig (1973); C redrawn from McLaughlin & Jensen (1996); H from Asakura (2001).

pleopods on pleomeres 2–4, pleopod 5 absent or rudimentary. Telson with posterior lobes separated by very small, shallow median cleft; terminal margins straight or somewhat concave, each with several to numerous spinules or small to very small spines.

Parapagurodes laurentae McLaughlin & Haig, 1973

Figs. 1B, 2B, 3B, 4C, D, 5B

Description by McLaughlin & Haig (1973:129–134, figs. 4b, 9–11).

Supplemental material examined.—U.S.A.: 3 ♂ (sl = 1.4–2.9 mm), 3 ♀ (sl = 1.7–2.9 mm), 2.5 mi SE Seal Rocks, Santa Catalina I, CA, 159–174 m, 25 Oct 1941, PMcL.

Diagnosis.—Gill lamellae essentially biserial but with or without very weak distal indentation or concavity. Rostrum acutely triangular. Maxillule with moderately well developed endopodal external lobe, not recurved. Right cheliped usually elongate, more so in large individuals; dorsal surface of palm convex; dorsal surface of

carpus with row of spines mesiad of midline. Left cheliped moderately long, dorsal surface of palm convex. Ambulatory legs similar, somewhat laterally compressed, dactyls as long or longer than propodi, slender, in dorsal view usually straight, with row of corneous spines on ventral margin; carpi each with dorsodistal spine. Fourth pereopods usually semichelate, occasionally subchelate; preungual process very small; propodal rasp with 1–3 irregular rows of corneous scales. Sternite of third pereopods (sixth thoracomere) subsemicircular. Sternite of fifth pereopods (eighth thoracomere) separated into two broad lobes by weak to moderate median depression; coxae of fifth pereopods symmetrical. Males with short or very short sexual tube developed from coxa of right fifth pereopod; left gonopore sometimes with papilla. No paired pleopods in either sex. Males usually with weakly biramous left pleopods on pleomeres 3 and 4, occasionally without unpaired pleopods. Females usually with moderately well developed, biramous pleopods on pleomere 2–4; pleopod 5 rudimentary, rarely absent. Telson with posterior lobes separated by very shallow median cleft; terminal margins concave or slightly oblique, each with row of very small spinules and 1–4 small spines at posterolateral angles.

Parapagurodes hartae McLaughlin & Jensen, 1996

Figs. 1C, 2C, 3C, 4E, 5C

Description by McLaughlin & Jensen (1996:844–847, figs. 1–4).

Supplemental material examined.—Canada: 1 ♂ (sl = 1.1 mm), 1 ♀ (sl = 1.5 mm), Taylor Inlet, Barkley Sound, British Columbia, 10 m, 10 Jun 1994, PMcL.

Diagnosis.—Gill lamellae essentially biserial but with or without very weak distal indentation or concavity. Rostrum acutely triangular. Maxillule with moderately well developed endopodal external lobe, not recurved. Right cheliped elongate in

large males; dorsal surface of palm convex; dorsal surface of carpus with row of spines mesiad of midline. Left cheliped with dactyl and fixed finger short and broad in small males and females, longer in large males; dorsal surface of palm convex. Ambulatory legs similar; dactyls slightly shorter to slightly longer than propodi, moderately slender, laterally compressed, in dorsal view straight, with row of corneous spines on ventral margin; carpi each with dorsodistal spine and row of low, sometimes spinulose protuberances on dorsal surface, rarely 1 dorsoproximal spines (second pereopods). Fourth pereopods usually semichelate, occasionally subchelate; preungual process very small; propodal rasp with 2–4 irregular rows of corneous scales. Sternite of third pereopods (sixth thoracomere) subsemicircular to subrectangular. Sternite of fifth pereopods (eighth thoracomere) separated into two broad lobes by weak to moderate median depression; coxae of fifth pereopods symmetrical. Males often with very short sexual tube developed from coxa of right fifth pereopod; left gonopore without papilla. No paired pleopods in either sex. Males with unequally biramous left pleopods on pleomeres 3–5. Females with moderately well developed, left biramous pleopods on pleomeres 2–4; pleopod 5 as in male. Telson with posterior lobes separated by shallow, U-shaped median cleft; terminal margins rounded or slightly oblique, each with row of very small spinules and 1 or 2 small spines at posterolateral angles.

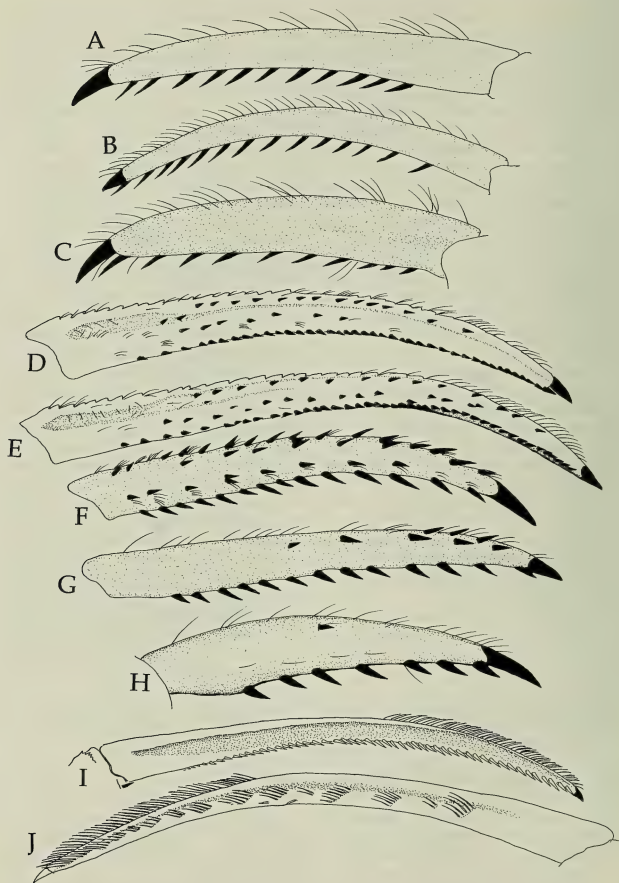
Parapagurodes gracilipes (Stimpson, 1858)

Figs. 1D, 2D, 3D, 4F, 5D

Redescription by Komai (1998:268–275, figs. 1A, 2–5, 7).

Supplemental material examined.—Japan: 2 ♂ (sl = 5.4, 9.0 mm), 1 ♀ (sl = 6.7 mm), off Choshi, Chiba, 10–20 m, 3 Sep 1996, CBM-ZC 2977.

Diagnosis.—Gill lamellae biserial. Rostrum acutely triangular. Maxillule with



somewhat produced endopodal external lobe, slightly to distinctly recurved. Right cheliped moderately (small specimens) to considerably elongate in large individuals; dorsal surface of palm weakly convex but with dorsomesial portion somewhat elevated; dorsal surface of carpus with row of spines mesiad of midline. Left cheliped with dorsal surface of palm somewhat flattened, dorsomesial and dorsolateral margins slightly elevated. Ambulatory legs similar; dactyls longer than propodi, strongly twisted; moderately broad, each with row of numerous corneous spines on ventral margin; carpi each with single or double row of multifid spines. Fourth pereopods semichelate; no preungual process; propodal rasp with several rows of corneous scales. Sternite of third pereopods (sixth thoracomere) subquadrate, weakly skewed, sulcate medially. Sternite of fifth pereopods (eighth thoracomere) separated into two subovate lobes by shallow median groove; coxae of fifth pereopods symmetrical. Males with very short sexual tube developed from coxa of right fifth pereopod; left gonopore without tube or papilla. No paired pleopods in either sex. Males with unequally biramous pleopods on pleomeres 3–5. Females with well developed, biramous pleopods on pleomeres 2–4; pleopod 5 with endopod noticeably reduced. Telson with posterior lobes separated by very small, or indistinct median cleft; terminal margins nearly horizontal, each with eight to ten small spines and two or three larger spines at posterolateral angles, lateral margins occasionally with spinules.

Parapagurodes nipponensis (Yokoya, 1933)

Figs. 1E, 2E, 3E, 4G, 5E

Redescribed by Komai (1998:275–279, figs 1B, 6, 7) only as similar to *P. gracilipes* with certain noted differences.

Supplemental material examined.—Japan: 4 ♂ (sl = 6.3–7.6 mm), 1 ♀ (sl = 5.3 mm), Kumano Nada, 50 m, Sep 1981, PML; 2 ♂ (sl = 8.0, 9.2 mm), off Kashima, Irakaki, 65 m, 24 Apr 1991, CBM-ZC 50; 1 ♂ (sl = 7.3 mm), off Kii Minabe, Kii Peninsula, 80–100 M, 24 Mar 1995, CBM-ZC 1162.

Diagnosis.—Gill lamellae biserial. Rostrum acutely triangular. Maxillule with somewhat produced external lobe, slightly to distinctly recurved. Right cheliped moderately (small specimens) to considerably elongate in large individuals; dorsal surface of palm weakly convex but with dorsomesial marginal area somewhat elevated; dorsal surface of carpus with row of spines mesiad of midline. Left cheliped with dorsal surface of palm somewhat flattened, dorsomesial and dorsolateral margins slightly elevated. Ambulatory legs similar; dactyls longer than propodi, strongly twisted; moderately slender to moderately broad; each with prominent longitudinal sulcus on lateral face and row of numerous very tiny corneous spines on ventral margin; carpi each with single or double row of multifid spines. Fourth pereopods semichelate; no preungual process; propodal rasp with several rows of corneous scales. Sternite of third pereopods (sixth thoracomere) sub-

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Fig. 3. Ambulatory dactyls. A–H, dactyl of left third pereopod (A–C lateral view, D–H, mesial view); I, dactyl of left second pereopod (mesial view); J, dactyl of right second pereopod (mesial view). A, *Parapagurodes makarovi* McLaughlin & Haig, 1973, ♂ (sl = 3.5 mm), LACM; B, *P. laurentae* McLaughlin & Haig, 1973, ♂ (sl = 3.2 mm), LACM; C, *P. hartae* McLaughlin & Jensen, 1996, ♂ (sl = 2.8 mm), RBCPM 974-00368-22; D, *P. gracilipes* (Stimpson, 1858), ♂ (sl = 9.0 mm), CBM-ZC 2977; E, *P. nipponensis* (Yokoya, 1933), ♂ (sl = 7.3 mm), CBM-ZC 1162; F, *P. constans* (Stimpson, 1858), ♂ (sl = 8.7 mm), CBM-ZC 59; G, H, *P. imaii* (Yokoya, 1939), ♂ (sl = 2.5 mm), CBM-ZC 2699, ovig. ♀ (sl = 1.6 mm), CBM-ZC 1911; I, J, *P. doederleini* (Doflein, 1902), ♂ (sl = 8.6 mm), ZSSM 274/1. A, B redrawn from McLaughlin & Haig (1973); C redrawn from McLaughlin & Jensen (1996); I, J from Asakura (2001).

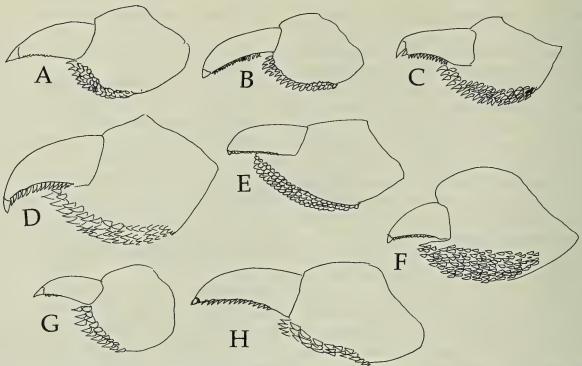


Fig. 4. Dactyl and propodus of left fourth pereopod (lateral view). A, *Parapagurodes makarovi* McLaughlin & Haig, 1973, ♂ (sl = 3.5 mm), LACM; B, *P. laurentae* McLaughlin & Haig, 1973, ♂ (sl = 3.4 mm), LACM; C, *P. hartae* McLaughlin & Jensen, 1996, ♂ (sl = 3.2 mm), RBCPM 974-00368-22; D, *P. gracilipes* (Stimpson, 1858), ♂ (sl = 9.0 mm), CBM-ZC 2977; E, *P. nipponensis* (Yokoya, 1933), ♂ (sl = 7.3 mm), CBM-ZC 1162; F, *P. constans* (Stimpson, 1858), ♂ (sl = 8.7 mm), CBM-ZC 59; G, *P. imaii* (Yokoya, 1939), ♂ (sl = 2.5 mm), CBM-ZC 2699; H, *P. doederleini* (Doflein, 1902), ♂ (sl = 8.6 mm), ZSSM 274/1. A, B redrawn from McLaughlin & Haig (1973); C redrawn from McLaughlin & Jensen (1996); H redrawn from Asakura (2001).

quadrate to subrectangular. Sternite of fifth pereopods (eighth thoracomere) separated into two subovate lobes by shallow median groove; coxae of fifth pereopods symmetrical. Males with very short sexual tube developed from coxa of right fifth pereopod; left gonopore without tube or papilla. No paired pleopods in either sex. Males with unequally biramous pleopods on pleomeres 3–5. Females with well developed, biramous pleopods on pleomeres 2–4; pleopod 5 with endopod noticeably reduced. Telson with posterior lobes separated by very small median cleft; terminal margins oblique, each with 8 or 9 small spines and 1 larger spine at posterolateral angles.

Parapagurodes constans (Stimpson, 1858)
Figs. 1F, 2F, 3F, 4H, 5F, G

Redescription by Komai (1999:80–88, figs. 1–4).

Supplemental material examined.—Japan: Hilgendorf collection, 1 ovig. ♀ (sl = 5.5 mm), ZMB 8650; 1 ♂ (sl = 11.1 mm), 1 ovig. ♀ (sl = 10.2 mm), Sagami Bay, ZMB 17800; 1 ♂ (sl = 8.7 mm), off Tone River mouth, Choshi, Chiba, 60 m, 21 Oct 1991, CBM-ZC 59; 2 ♂ (sl = 6.3, 10.7 mm), Hakodate Bay, 10–20 m, 17 Mar 1995, CBM-ZC 2362.

Diagnosis.—Gill lamellae biserial. Rostrum triangular. Maxillule with moderately well developed external lobe, not recurved. Right cheliped somewhat suboval in dorsal view; dorsal surface of palm weakly convex; dorsal surface of carpus with scattered spines mesiad of midline. Left cheliped with dorsal surface of palm weakly convex. Ambulatory legs similar; dactyls slightly longer than propodi, moderately slender, laterally compressed, in dorsal view slightly to prominently twisted, with longitudinal

sulcus on lateral face and row of corneous spines on ventral margin; carpi each with dorsodistal spine and row of low protuberances on dorsal surface. Fourth pereopods semichelate, preungual process apparently absent; propodal rasp with several rows of corneous scales. Sternite of third pereopods (sixth thoracomere) subrectangular. Sternite of fifth pereopods (eighth thoracomere) separated into two somewhat flattened, rounded lobes by shallow median depression; coxae of fifth pereopods symmetrical. Males with papilla or very short sexual tube developed from coxa of both right and left fifth pereopods. No paired pleopods in either sex. Males with unequally biramous left pleopods on pleomeres 3–5. Females with moderately well developed, biramous pleopods left on pleomeres 2–4; pleopod 5 reduced. Telson with posterior lobes separated by shallow median cleft; terminal margins broadly rounded, each unarmed or with few very small spinules adjacent to cleft.

Parapagurodes imaii (Yokoya, 1939)

Figs. 1G, 2G, H, 3G, 4I, 5H

Redescription by Komai (1994:33–38, figs. 1–3).

Supplemental material examined.—Japan: 1 ♂ (sl = 2.1 mm), 1 ovig. ♀ (sl = 1.6 mm), Funakoshi Bay, Iwate, Sanriku, 66 m, 25 May 1995, CM-ZC 1911; 1 ♂ (sl = 2.5 mm), off Takeoka, Boso Peninsula, ca 80 m, 2 Mar 1995, CBM-ZC 2699.

Diagnosis.—Gill lamellae biserial, but with slight terminal concavity, cleft or depression. Rostrum triangular. Maxillule with moderately well developed external lobe, not recurved. Right cheliped elongate in large males, dorsal surface of palm convex; dorsal surface of carpus with two longitudinal rows of spines. Left cheliped with dorsal surface of palm elevated in midline. Ambulatory legs somewhat dissimilar, third sexually dimorphic; dactyls of second and third right slightly shorter to slightly longer than propodi, moderately slender, laterally

compressed, in dorsal view barely twisted, with row of corneous spines on ventral margin, third left of females broadened, propodus with prominent ventral spine; carpi each with dorsodistal spine and row of low, sometimes spinulose protuberances on dorsal surface. Fourth pereopods semichelate; preungual process absent; propodal rasp with 2 or 3 rows of corneous scales. Sternite of third pereopods (sixth thoracomere) subcircular to subovate, slightly skewed. Sternite of fifth pereopods (eighth thoracomere) separated into two somewhat flattened, rounded lobes by shallow median depression; coxae of fifth pereopods symmetrical. Males with very short sexual tube developed from coxa of both right and left fifth pereopods. No paired pleopods in either sex. Males with unequally biramous left pleopods on pleomeres 3–5. Females with moderately well developed, biramous left pleopods on pleomeres 2–4; pleopod 5 reduced. Telson with posterior lobes separated by shallow median cleft; terminal margins oblique, each with 3 or 4 moderate to strong spines.

Parapagurodes doederleini (Doflein, 1902)

Figs. 1H, 2I, J, 3H, 4J, 5I

Redescription by Asakura (2001:885–888, figs. 45–47).

Supplemental material examined.—Japan: 2 ♂ (sl = 8.1, 9.2 mm), off Kochi, Tosa Bay, 190 m, 10 Aug 1991, CBM-ZC 184.

Taiwan: 1 ♂ (sl = 9.3 mm), 1 ♀ (sl = 7.8 mm), Su-Aou, 100–200 m, 6 Aug 1996, CBM-ZC 2922.

Diagnosis.—Gill lamellae biserial. Rostrum triangular. Maxillule with moderately well developed endopodal external lobe, not recurved. Right cheliped stout, dorsal surface of palm slightly convex; dorsal surface of carpus with covering of spines and spinulose tubercles. Left cheliped with dorsal surface of palm very slightly elevated in midline. Ambulatory legs dissimilar, dac-

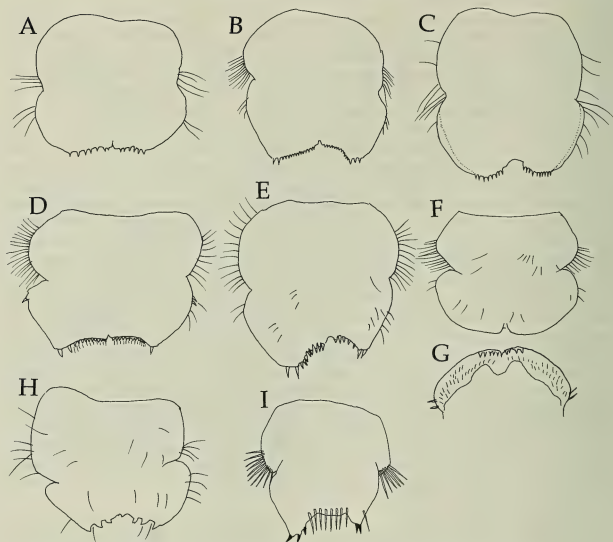


Fig. 5. Telson (A-F, H, I, dorsal view, G, ventral view of posterior portion). A, *Parapagurodes makarovi* McLaughlin & Haig, 1973 ♂ (sl = 3.5 mm), LACM; B, *P. laurentae* McLaughlin & Haig, 1973, ♂ (sl = 3.4 mm), LACM; C, *P. hartae* McLaughlin & Jensen, 1996, ♂ (sl = 3.2 mm), RBCPM 974-00368-22; D, *P. gracilipes* (Stimpson, 1858), ♂ (sl = 9.0 mm), CBM-ZC 2977; E, *P. nipponensis* (Yokoya, 1933), ♂ (sl = 7.3 mm), CBM-ZC 1162; F, G, *P. constans* (Stimpson, 1858); ♂ (sl = 8.7 mm), CBM-ZC 59; H, *P. imaii* (Yokoya, 1939), ♂ (sl = 2.5 mm), CBM-ZC 2699; I, *P. doederleini* (Doflein, 1902), ♂ (sl = 8.6 mm), ZSSM 274/1. A, B redrawn from McLaughlin & Haig (1973); C redrawn from McLaughlin & Jensen (1996); I from Asakura (2001).

tyls longer than propodi, strongly twisted, second left with row of 40–60 well developed, comb-like corneous spines on ventral margin; second right and third each with longitudinal row of short transverse rows of setae; carpi each with row of spines on dorsal surface. Fourth pereopods subchelate; preungual process absent; propodal rasp with 3 or 4 rows of corneous scales. Sternite of third pereopods (sixth thoracomere) rectangular. Sternite of fifth pereopods

(eighth thoracomere) as narrow rod with pair of rounded lobes anteriorly; coxae of fifth pereopods asymmetrical. Males with very short sexual tube developed from coxa of right fifth pereopod, left sometimes with papilla. No paired pleopods in either sex. Males with unequally biramous left pleopods on pleomeres 3–5. Females with moderately well developed, biramous left pleopods on pleomeres 2–4; pleopod 5 reduced. Telson with posterior lobes separated by

broad, deep median concavity; terminal margins oblique, each with 1–5 moderate to strong corneous spines.

Results

In her discussion of significant generic characters, de Saint Laurent-Dechancé (1966) listed three that are pertinent to our investigation: sexual tube development, development of the external lobe of the maxillulary endopod, and pleopod number and development. Perusal of the abbreviated diagnoses of the eight species currently assigned to *Parapagurodes* shows that attributes of these three characters are not universally shared.

While sexual tube length (Fig. 1) varies from very short to short in *P. makarovi* (Figs. 1A, B) and *P. laurentae* (Fig. 1C, D) only very short tubes develop in the other six species (Figs. 1E–J), and occasionally are not apparent at all. However, recent studies have shown that sexual tube development is known to vary within genera (e.g., McLaughlin 1997, 2003; McLaughlin & Lemaitre 2001; Lemaitre & McLaughlin 2003a, 2003b). Nevertheless, *P. doederleini* is more importantly distinguished from the other seven species because in addition to the very short right sexual tube, the coxae of the male fifth pereopods are asymmetrical (Fig. 1J).

The external lobe of the maxillulary endopod (Fig. 2) is moderately well developed in all eight species, but is slightly to distinctly recurved only in *P. gracilipes* and *P. nipponensis* (Figs. 2D, E).

Parapagurodes was initially characterized as having unpaired male pleopods varying from reduced on pleomeres 3–5 to completely absent, and female unpaired pleopods often being reduced on pleomeres 2–4 and absent on pleomere 5. All subsequently assigned taxa are described as having at least moderately well developed unpaired, unequally biramous pleopods on male pleomeres 3–5 and on female pleomeres 2–5.

Several other characters frequently included in generic diagnoses also have been examined. Rostral development, for example is generally similar among species within a single genus. All eight species have an acutely developed rostrum, but then so do many species assigned to other genera.

With the exception of *P. constans*, all of the species under consideration herein are described as having an elongate right cheliped, at least in large males. In *P. hartae* and *P. imaii* this elongation is considered a sexually dimorphic character (McLaughlin & Jensen 1996, Komai 1999), whereas in *P. gracilipes* and *P. nipponensis* apparently the elongation is growth related (Komai 1998). Similar lengthening of the left cheliped is reported for these species. In contrast, the chelipeds are typically elongate regardless of sex or size in *P. makarovi*, *P. laurentae* and *P. doederleini*. That cheliped elongation is comparable among the eight taxa is doubtful.

Major differences among the eight species can be observed in the shape and armature of the dactyls of the ambulatory legs (Fig. 3). In *P. makarovi* and *P. laurentae* the dactyls (Figs. 3A, B) are moderately long, slender, laterally compressed, and in dorsal view appear straight; the dorsal surfaces of the carpi are armed only with a dorsodistal spine. The dactyls are similarly straight in *P. hartae* (Fig. 3C), but vary in length from shorter to only slightly longer than the propodi; the carpi each have a row of low protuberances on the dorsal surface in addition to the dorsodistal spine. The dactyls of *P. gracilipes* and *P. nipponensis* (Figs. 3D, E), although moderately long and laterally compressed, are moderate to broad and strongly twisted, the ventral margins of each are provided with a row of numerous small corneous spines; the dorsal surfaces of the carpi are provided with one or more rows of small spines. In contrast, while the dactyls of *P. constans* (Fig. 3F) are longer than the propodi and slightly to noticeably twisted, the ventral margins each are armed with fewer and much larger cor-

neous spines; each carpus is armed only with a row of low protuberances in addition to the dorsodistal spine. The dactyls of *P. imaii* and *P. doederleini* are dimorphic, but do not represent comparable conditions. As reported by Komai (1999), the third left dactyl and propodus of females of *P. imaii* differ from those of males. In males the dactyl and propodus of the third left (Fig. 3G) are moderately long and slender as they are on the second and third right. The female dactyl (Fig. 3H) is broad and prominently flattened; a well developed calcareous spine is present on the ventrodistal margin of the propodus. The dimorphism in *P. doederleini* involves the dactyls of the second pereopods. The left is provided with a ventral row of closely-spaced, corneous spines that present a comb-like appearance (Fig. 3I); the right, and the dactyls of the third pereopods completely lack spines, and instead are provided with short transverse rows of setae over the entire length of the mesial faces (Fig. 3J).

The shape of the anterior lobe of the sternite of the third pereopods and the configuration of the sternite of the fifth pereopods have been proposed as generic or at least group characters (e.g., McLaughlin 1981, 2003; Lemaitre et al. 1982). The anterior lobe of the sternite of the third pereopods is subsemicircular in *P. makarovi*, *P. laurentae*, and *P. hartae*, semicircular or subovate in *P. imaii*, but subquadrate to subrectangular in *P. gracilipes* and *P. nipponensis* and subrectangular in *P. constans* and *P. doederleini*. The sternites of the fifth pereopods are less clearly definable in these eight taxa.

The fourth pereopods (Fig. 4) are subchelate or only very weakly semichelate in *P. makarovi* and *P. laurentae* and *P. doederleini*, but semichelate in the remaining species. The number of rows of corneous scales making up the propodal rasps of these appendages exhibit overlapping intraspecific variation in all eight species.

The telsons of *P. makarovi* and *P. laurentae* (Figs. 5A, B) have straight to weakly

concave or very slightly oblique terminal margins that are armed with small spines or spinules. Similar conformation and armature are seen in *P. gracilipes* (Fig. 5D) and to a lesser extent in *P. nipponensis* (Fig. 5E). In contrast, the terminal margins of the telsons of *P. hartae* (Fig. 5C) and *P. constans* (Fig. 5F, G) are broadly rounded and unarmed or only weakly armed. The telson of *P. imaii* (Fig. 5H) differs in having distinctly oblique terminal margins, each armed with prominent spines, and the telson of *P. doederleini* (Fig. 5I) is plainly different from the other seven.

Conclusions

From the evidence presented, there can be little doubt that *Parapagurodes*, as presently constituted, represents a heterogeneous collection of taxa. Consequently, we restrict *Parapagurodes* to the two species initially assigned, *P. makarovi* and *P. laurentae*. *Parapagurodes hartae* is herein transferred to *Pagurus* and the four species formerly included in *Pagurus* are returned to it.

We concur with Komai (1998) that *P. gracilipes* and *P. nipponensis* are closely allied to the *bernhardus* group of *Pagurus*, and undoubtedly should be included in that group. We do not advocate separating the *bernhardus* group from the admittedly polyphyletic *Pagurus* at this time, as *Pagurus bernhardus* (Linnaeus, 1758) is the type species of the genus. To remove *P. bernhardus* and its allied species would leave the remaining 80 or so species without generic union. Consequently, until such time as all species currently assigned to *Pagurus* have been thoroughly recognized and defined, this genus necessarily must remain a "catch-all". In contrast, there is ample justification to establish a new genus for the very distinctive *P. doederleini* as is done herein.

Dofleinia gen. nov.

Catapagurus: Doflein 1902:624 (in part).—
Miyake 1978:78 (key, in part), 141 (in

part); 1982:232 (key, in part); 1991:232 (key, in part); 1999:232 (key, in part).

Parapagurodes: Asakura 2001:885 (in part).

Diagnosis.—Gills biserial; 11 pairs. Rostrum well developed, acute. Antennal peduncles with supernumerary segmentation. Maxillule with external lobe of endopod moderately well developed, not recurved. Third maxilliped with well developed crista dentata, 1 accessory tooth. Sternite of third maxillipeds unarmed. Chelipeds subequal, right stronger but not necessarily longer. Second pereopods dimorphic, left with row of closely-spaced comb-like corneous teeth on ventral margin, right with ventral margin unarmed. Third pereopods similar; sternite with subrectangular anterior lobe. Fourth pereopods subchelate; dactyl with well developed preungual process; propodal rasp consisting of 3 or 4 rows of corneous scales. Fifth pereopods chelate; coxae of males asymmetrical. Males with very short sexual tube developed from right gonopore, papilla frequently produced from left.

Abdomen well developed, twisted; columnar muscle usually prominent. Males without paired first or second pleopods; with unequally biramous unpaired left pleopods 3–5. Females without paired first pleopods, with subequally biramous, unpaired, left pleopods 2–4, pleopod 5 as in male. Uropods asymmetrical. Telson with distinct lateral indentations; posterior lobes separated by very broad median cleft.

Type species.—*Catapagurus doederleini* Doflein, 1902.

Etymology.—Named after F. Doflein who first described the type species; gender feminine.

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***Pseudopaguristes bicolor*, a new species of hermit crab (Crustacea: Decapoda: Diogenidae) from Japan, the third species of the genus**

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Abstract.—*Pseudopaguristes bicolor*, a new species of the recently established diogenid genus *Pseudopaguristes* McLaughlin, is described and illustrated from Okinawa, Japan. This is the third species assigned to this genus.

The recently established diogenid genus *Pseudopaguristes* McLaughlin, 2002, is characterized by eight functional gills, male chelipeds with the right larger than the left and dissimilar in armature, female chelipeds similar from left to right, fourth pereopods with a clump of long capsulate setae on the carpi, and the paired first and second pleopods modified as gonopods. The type species, *P. janetkae* McLaughlin, 2002, was recorded from Guam, the Mariana Islands. A second species, *P. bollandi* Asakura & McLaughlin, 2003, was recorded from Okinawa, tropical Japan. The present authors recently found the third species of this genus, again from Okinawa. The new species is very easily separated from both *P. janetkae* and *P. bollandi* by its characteristic coloration and morphology of the male chelipeds.

The holotype is deposited in the Natural History Museum and Institute, Chiba (CBM-ZC). The terminology used follows McLaughlin (1974, 2002) with the exception of the fourth pereopods as defined by McLaughlin (1997), gill structure by McLaughlin & de Saint Laurent (1998), and the posterior carapace by McLaughlin (2000). Abbreviations used are; coll., collector; and SL, shield length as measured from the tip of the rostrum to the posterior margin of the shield.

***Pseudopaguristes bicolor*, new species**
Figs. 1–8

Material.—Holotype: male, SL = 2.65 mm, 78 m, 24°25.5'N, 124°03.3'E, off Yarabu-zaki, Ishigaki-jima Island, Okinawa, 21 Nov. 2002, coll. T. Kosuge, CBM-ZC 6759.

Description.—Eight functional pairs of quadriserial, phyllobranchiate gills (Fig. 1A). Shield (Fig. 1B) 1.30 times longer than broad; anterior margin between rostrum and lateral projections concave; lateral projections triangular, with strong submarginal spine; anterolateral angles each with strong corneous spine; lateral margins convex; posterior margin truncate; dorsal surface slightly convex, with elevated area present on each anterolateral portion; scattered tufts of short setae. Rostrum (Fig. 1B) prominent, triangular, reaching nearly to apices of ocular acicles, with terminal spine. Posterior carapace lateral elements (Fig. 1B) small, well calcified, unarmed. Branchiostegites (Fig. 1C) each with row of spines on dorsal margin anteriorly.

Ocular peduncles (Fig. 1B) moderately long, 0.75 length of shield. Corneas (Fig. 1B, C) very slightly dilated. Ocular acicles (Fig. 1B) each terminating in strong, bifid corneous spines; separated basally by more than breadth of rostrum.

Antennular peduncles (Fig. 1D) stout, with few setae on each segment; when fully

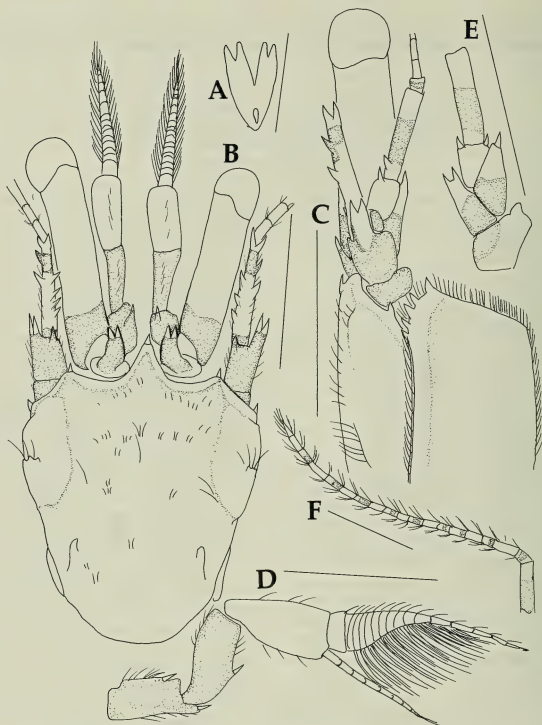


Fig. 1. *Pseudopaguristes bicolor*, new species: holotype male (CBM-ZC 6759), SL = 2.65 mm, off Yarabuzaki, Ishigaki-jima Is., Okinawa. A, arthrobranch gill lamella; B, shield and cephalic appendages, dorsal; C, distal half of cephalothorax and cephalic appendages, right, lateral; D, right antennule, lateral; E, right antennal peduncle, ventral; H, right antennal flagellum. Scales equal 0.5 mm (A) and 1 mm (B-F).

extended, distal margins of ultimate segments reaching distal margins of corneas; ultimate segments unarmed; penultimate segments with ventral margins each bearing acute spine; basal segments with ventrod-

istal angles each bearing acute spine and dorsolateral margins each bearing acute subdistal spine.

Antennal peduncles (Fig. 1B, C, E) moderately long, when fully extended, reaching

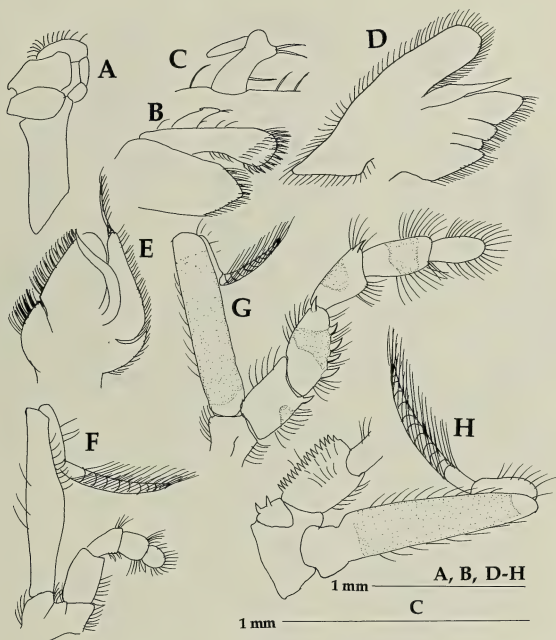


Fig. 2. *Pseudopaguristes bicolor*, new species: holotype male (CBM-ZC 6759), SL = 2.65 mm, off Yarabuzaki, Ishigaki-jima Is., Okinawa. Right mouthparts: A, mandible, internal; B, maxillule, external; C, same, endopod; D, maxilla, external; E, first maxilliped, internal; F, second maxilliped, external; G, third maxilliped, external; H, same, internal.

distal 0.30 of ocular peduncles, scarcely setose; fifth segments with dorsal margins each bearing acute subproximal spine; fourth segments with dorsodistal margins each bearing acute spine and ventrodistal margins each bearing another acute spine; third segments with prominent spine at ventrodistal margin; second segments with dorsolateral distal angles produced, terminating in prominent bifid spine, dorsomesial distal

angles each with acute corneous spine; first segment unarmed. Antennal acicles moderately long, straight; dorsomesial margins each with 3 (right) or 4 (left) spines; dorsolateral margins each with 2 strong spines; distal margins each with 2 strong spines. Antennal flagella (Fig. 1F) consisting of about 18 articles, each article with several short setae.

Mandible (Fig. 2A) without distinguish-

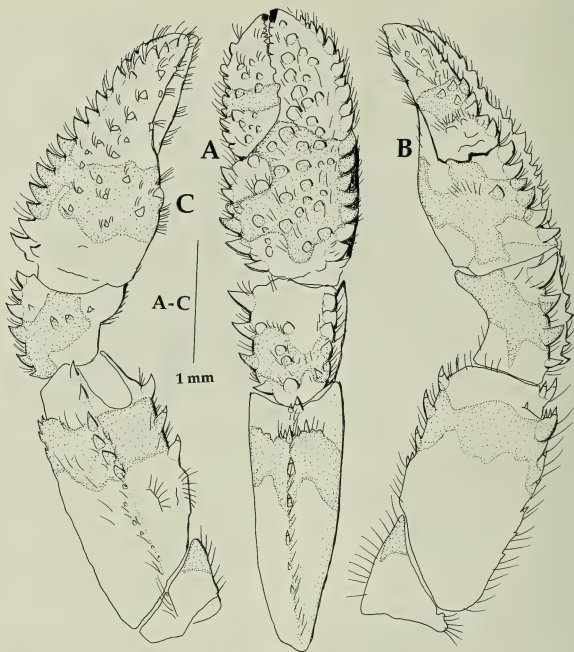


Fig. 3. *Pseudopaguristes bicolor*, new species: holotype male (CBM-ZC 6759), SL = 2.65 mm, off Yarabuzaki, Ishigaki-jima Is., Okinawa. Right cheliped: A, dorsal; B, mesial; C, lateral.

ing characters. Maxillule (Fig. 2B, C) with external lobe of endopod well developed, articulated, and recurved; internal lobe with 2 bristles. Maxilla (Fig. 2D) with moderately narrow scaphognathite. First maxilliped (Fig. 2E) with well developed, setose epipod. Second maxilliped (Fig. 2F) without distinguishing characters. Third maxilliped (Fig. 2G, H) with carpus bearing dorsodistal spine; merus with dorsodistal spine,

ventral margin bearing 4 spines; ischium with strong ventrodistal spine, crista dentata well-developed, no accessory tooth; basis with 2 sharp spines.

Chelipeds subequal; right (Fig. 3) larger than left. Dactyl as long as palm; terminating in broad corneous claw; dorsal face flat, with scattered large tubercles; cutting edge with several calcareous teeth. Fixed finger terminating in corneous claw; dorsal face

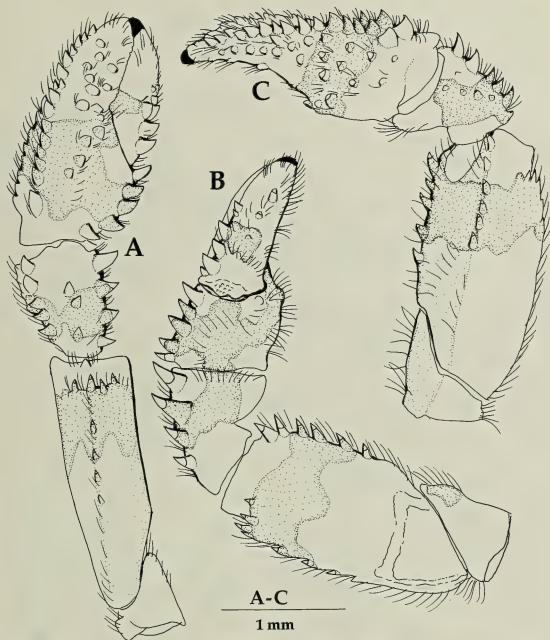


Fig. 4. *Pseudopaguristes bicolor*, new species: holotype male (CBM-ZC 6759), SL = 2.65 mm, off Yarabuzaki, Ishigaki-jima Is., Okinawa. Left cheliped: A, dorsal; B, mesial; C, lateral.

flat, with scattered large tubercles; cutting edge with several calcareous teeth. Palm 1.07 length of carpus; dorsal surface flat, with scattered large tubercles; dorsomesial margin with row of very strong spines; dorsolateral margin of palm and fixed finger with row of strong spines. Carpus 0.50 length of merus; dorsal face with scattered large tubercles, dorsolateral margin with row of strong conical-shaped spines, dorsomesial margin with row of very strong

spines. Merus with dorsal face bearing 2 distal spines, subdistal transverse row of several spines, and row of spines on remainder of dorsal margin, tips semitransparent; ventromesial margin with 3 widely-separated strong spines, tips semitransparent, ventrolateral margin with row of spines or tubercles. Ischium unarmed. Coxa with acute spine ventromesially.

Left cheliped (Fig. 4) slenderer than right. Dactyl with dorsal face without tu-

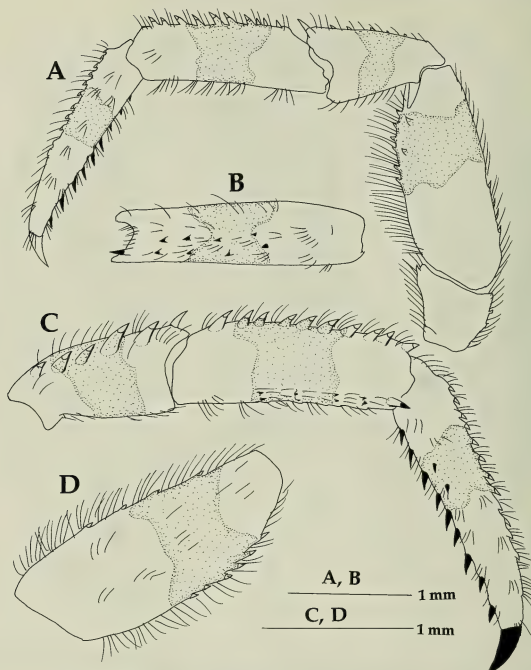


Fig. 5. *Pseudopaguristes bicolor*, new species: holotype male (CBM-ZC 6759), SL = 2.65 mm, off Yarabuzaki, Ishigaki-jima Is., Okinawa. Second left pereopod: A, lateral; B, propodus, ventral; C, dactyl, propodus, and carpus, mesial; D, merus, mesial.

bercles; number of tubercles or spines on dorsal faces of palm and carpus fewer; merus with ventromesial and ventrolateral margins bearing 6 and 5 spines, respectively; other surfaces similar to right.

Second pereopods (Fig. 5) with armature similar from left to right; right 1.10 length of left. Basically, spines on ambulatory pereopods with semitransparent tips. Dactyls

1.10 (left) or 1.25 (right) length of propodi, each terminating in strong corneous claw; dorsal margins each with row of strong spines; ventral margins each with row of 9 strong corneous spines and, on left, accompanied with 2 tiny corneous spines mesially. Propodi 1.60 (left) or 1.55 (right) length of carpi, each with row of 10 strong spines on dorsal margin; ventral faces each with 2

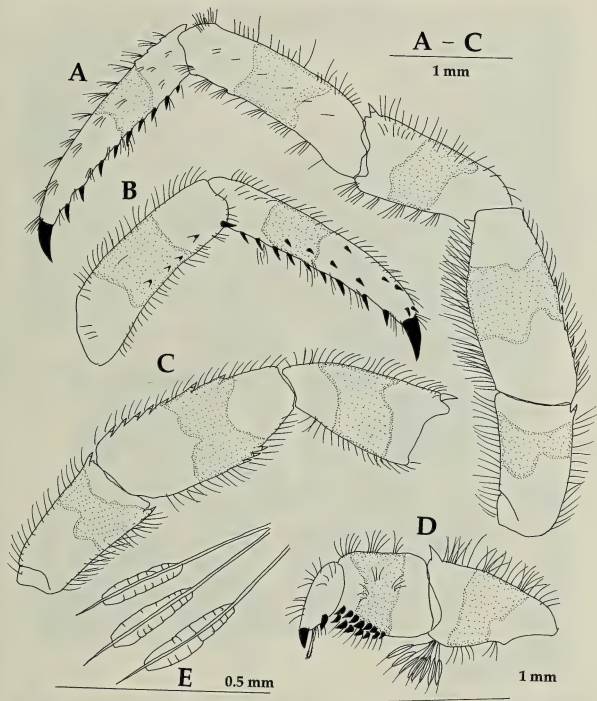


Fig. 6. *Pseudopaguristes bicolor*, new species: holotype male (CBM-ZC 6759), SL = 2.65 mm, off Yarabuzaki, Ishigaki-jima Is., Okinawa. Third left pereopod: A, lateral; B, dactyl and propodus, mesial (propodus slightly ventral view); C, carpus, merus and ischium, lateral. Fourth left pereopod: D, dactyl, propodus and carpus, lateral; E, ventral setae of carpus.

irregular rows of widely-separated, tiny corneous spines, ventromesial distal margins with 1 (right) or 2 (left) acute corneous spines. Carpi 0.55 (left) or 0.60 (right) length of meri, each with strong, corneous or corneous-tipped, slender spine at dorso-

distal angle and row of 5 slender spines on dorsal face mesially. Meri with ventral margins each with row of slender spines and, on left, accompanied with 2 small spines mesially; dorsal margins each with row of spines. Ischia each with few, slender cor-

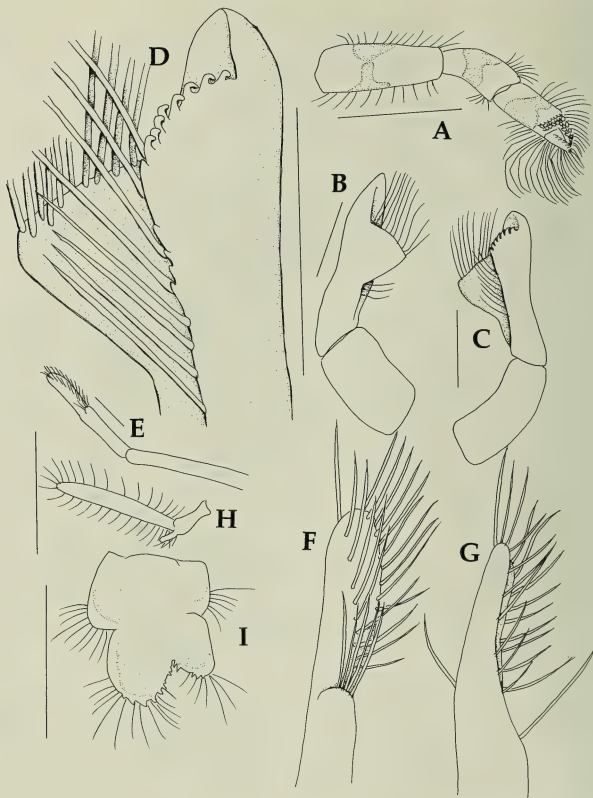


Fig. 7. *Pseudopaguristes bicolor*, new species: holotype male (CBM-ZC 6759), SL = 2.65 mm, off Yarabuzaki, Ishigaki-jima Is., Okinawa. A, right fifth pereopod. Left first pleopod: B, external; C, internal; D, distal portion, internal, enlarged. Left second pleopod: E, external; F, distal portion, enlarged, external; G, same, mesial. H, third pleopod. I, telson. Scales equal 1 mm (A, H, I) and 0.2 mm (B-E).

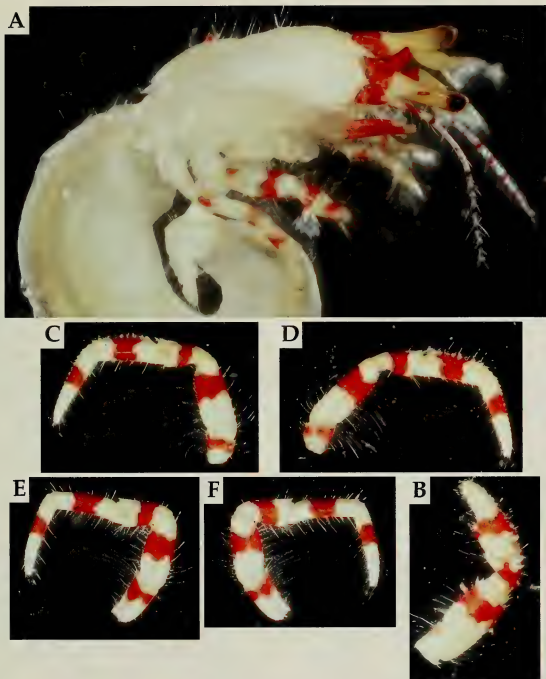


Fig. 8. *Pseudopaguristes bicolor*, new species: holotype male (CBM-ZC 6759), SL = 2.65 mm, off Yarabuzaki, Ishigaki-jima Is., Okinawa. A, dorsolateral view; B, right cheliped, mesial; C, left second pereopod, lateral; D, same, mesial; E, left third pereopod, lateral; F, same, mesial. Photo by A. Asakura.

neous-tipped spines dorsally and small spine at ventromesial distal angle. Coxae unarmed.

Third pereopods (Figs. 6A–C) with armature similar from left to right, right 1.05 length of left. Dactyls 1.20 (left) or 1.25 (right) length of propodi, each terminating in strong corneous claw; mesial faces each

with row of small corneous spines ventrally and 4 (left) or 2 (right) small spines dorsally; dorsal margins with few tiny spines on proximal 0.25; ventral margins each with row of 9 strong corneous spines. Propodi 1.60 length of carpi; dorsal faces unarmed (left) or row of small tubercles or spines (right); ventral faces each with row of

small, widely-separated corneous spines, ventromesial distal angles each with 1 (left) or 2 (right) acute corneous spines. Carpi 0.70 (left) or 0.80 (right) length of meri, each with strong spine at dorsodistal angle; dorsal margin unarmed (left) or with minute subproximal spine (right). Meri with ventral margins each bearing 3 (left) or 2 (right) small spines; dorsal margins each with row of spines. Ischia each with small dorsodistal spine and another small ventrodistal spine. Coxae unarmed.

Sternite of third pereopods with anterior lobe rectangular, unarmed.

Fourth pereopod (Fig. 6D) subchelate. Dactyl terminating in strong corneous claw; prominent preungual process present at base of claw; ventral face with 1 corneous spine laterally. Propodal rasp with 2 rows of corneous scales. Carpus with large dorsodistal spine; ventral face with clump of long capsulate setae (Fig. 6E).

Fifth pereopod (Fig. 7A) chelate; dactyl and propodus with well-developed rasps.

Male first pleopods (Fig. 7B–D) paired, modified as gonopods; basal lobe bearing few setae at superior mesial angle; inferior lamella with distal margin bearing row of short, hooked spines, and lateral margin with row of setae; internal lobe with row of setae on mesial margin; external lobe distinctly exceeding inferior lamella in distal extension. Second pleopods (Fig. 7E–G) paired, modified as gonopods; basal segment naked; endopod with several long setae; appendix masculina twisted; lateral and distal margins and inferior face with moderately long setae. Third (Fig. 7H) to fifth left pleopods each with exopod well developed, endopod reduced.

Uropods asymmetrical, left larger than right; rasps of exopods and endopods well developed; protopods each with row of spines posteriorly.

Telson (Fig. 7I) with lateral constrictions; anterior portion unarmed; posterior lobes separated by deep median cleft, left lobe larger than right, terminal margins fringed with spines.

Female unknown.

Color in life (Fig. 8).—Shield white; antennules with flagella and ultimate segment yellow, setae on flagella blue, penultimate and basal segments red; antennae with flagella bearing alternative red and white bands, fifth segment with middle red band, proximal half of third segment red, second segment red except for white distal spines, first segment red except for ventral face, antennal acicle with subdistal red band, other surfaces of antennae white; ocular peduncles yellow, each with red band on proximal 0.25; ocular acicles red except for white distal spines; third maxillipeds with propodus, carpus, and merus and penultimate segment of exopod each bearing middle red band, other surfaces white; second maxillipeds with middle red band on penultimate segment of exopod. Both chelipeds and second through fifth pereopods with irregular red area on each segment.

Etymology.—From the Latin *bicolor*, two colors, in reference to the alternating red and white color bands on the pereopods characteristic to this species.

Distribution.—Known only from the type locality.

Remarks.—Despite their general similarities in morphology, the new species, *P. bicolor*, is readily distinguished from both *P. janetkae* and *P. bollandi* by differences in coloration in life. The chelipeds and the second and third pereopods in *P. bicolor* have alternating red and white bands. These appendages are uniformly red in *P. bollandi*, and, in *P. janetkae*, the meri and carpi and proximal half of palm of the chelipeds are cranberry-red and the carpi, propodi and dactyls of the second and third pereopods are light cream, tinged with yellow.

Morphologically, *P. bicolor* is similar to both *P. janetkae* and *P. bollandi*, but some differences are seen among them. The most striking difference that separates *P. bicolor* from both *P. janetkae* and *P. bollandi* is the degree of dissimilarity in the chelipeds in males. In male *P. janetkae* and *P. bollandi*, the chelipeds are very unequal, and arma-

tures are much stronger in the right than in the left. However, in male *P. bicolor*, the chelipeds are subequal and the dissimilarity of the armature is not so large as in those in *P. janetkae* and *P. bollandi*. Furthermore, the dorsal surfaces of the chelae are provided with tubercles in *P. bicolor* and *P. bollandi* but with spines in *P. janetkae*.

Other minor difference includes the fact that, although a preungual process is absent in *P. bollandi*, both *P. bicolor* and *P. janetkae* have a very prominent preungual process developed at the base of the claw, giving the dactyl a quasi-chelate appearance. However, so few specimens have been reported in any of these species (four specimens in *P. janetkae*, one in *P. bollandi* and one in *P. bicolor*), it is not possible to evaluate variability. Thus, we expect future collection efforts to provide more precise information on morphological discrimination between the species.

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**A new species of axiid shrimp from chemosynthetic communities of
the Louisiana continental slope, Gulf of Mexico
(Crustacea: Decapoda: Thalassinidea)**

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Abstract.—*Calaxius carneyi*, new species (Axiidae), is described from two male specimens collected by manned submersibles working near hydrocarbon seeps in deep waters (544 m) on the continental slope off Louisiana, in the northern Gulf of Mexico. Both specimens were taken adjacent to communities of clams that comprise a major constituent of chemosynthetic assemblages at the collection site. The new species is characterized in part by ventrally truncate abdominal pleura, as opposed to the acutely triangular or broadly rounded pleura found in other known members of *Calaxius*, only one of which is known to occur in the Atlantic Ocean. The new species is readily distinguished from its congeners by unique dentition of its heavy triangular rostrum and postrostral carapace, its short eyestalks and antennal acicle, the absence of well-defined teeth on the massive chelipeds, and the narrow, subtriangular telson. Chelipeds, pleopods and uropods of the two known specimens herewith described are covered extensively by long setae, many of which are plumose and densely fouled by flocculent debris.

Recent investigations of methane cold seeps in the Gulf of Mexico have discovered a number of previously undescribed taxa associated with chemosynthetic communities in deep waters of the continental slope (e.g., Gustafson et al. 1998). However, some collections from these unique habitats consist of single specimens, and comparative studies have been deferred pending recovery of additional materials. One such case was presented by the collection of a single, somewhat fragmented, molted integument from the male of an apparently undescribed axiid mud shrimp, collected in 1988 during a dive of the manned submersible *Pisces II*. A second, smaller, intact male specimen, was obtained

from an adjacent site in 1992 with a shallow core sampler deployed by the *Johnson Sea-Link* manned submersible. Collections on subsequent dives by submersibles and vessel-based box coring in this area have brought no additional materials to our attention.

While the female of this species remains unknown, it is readily apparent that the species is undescribed. The marked size difference between the intact specimen and the earlier recovered exuvia provides a glimpse of ontogenetic variation in characters, and allows us to select diagnostic characters that should apply to a wide size range. Also, from familiarity with typical sexual dimorphism in congeneric species, we expect that the description here provided will serve adequately for identification of female specimens, if encountered.

* Deceased.

Upon arrival at the surface, specimens were fixed in 10% formalin (with Rose Bengal stain for only the 1992 collection), transferred to 80% ethyl alcohol, and finally archived in 70% ethyl alcohol. Carapace length (CL) was measured from the posterior margin of the orbit to the posterior margin of the carapace midline. Total length (TL) was measured from the tip of the rostrum to the tip of the extended telson. Specimens are archived in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

Family Axiidae Huxley, 1879

Calaxius Sakai & de Saint Laurent, 1989

Calaxius carneyi, new species

Figs. 1 & 2

Material examined.—Holotype, USNM 1009165, male, CL 10.1 mm, TL 26.5 mm, *Johnson Sea-Link* submersible sta 3269, box core B, deployed from submersible about 2 m from chemosynthetic mussel community, Bush Hill site, 544 m, Louisiana continental slope, northern Gulf of Mexico, 27°46.904'N, 91°30.286'W, 11 Aug 1992. Paratype, USNM 1009166, exuvia of male, CL 18.3 mm, TL 50.5 mm, submersible *Pisces II* sta 880031 (8831), location and depth same as for holotype, Aug 1988.

Diagnosis.—Rostrum heavy, triangular, extending slightly more than twice length of eyes, bearing flattened, upturned terminal spine and pair of similar upturned subterminal spines. Antennal acicle short, overreaching proximal third of penultimate (fourth) peduncular article. Chelipeds massive, lacking well defined teeth. Carapace bearing dentate lateral and submedian carina. Pereopodal epipods and pleurobranchs present. Abdomen with pleura 3–5 ventrally truncate, bearing small anterior and posterior marginal denticles; lacking male pleopod 1; appendices internae on pleopods 2–5; uropodal exopod bearing transverse suture; terminated by narrow, subtriangular telson.

Description of holotype.—Integument firm but pliable, with numerous clumps of elongate, plumose, fouled setae, often obscuring underlying structures on chelae, pleopods, uropods, and telson; calcification most heavy in carapace teeth and chelae. Carapace with posterior midline elevated, bracketed on either side by paired setose punctae, midline elevation becoming a rounded crest in cardiac region where surmounted by a slight but distinct prominence or tubercle, marked dorsally by translucent or worn area (Fig. 1a); rostrum heavily calcified, triangular, slightly more than twice length of eyes, terminal spine subacute, upturned, dorsoventrally flattened, triangular in dorsal view; subterminal pair of spines similar to terminal, also upturned, imparting concave appearance to flattened dorsal surface of rostrum (Fig. 1b, c); supraocular spines (lacking in the paratype, a larger specimen) and supraorbital spines strong, similar in calcification, shape and orientation to subterminal pair; lateral carina originating from supraorbital spine, diminishing immediately anterior to second spine or tooth, continuing as a low ridge toward posterior; submedian carina originating from posteriormost of two slightly offset submedian teeth, becoming ill-defined toward posterior; median carina a weak crest bearing a worn tubercle near its posterior end, and otherwise lacking ornamentation.

Sternite of fourth pereopods (seventh thoracic somite) with deep median slit, thoracic shield produced to form acute, marginally sinuate, triangular flange to either side; 3-branched carina set between articulations of fourth pereopods (Fig. 2a). Abdominal pleuron 1 narrowed, acute ventrally (Fig. 1a); pleuron 2 ventrally broad, with an angular tooth or acute corner at the posteroventral end; pleura 3–5 ventrally truncate, with small acute tooth on anteroventral margin and another on posteroventral margin; pleuron 6 with small acute tooth on anteroventral margin and broad triangular flange at posteroventral margin.

Eyestalks small, subcylindrical, reaching

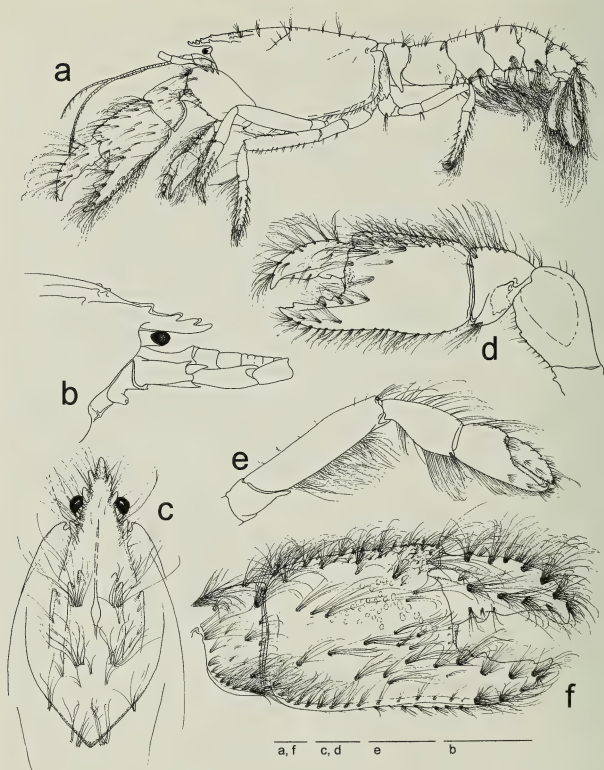


Fig. 1. *Calaxius carneyi*, new species (where setation is shown, setules and flocculent coating of plumose appendages not fully illustrated). a–e, holotype male, USNM 1009165: a, carapace, abdomen, left pereopods 1 and 3–5 in lateral view, with right pereopod 2 internal surface; b, anterior carapace, eyes and antennal peduncles, right side, lateral view, setation not shown; c, anterior of carapace in dorsal view; d, right pereopod 1 or major cheliped, internal surface; e, right pereopod 2, external surface. f, paratype male, USNM 1009166: right pereopod 1 or major cheliped, external surface. Scale bars indicate 2.0 mm.

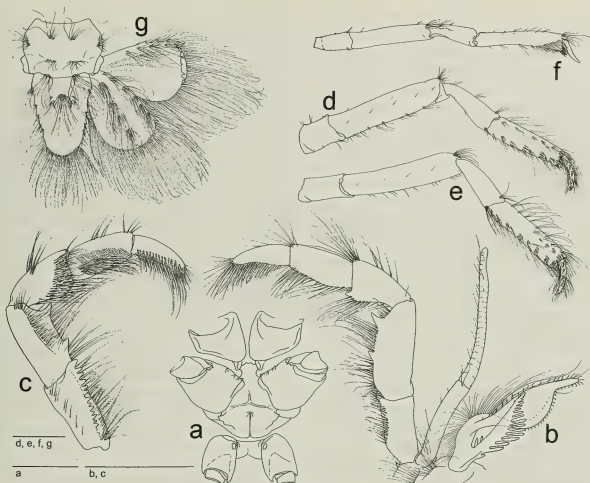


Fig. 2. *Calaxius carneyi*, new species, holotype male, USNM 1009165 (where setation is shown, setules and flocculent coating of plumose appendages not fully illustrated). a, posterior thoracic sternites and coxae of pereopods 3-5, ventral view, setation not shown; b, left maxilliped 3, external surface; c, endopod of left maxilliped 3, internal surface; d, pereopod 3, external surface; e, pereopod 4, external surface; f, pereopod 5, external surface; g, abdominal somite 6, telson and uropods, dorsal surface. Scale bars indicate 2.0 mm.

almost to midlength of rostrum (Fig. 1a, b, c). Cornea terminal, slightly globose, diameter equal to or slightly exceeding that of eyestalk.

Antennular peduncle reaching well beyond rostrum (Fig. 1b). Antennal peduncle bearing produced nephridiopore proximoventrally, second article bearing dorsodistal spine overreaching much of acicle, acicle short, not bifid, overreaching proximal third of penultimate (fourth) peduncular article, third peduncular article distally bearing strong ventromesial spine. Maxilliped 3 basis bearing short, acute mesial spine (Fig. 2b); ischium of endopod with strong, distally elevated crista dentata on internal surface, bearing about 16 spines, distalmost of

which are largest and most strongly directed mesiad (Fig. 2c); merus with two mesial spines, one near or just short of midlength, the other larger and in distal third; carpus with short triangular tooth at distal extreme of flexor margin; all articles of endopods bearing fields of long setae, many dense and heavily plumose, especially on mesiad and internal surfaces.

Pereopods 1-4 bearing epipods. Pereopods 2-4 with pleurobranches above coxae (on thoracic somites 5-7).

Chelipeds (pereopod 1) similar in form and ornamentation on the 2 sides, right the heaviest (Fig. 1a, d); ischium with single well-defined spine on inferior margin; merus with single flattened spine near mid-

length of inferior margin, which is weakly marked by adjacent sinuation or serration, distal corner of flexor margin on external side forming short, heavy raised spine (Fig. 1a); carpus very short, bearing numerous patches of long setae on external surface, dorsal margin weakly tuberculate, terminating distally in blunt tooth, ventral carina of external surface forming flange distally which terminates in flattened, weakly hooked tooth; propodus very thick and heavily calcified, lacking well-defined teeth on weakly tuberculate dorsal margin, bearing numerous patches of long setae on external surface, including among tubercles of dorsal surface, along well-marked carina of ventral margin, below cutting edge of fixed finger, and proximal to gape, external surface proximal to dactylus with scattered low tubercles and granules, fixed finger bearing two erect teeth on proximal half and single less erect tooth in distal half, terminus spiniform, internal surface with weak carina adjacent to and slightly below cutting edge; movable finger very thick and heavy, with dense patches of long setae externally and dorsally, cutting edge bearing rounded to lobiform tooth in proximal third, broad ill-defined tooth or sinuous lobe in distal two-thirds, terminus weakly hooked and subacute, a carina above cutting edge on internal surface. Pereopod 2 (Fig. 1e) merus lacking marginal spines, combined length of ischium and merus about equal to combined length of carpus and propodus, length of dactyl about half total length of propodus, opposable cutting edges of fingers corneous, finely pectinate, distinctly spooned distally. Pereopod 3 (Fig. 2d) merus lacking marginal spines, external surface of propodus bearing five sets of corneous spiniform setae, set individually or in short transverse rows of two or three near inferior margin, fewer sets and few such setae near superior margin, falcate dactylus with three distinct corneous spiniform setae on external surface, distally with two more very small ones set near flexor margin, and a sharp corneous spine forming terminus. Pe-

reopod 4 (Fig. 2e) merus lacking marginal spines, external surface of propodus bearing six sets of corneous spiniform setae, set individually or in transverse rows of two to four near inferior margin, four such sets of one to three setae near superior margin, falcate dactylus with five distinct corneous spiniform setae on external surface, distally with additional very small corneous seta, sharp corneous spine forming terminus. Pereopod 5 (Fig. 2f) merus and propodus lacking marginal spines, propodus bearing stiff bristles at distal inferior end of propodus, concealed by dense distal fields of setae; lanceolate dactylus twisted laterally, opposed to terminal bristles of propodus when flexed.

Pleopod 1 absent, posterior pleopods all bearing dense cover of long, plumose, heavily fouled setae; appendix interna present on pleopods 2-5. Uropodal exopod (Fig. 2g) bearing four spines along external margin and an articulated spine where this margin meets the transverse suture, five additional spines along transverse suture, and no spines on dorsal surface, long setae forming dense fringe on margins, but on dorsal surface limited to few patches near external margin; endopod with single strong spine at distal end of external margin and another small spine overreaching distal margin at end of weak median ridge, long setae forming dense fringe on margins, and distributed in patches on dorsal surface near external margin and along medial ridge. Telson length distinctly greater than its basal width, tapering toward posterior, widest at lateral lobes in proximal one-quarter of length, single pair of strong fixed dorsal spines in anterior half, two to four fixed marginal serrations or spines posterior to proximal lobes, and two pairs of short, articulated marginal spines in distal third of lateral margins, distal margin evenly convex, densely setose.

Variations.—Paratype: Spination and tuberculation in the exuvia of this larger specimen differ in several minor ways from ornamentation in the holotype. There are few-

er spines on the margin of the rostrum, as the supraoculars are not present. The margin of the rostrum is somewhat broadly concave in this region on the paratype, although it retains an overall triangular shape. Dorsal tuberculation of the propodal palm is less evident than in the holotype. Spines on the cutting edge of the major chela differ slightly in shape from those on the holotype, but the pattern and placement of this spination is conserved (Fig. 1f). Granulation on the internal surface of the propodus in the paratype is stronger than that in the holotype. The external margin of the uropodal exopod in the paratype male bears five rather than four fixed spines, while the external margin of the endopod bears three spines rather than a single one. Lateral margins the telson bear up to five serrations or fixed lateral spines in the paratype, and the pairs of articulated marginal spines are relatively smaller than in the holotype and very difficult to discern. Small angular, acute corners or teeth on the anteroventral margins of abdominal pleurae 3–5 are also more difficult to discern in the holotype. These appear to be somewhat worn or smoothed off in the paratype, although the acute posteroventral margins remain readily evident.

Etymology.—The species is named for Robert S. Carney, Louisiana State University, Baton Rouge, who oversaw collections of the specimens and made these materials available for our study. His own work on hydrocarbon vent communities of the Gulf of Mexico (see Carney 1994) has brought needed attention to these remarkable assemblages of marine organisms.

Remarks.—Ten species were listed in a recent review of *Calaxius* by Kensley & Hickman (2001). The present description accounts for the eleventh known member and only the second species to be found in the Atlantic Ocean. There seems little doubt as to the generic placement of this new species, given the dentate rostrum twice as long as the eyestalks, the dentate carapace carinae, the transverse suture on the uro-

podal exopod, presence of pereopodal epipods and pleurobranchs, the absence of pleopod 1 in the male, and the presence of appendices internae on pleopods 2–5 (see Poore 1994:97). The specimens lack strong dentition on the dorsal surface of the first chelipeds, as seen in *Acanthaxius* Sakai & de Saint Laurent, 1989, which they somewhat resemble.

In contrast to the known congeners and the original generic definition (Sakai and de Saint Laurent 1989:84), the rostrum of *C. carneyi* is heavier and more broadly triangular, the eyestalks and antennal acicle are comparatively shorter, and the palm of the cheliped lacks well-separated and defined teeth dorsally, having at most a covering of low tubercles, and the telson is distinctly narrowed posteriorly or subtriangular. The abdominal pleura of *C. carneyi* resemble neither the acutely triangular plates seen in four other previously described species nor the broadly rounded plates seen in five other species; rather, pleura 3–5 are ventrally truncate with small anterior and posterior marginal denticles.

The only species of *Calaxius* previously reported from the broad geographic area of the Gulf of Mexico and contiguous regions is *C. oxyleura* (Williams, 1974), recorded from the Straits of Florida. This species has abdominal pleura 3–5 ventrally angular or acute, rather than truncate, and a narrow dentate rostrum unlike that of *C. carneyi*.

Ecology.—A dense cover of flocculent materials on plumose setae of both the holotype and paratype exuvia (much of which has disintegrated over time in alcohol, or which was brushed free in the course of morphological studies) may derive from the unique environments inhabited by these animals, but nothing is known of the burrow structure or feeding behavior. The flocculent coatings on the axiid setae could be a passive result of these animals' trophic ties to members of the chemosynthetic community, at a primary or secondary consumer level. Accumulations of mussels and worms near hydrocarbon seeps in the north-

ern Gulf of Mexico do in varied ways depend upon methanotrophic or sulfur-oxidizing bacteria for metabolic resources (see Van Dover 2000:363–366). These bacteria occur in animal tissues as endosymbiotic cells or as scattered mats immediately surrounding the seeps. They may directly exploit methane as both a carbon and energy source or, much as in hydrothermal vent environments, directly oxidize rich cold-seep sources of sulfides for metabolic energy. Precipitates and bacteria might simply accumulate on or among the setules of highly plumose setae, perhaps as these axiids move about or ventilate burrows in these matted settings. While the flocculent materials could simply mask movements among bacterial mats or mussel communities, we cannot rule out that the axiids themselves may directly consume accumulations of chemosynthetic bacteria, either by accessing exposed mats or undertaking behaviors that favor the forming of such accumulations within and along walls of their burrows. It is suspected that other thalassinideans engage in burrow-modulated feeding behaviors that are microbially based, albeit in reduced interstitial waters of shallow hypoxic environments (Felder 2001) where at least one species lives in apparent association with lucinid bivalves harboring chemosynthetic gill bacteria.

Even if *C. carneyi* could be shown to depend upon the chemosynthetic community as a nutritional resource, perhaps by stable isotope measurements, this would not necessarily confirm its restriction to occurrence with chemosynthetic communities of hydrocarbon seeps. As has recently been reported for infaunal worms associated with methane seeps off California (Levin et al. 2000), infaunal thalassinideans are also likely pre-adapted to organic-rich, reducing environments, and may in fact be widely distributed forms that do not strictly exhibit chemosynthesis-based trophic specializations. Owing to very limited general sampling for infaunal macrocrustaceans from slope environments in the Gulf of Mexico

to date, its occurrence in sediments other than those near cold seeps cannot be ruled out.

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Description of a new *Synidotea* species (Crustacea: Isopoda: Valvifera: Idoteidae) from Hawaii

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Abstract.—This paper provides the first description of a Hawaiian isopod of the genus *Synidotea*, *S. oahu* n. sp. This species is most similar to *S. laeviodorsalis* (Miers, 1881) and *S. harfordi* Benedict, 1897. A list of *Synidotea* species described to date with biogeographic information, and a list of all marine isopods described from the Hawaiian Islands, are provided.

This paper provides the first description of a *Synidotea* species from the Hawaiian Islands. The isopod genus *Synidotea* Harger, 1878 currently contains 57 species, including the species herein described (see Table 1). The following characters define this genus: penes fused forming penial plate, fifth oostegites absent, and sexually dimorphic mouthparts (Poore 2001). In addition, *Synidotea* species possess the following combination of characters: antennae 2 flagellum multiarticulate, maxillipedal palp triarticulate, pleon with one partial suture, pereonites 2–4 coxal plates not visible in dorsal aspect and (unlike most other valviferan genera) pereonites 5–7 tergite-coxal plate sutures can be either present or absent.

The Californian species of *Synidotea* were reviewed by Menzies & Miller (1972), who also included a biogeographic account of the genus that, at the time, contained 36 species. The phylogeny and biogeography of the 22 idoteid genera, including *Synidotea*, were discussed by Brusca (1984). Poore (2001) redefined and inferred the phylogeny of the families within the Valvifera.

Most *Synidotea* species occur in the Arctic and in boreal waters (39 of the 57 described species); 13 species have been described from tropical/subtropical waters. To date, only one other *Synidotea* species has been described from the islands of the trop-

ical Pacific, *S. pacifica* Nobili, 1906 from the Tuamotu Islands. *Synidotea oahu* n. sp. is one of only 29 marine isopods known from the Hawaiian islands (see Table 2). The only other known Hawaiian valviferan is *Colidotea edmondsoni* Miller, 1940.

Nine species in this genus belong to the *Synidotea hirtipes* species-group (Monod 1931, Menzies & Miller 1972): *S. hirtipes* (H. Milne Edwards, 1840), *S. laeviodorsalis* (Miers, 1881), *S. laticauda* Benedict, 1897, *S. harfordi* Benedict, 1897, *S. marplatensis* Giambiagi, 1922, *S. brunnea* Pires & Moreira, 1975, *S. keablei* Poore & Lew Ton, 1993, *S. grisea* Poore & Lew Ton, 1993, and *S. oahu* n. sp. Members of the *S. hirtipes* species-group share the following distinguishing characters: pereon smooth, frontal margin of head entire or slightly excavate, and posterior border of pleotelson with median excavation. Because *S. oahu* n. sp. possesses these characters I herein consider it a member of this group. Species boundaries within the *S. hirtipes* group have been disputed in the literature. Chapman & Carlton (1991, 1994) argued that *S. laeviodorsalis* is a widespread species, which has been widely introduced to many coastlines from Japan by the shipping industry. Chapman & Carlton (1991, 1994) have thus suggested the synonymy of seven of the nine species within this group. However, their taxonomic justification for the synonymies



Fig. 1. Holotype, dorsal view.

was weak, based entirely on an analysis of length-width ratios of various body parts of the dorsal aspect of these species. Poore (1996) refuted the synonyms; through careful comparison of the pleotelson, penial plate and pereopod 1, he clearly demonstrated that the populations described from various Indo-Pacific coastlines represent valid and separate species. He also noted that the species boundaries are further sup-

ported by different ecological distributions of the species in this group. This case underscores the importance of detailed, accurate taxonomy in the pursuit of successfully identifying translocated species. Taxonomists are accustomed to the challenging task of recognizing species boundaries within groups that contain many similar species; oftentimes differences between species, although solid and obvious once made explicit, are not apparent to the untrained eye.

Order Isopoda Latreille, 1817

Suborder Valvifera Sars, 1882

Family Idoteidae Samouelle, 1819

Genus *Synidotea* Harger, 1878

Synidotea oahu, new species

Figs. 1–6

Type material examined.—Holotype, ovigerous female, USNM 1009176. Hawaii: Oahu Is., 0.8 km from town of Kailua, collected from small batches of seaweed by Ray Greenfield, August 20, 1950. Paratype, female, USNM 99384. Hawaii: Oahu Is., Ewa Beach, 32 km from Honolulu, collected from seaweed by Ray Greenfield, August 1, 1954.

Etymology.—The specific epithet *oahu* derives from the poetic vowel-rich Hawaiian language, providing this binomen, *Synidotea oahu*, with every vowel in the English alphabet. In Hawaiian, *oahu* means “the gathering place.” Oahu is also the name of the second largest island in the Hawaiian archipelago and the type locality of this species. This word is used here as a noun in apposition.

Diagnosis.—Cephalon dorsal surface with a weak, transverse depression in front of eyes. Pereonites 1–7 with mesial, broadly rounded grooves on dorsal surface. Maxilla 1 mesial lobe with two unique, stout, distally-serrate robust setae with mesial setules. Mandibles (both right and left) with four-toothed incisors and four-toothed lacinia mobili with additional large serrate spine-like process. Ratio of head width to

Table 1.—Described species in the genus *Synidotea* Hager, 1878.

Species and author	Biogeographic region	Ocean (recorded distribution)	Depth (meters)
<i>S. angulata</i> Benedict, 1897	Boreal	NE Pacific (British Columbia to California)	6-117
<i>S. bathyalis</i> Gurjanova, 1955	Arctic, Boreal	Arctic Sea, NW Pacific	196-430
<i>S. berolzheimeri</i> Menzies & Miller, 1972	Boreal	NE Pacific (California)	intertidal
<i>S. bicuspida</i> (Owen, 1839)	Arctic, Boreal	NE Pacific (Bering Sea, Alaska), Arctic, N Atlantic (Labrador)	6-250
<i>S. birseini</i> Kussakin, 1971	Boreal	NW Pacific	910-2820
<i>S. bogorovi</i> Gurjanova, 1955	Arctic, Boreal	NW Pacific (Sea of Okhotsk)	2300
<i>S. brazhnikovi</i> Gurjanova, 1933	Arctic	NW Pacific (Sea of Japan)	5-25
<i>S. brunnea</i> Pires & Moreira, 1975	Tropical	SW Atlantic (Brazil)	intertidal
<i>S. calcarata</i> Schultz, 1966	Warm Temperate	NE Pacific (S California)	813
<i>S. cinerea</i> Gurjanova, 1933	Arctic	NW Pacific (Sea of Okhotsk)	12-22
<i>S. consolidata</i> (Stimpson, 1857)	Boreal	NE Pacific (Alaska to California)	intertidal-20
<i>S. cornuta</i> Rafn & Laubitz, 1990	Boreal	NE Pacific (British Columbia)	intertidal
<i>S. epimerata</i> Richardson, 1909	Arctic	NW Pacific (Sea of Okhotsk)	20-80
<i>S. erosa</i> Benedict, 1897	Boreal	NE Pacific (Alaska)	869
<i>S. ezoensis</i> Nunomura, 1991	Boreal	NW Pacific (Japan)	intertidal
<i>S. fecunda</i> Javed & Yasmeen, 1994	Tropical	Indian (Pakistan)	intertidal
<i>S. fluvialilis</i> Pillai, 1954	Tropical	Indian (India; Chulka Lae, Quillon, Cochín)	esuarine
<i>S. francesae</i> Brusca, 1983	Subtropical	NE Pacific (upper Gulf of California)	intertidal
<i>S. grisea</i> Poore & Lew Ton, 1993	Warm Temperate	SW Pacific (New South Wales, Victoria)	7-10
<i>S. hanumantharaoi</i> Kumari & Shiyamasundari, 1983	Tropical	Indian (India)	intertidal
<i>S. hafordii</i> Benedict, 1897	Boreal/Warm Temperate	NW Pacific (Sea of Japan), NE Pacific (S California, Baja California)	intertidal-12
<i>S. hikigawaensis</i> Nunomura, 1974	Boreal	NW Pacific (Japan, Korea)	3-4
<i>S. hirripes</i> (H. Milne Edwards, 1840)	Tropical/Warm Temperate	SE Atlantic (S Africa, Namibia), Indian (Red Sea)	5-200
<i>S. indica</i> Javed & Yasmeen, 1994	Tropical	Indian (Pakistan)	intertidal
<i>S. ishmarui</i> Nunomura, 1991	Boreal	NW Pacific (Japan)	intertidal
<i>S. keablet</i> Poore & Lew Ton, 1993	Warm Temperate	SW Pacific (New South Wales)	8-18
<i>S. laeviodorsalis</i> (Miers, 1881)	Boreal	NW Pacific (Japan)	15-17
<i>S. laevis</i> Benedict, 1897	Boreal	NE Pacific (Alaska)	52-66
<i>S. lata</i> Gurjanova, 1933	Boreal	NW Pacific	intertidal-20
<i>S. laticauda</i> Benedict, 1897	Boreal	NE Pacific (California, Washington)	intertidal-12.5
<i>S. littoralis</i> Pires & Moreira, 1975	Tropical	SW Atlantic (Brazil)	intertidal
<i>S. longicirra</i> Gurjanova, 1933	Arctic	NW Pacific (Sea of Okhotsk)	30-141

Table 1.—Continued.

	Species and author	Biogeographic region	Ocean (recorded distribution)	Depth (meters)
	<i>S. magnifica</i> Menzies & Barnard, 1959	Boreal	NE Pacific (California)	55–91
	<i>S. marmorata</i> (Packard, 1867)	Boreal	N Atlantic (Labrador)	14–360
	<i>S. marplatensis</i> Giambiagi, 1922	Tropical	S Atlantic (S Brazil, Argentina)	intertidal–30
	<i>S. media</i> Iverson, 1972	Boreal	NE Pacific (California)	183
	<i>S. minuta</i> Rafi & Laubitz, 1990	Boreal	NE Pacific (British Columbia)	intertidal
	<i>S. muricata</i> (Harford, 1877)	Arctic, Boreal	N Pacific (Bering Sea)	45–150
	<i>S. nebulosa</i> Benedict, 1897	Boreal	NE Pacific (Alaska)	intertidal–380
	<i>S. neglecta</i> Birstein, 1963	Boreal	NW Pacific	1693
	<i>S. nipponensis</i> Nunomura, 1985	Boreal	NW Pacific (Japan; Toyama Bay)	?
	<i>S. nodulosa</i> (Kroyer, 1846)	Arctic, Boreal	NE Pacific (Alaska, British Columbia), NW Pacific (Sea of Okhotsk), Arctic, N Atlantic (Greenland)	5–343
	<i>S. oahu</i> n. sp.	Subtropical	Central Tropical Pacific (Hawaii: Oahu Is.)	intertidal
	<i>S. otsuchiensis</i> Nunomura, 1985	Boreal	NW Pacific (Japan)	shallow
	<i>S. pacifica</i> Nobili, 1906	Tropical	Central Tropical Pacific (Tuamotu Is.)	?
	<i>S. pallida</i> Benedict, 1897	Boreal	NE Pacific (Alaska)	1380–1641
	<i>S. pettiboneae</i> Hatch, 1947	Boreal	NE Pacific (British Columbia, Washington)	intertidal–55
	<i>S. picta</i> Benedict, 1897	Boreal	NE Pacific (Alaska)	10–40
	<i>S. pulchra</i> Birstein, 1963	Boreal	NW Pacific	2887–2917
	<i>S. ritteri</i> Richardson, 1904	Boreal	NE Pacific (California)	intertidal
	<i>S. sculpita</i> Gurjanova, 1955	Arctic	NW Pacific (Sea of Okhotsk)	60–284
	<i>S. setifer</i> Barnard, 1914	Tropical	SW Indian (S. Africa)	7–80
	<i>S. submarmorata</i> Kussakin & Mezhev, 1979	Boreal	NW Pacific (Russia: Kurile Is.)	50–425
	<i>S. tuberculata</i> Richardson, 1909	Arctic	NW Pacific (Sea of Okhotsk)	120–135
	<i>S. variegata</i> Collinge, 1917	Tropical	Indian (India, Sri Lanka), SW Indian (South Africa, Mozambique, Madagascar)	1–20
	<i>S. watsonae</i> Poore & Lew Ton, 1993	Subantarctic	Southern Ocean (W. Australia, Victoria)	7–35
	<i>S. worlensis</i> Joshi & Bal, 1959	Tropical	Indian (India: Bombay)	intertidal

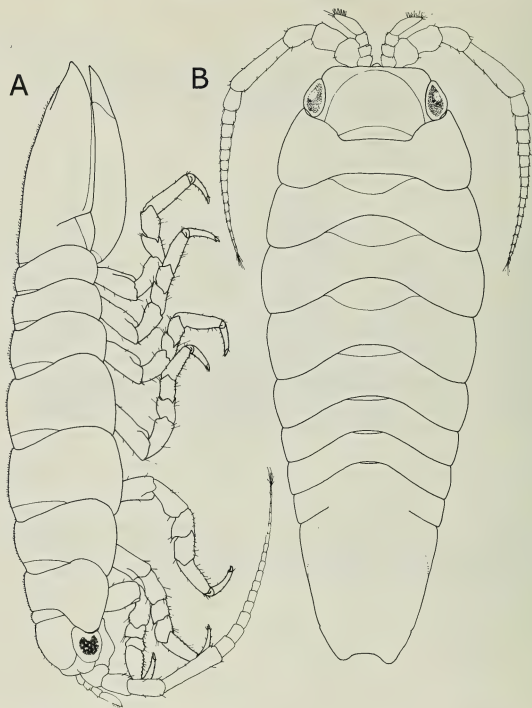


Fig. 2. Paratype. A, lateral view; B, dorsal view.

pereonite 4 width is 0.69. Pleotelson (fused pleonites and telson) 1.26 times longer than wide (measured along lateral margin, from posterior margin of coxa of pereonite 7 to distal-most tip of telson).

Description.—Body length: ovigerous female holotype, 8 mm, non-ovigerous fe-

male paratype, 7.5 mm. Body yellowish tan in alcohol.

Cephalon dorsal surface with a weak, transverse depression in front of eyes. Frontal margin straight. Eyes bulge outward, forming part of contour of lateral margin of head. Ratio of head width to pereonite 4

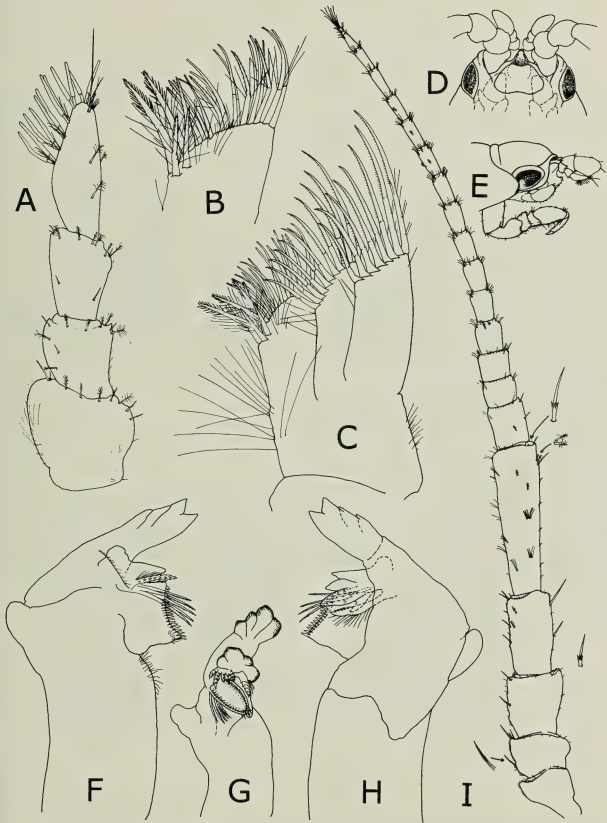


Fig. 3. Holotype. A, right antenna 1; B, left maxilla 2 close-up of inner lobe; C, left maxilla 2; D, head, ventral view; E, head, lateral view; F, left mandible, dorsal view; G, left mandible, mesial view; H, left mandible, ventral view, I, right antenna 2.

Table 2.—A list of all marine isopods reported to occur in the waters surrounding the Hawaiian Islands.

Suborder family	Species and author	Recorded distribution
ANTHURIDEA		
Anthuridae	<i>Amakusanthura inornata</i> (Miller & Menzies, 1952)	Hawaiian Islands
	<i>Mexanthura hieroglyphica</i> Miller & Menzies, 1952	Hawaiian Islands
Paranthuridae	<i>Paranthura bellicauda</i> Miller Menzies, 1952	Hawaiian Islands
	<i>Paranthura ostergaardi</i> Miller & Menzies, 1952	Hawaiian Islands
ASELLOTA		
Janiridae	<i>Caecijaera horvathi</i> Menzies, 1951	Hawaiian Islands, California, Cuba, Thailand
	<i>Carpis atgicola</i> (Miller, 1941)	Hawaiian Islands, Caribbean, Gulf of Mexico, India, Aldabra Atoll Comoro Is., Red Sea, Mauritius
	<i>Hawaianira peleae</i> Miller, 1967	Hawaiian Islands
Joeropsidae	<i>Joeropsis hawaiiensis</i> Miller, 1941	Hawaiian Islands
Munnidae	<i>Uromunna acarina</i> (Miller, 1941)	Hawaiian Islands
Steneriidae	<i>Hansenium medipacificum</i> (Miller, 1941)	Hawaiian Islands
EPICARIDEA		
Bopyridae	<i>Enophilus omnitectus</i> Richardson, 1903	Hawaiian Islands, Madagascar
	<i>Gigantione hawaiiensis</i> Danforth, 1967	Hawaiian Islands
	<i>Ionella murchisoni</i> Danforth, 1970	Hawaiian Islands
	<i>Scyraepon hawaiiensis</i> Richardson, 1910	Hawaiian Islands
Cryptoniscidae	<i>Faba glabra</i> Nierstrasz Brener a Brandis, 1930	Hawaiian Islands
Dajidae	<i>Zonophryxus retrodens</i> Richardson, 1903	Hawaiian Islands
FLABELLIFERA		
Aegidae	<i>Aega deshayesiana</i> (H. Milne Edwards, 1840)	Hawaiian Islands, Pacific Costa Rica, Japan, Cape Verde, Tristan da Cunha, NW Africa, Seychelles, Azores, Antilles Is., Mediterranean
	<i>Aega quadratistinus</i> Richardson, 1903	Hawaiian Islands
	<i>Rocinela hawaiiensis</i> Richardson, 1904	Hawaiian Islands
Cymothoidae	<i>Creniela breviceps</i> (Schioedte & Meinert, 1881)	Hawaiian Islands
	<i>Cymothoa recta</i> Dana, 1853	Hawaiian Islands
	<i>Glossobius anctus</i> Bruce & Bowman, 1989	Hawaiian Islands, W Australia, Queensland, Japan
	<i>Ichthyoxenus puihi</i> (Bowman, 1962)	Hawaiian Islands
	<i>Mothocya melanosticta</i> (Schioedte & Meinert, 1884)	Hawaiian Islands, S Australia, Japan, Mozambique, S Africa, Red Sea

Table 2.—Continued.

Suborder family	Species and author	Recorded distribution
Linnoriidae	<i>Paralimnoria andrewsi</i> (Calman, 1910)	Hawaiian Islands, Samoa, Japan, Christmas Is., Andaman Is., Aldabra Atoll, Caribbean
Sphaeromatidae	<i>Cymodocella hawaiiensis</i> Bruce, 1994 <i>Neonaesa rugosa</i> Harrison & Holdich, 1982	Hawaiian Islands Hawaiian Islands, Society Islands, New Guinea, Queensland
VALVIFERA		
Idoteidae	<i>Colidotea edmondsoni</i> Miller, 1940 <i>Synidotea oahu</i> n. sp.	Hawaiian Islands Hawaiian Islands

width is 0.69. Antenna 1 with triarticulate peduncle and uniaarticulate flagellum with six pairs of jointed aesthetascs. Antennae 2 extended to third pereonite; with five-articulate peduncle, article 5 at least twice as long as any other peduncular article; flagellum with 15–17 articles, terminal two articles very small.

Maxilliped with a triarticulate maxillipedal palp, single coupling hook on the left maxilliped only (holotype). The paratype has one coupling hook on both left and right maxilliped. Maxilla 1 mesial lobe with two stout distally-serrate robust setae with mesial setules; lateral lobe with ten serrate robust setae and many simple setae along lateral and mesial margins. Maxilla 2 with plumose, simple and comb setae as figured. Mandibles with four-toothed incisors and large molar processes with short spines surrounding margins. Lacinia mobilis of left and right mandible four-toothed with an additional large serrate spine-like process.

Pereonites 1–7 with mesial, broadly rounded grooves on dorsal surface, otherwise dorsal surface and lateral margins smooth, without rugae, tubercles, or scales. Pereonite 3 widest. Lateral margins of pereonite 1–3 evenly convex, 4–7 straighter but not sharply angulate. Pereopods setose. Pereopod 1 with dactyl as long as propodus; two stout setae arise from base of unguis; distal lateral surface of propodus covered with serrate setae. Pereopods 2–7 with setation patterns as figured.

Pleotelson 1.26 times longer than wide; dorsal surface evenly convex; posterior border with median excavation. Pleopods 1 and 2 with plumose marginal setae on endopods and exopods, both rami without sutures. Pleopods 1–3 with coupling setae on mesial margin of peduncle. Pleopods 3–5 with plumose marginal setae on exopods only; the number of setae decrease from pleopods 3 to pleopods 5; exopods with partial sutures on lateral margins, Uropod with an oblique ridge and 3 plumose setae at mesial junction of protopod and exopod. Uropod exopod length to width ratio is 0.96.

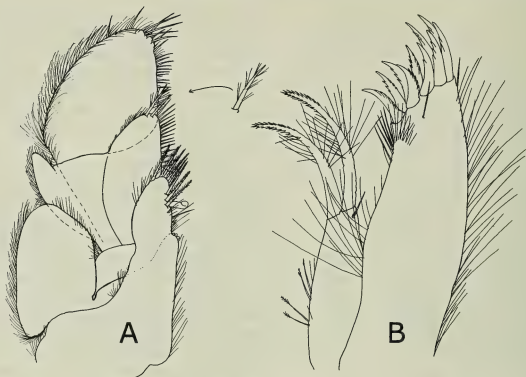


Fig. 4. Holotype. A, left maxilliped; B, left maxilla 1.

Discussion.—*Synidotea oahu* males are unknown. This species superficially resembles other members of the *S. hirtipes* species-group, particularly *S. laevidorsalis* and the widely distributed species *S. harfordi*. These three species are possibly closely related, however, a phylogenetic analysis of this large genus is needed to test this hypothesis.

Synidotea oahu differs from *S. harfordi* and *S. laevidorsalis* most strikingly in its smaller body size (*S. oahu*, 7.5–8.0 mm; *S. laevidorsalis*, 12.3–35 mm, *S. harfordi*, 18 mm). Menzies & Miller (1972) noted that *Synidotea* species follow a general trend of increasing body size with increasing latitude. Wallerstein & Brusca (1982) showed the same trend for all intertidal isopods occurring in the northeast Pacific. Species within *Synidotea* range in length from the 3 mm tropical Pacific *S. pacifica*, to the 32 mm *S. bicuspidata* and 35 mm *S. laevidorsalis* from Arctic and boreal waters. *Synidotea oahu* fits this pattern, with a body size

of 7.5–8 mm, the average body size for tropical *Synidotea* (Menzies & Miller 1972).

S. oahu also differs from other members of the *S. hirtipes* species-group in the following characters: *S. oahu* has unique stout distally-serrate robust setae with mesial setules on the mesial lobe of maxilla 1 and a four-toothed mandibular incisor, whereas *S. harfordi* and *S. laticauda* both have a two-toothed mandibular incisor. *Synidotea oahu* also differs from *S. harfordi* in its broadly rounded median dorsal impressed lines on pereonites 2–4, whereas in *S. harfordi* these lines are distinctly triangulate. Also, the dactyl of pereopod 1 in *S. oahu* is nearly as long as the propodus, whereas in *S. harfordi* it is much longer than the propodus.

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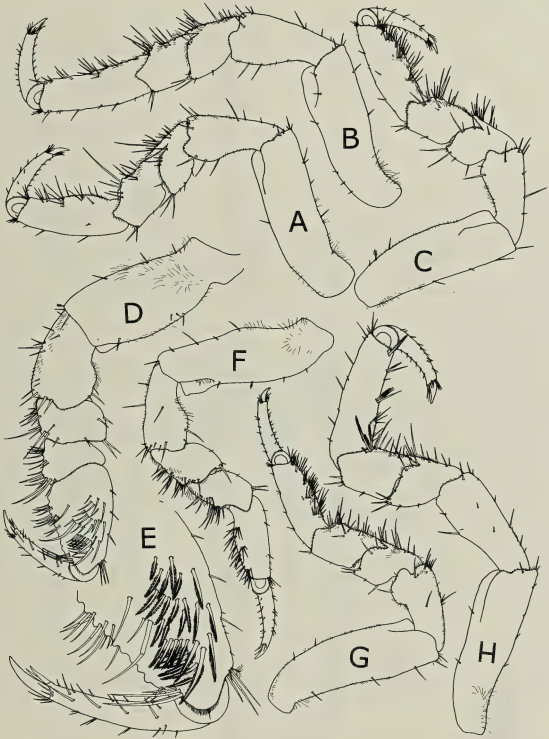


Fig. 5. Holotype. A, right pereopod 5; B, right pereopod 7; C, right pereopod 6; D, right pereopod 1; E, right pereopod 1, close-up of propodus and dactyl; F, right pereopod 2; G, right pereopod 3; H, right pereopod 4.

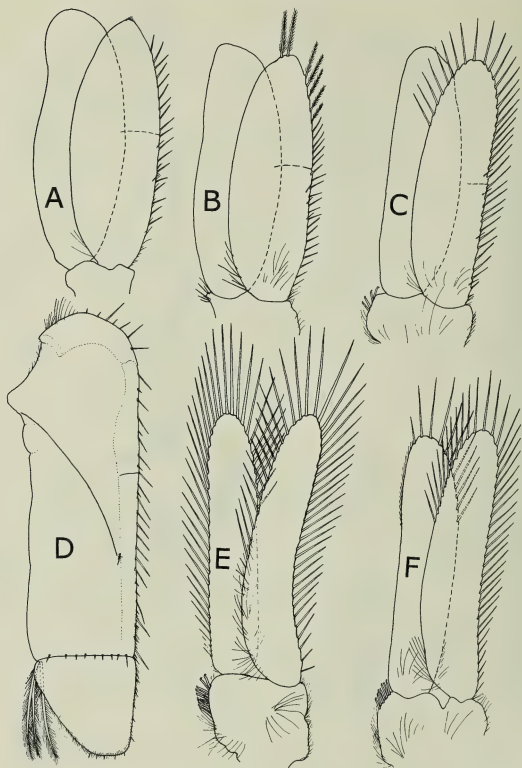


Fig. 6. Holotype, A, right pleopod 5; B, right pleopod 4; C, right pleopod 3; D, right uropod; E, right pleopod 1; F, right pleopod 2.

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A new species of *Synidotea* (Crustacea: Isopoda: Valvifera) from the northern Gulf of Mexico

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Abstract.—*Synidotea fosteri*, n. sp., the sixth known member of the genus *Synidotea* from the western Atlantic Ocean, is described from shallow waters (1–2 m) adjacent to open beaches in the northern Gulf of Mexico. Its current range extends from western Florida westward to Texas. The new species is distinguished from other related species by small size, fairly straight lateral margins of first pereonite, having the posterior margin of pleotelson straight to very slightly emarginate and by details of the appendix masculina. A key to the known western Atlantic species of the genus *Synidotea* is also given.

Introduction

The presence of an undescribed species belonging to the valviferan genus *Synidotea* has been known from the Gulf of Mexico for over 20 years. Although there are only two published records listed as “*Synidotea* sp.” and “*Synidotea* sp. A” from Texas and Florida, respectively (Clark & Robertson 1982, Rakocinski et al. 1996), it has also been observed in beach habitats at Grand Island, Louisiana and Gulf Shores, Alabama (R. Heard, pers. obs.). More recent collections of *Synidotea* made near Panama City, Florida, have made possible the determination of a new species, which is the subject of this report. In the most recent discussion of the 56 nominal world species of *Synidotea*, Poore (1996) lists the relevant characters used to differentiate several species in this genus which closely resemble *S. laevidorsalis* (Miers, 1881), as does the present new species.

Family Idoteidae Samouelle, 1819

Genus *Synidotea* Harger, 1878

Synidotea Harger, 1878:374; Richardson, 1905:376; Rafi and Laubitz, 1990:2672; Poore and Lew Ton, 1993:261–262.

Diagnosis.—Body about twice as long as wide, integument sometimes setose or with sculpturing; cephalon narrower than pereonite 1; body width greatest at pereonite 4. Pleon lacking articulating pleonites, pleonite 1 indicated by single, small ventrolateral suture; apex acute, rounded or excavate. Antenna 2 multiarticulate. Mandible with secondary tooth on lacinia mobilis. Maxillipedal palp, with articles 2 and 3 fused, 4 and 5 also fused. Coxae 2–4 without dorsal coxal plates; coxae 5–7 with expanded dorsal plates. Penes fused completely and swollen distally, attached to posterior margin of pleonite 1. Oostegites forming brood-pouch on pereonites 1–4.

Key to the Species of *Synidotea* from the Western Atlantic Region

- 1a. Pleotelson tapers to narrowly rounded, produced apex *S. nodulosa*
- 1b. Pleotelson faintly to deeply emarginate at apex, not produced 2
- 2a. Cephalon bearing two convexities separated by narrow groove and 2 small, medial tubercles anteriorly; lateral margins of pereonites 1–4 angular
..... *S. littoralis*

- 2b. Cephalon smooth, lacking sculpturing; lateral margins of pereonites not angular 3
- 3a. Lateral margins of pleotelson almost parallel for first 2/3 of length; angled medially in distal one-third with broad, shallow emargination on distal margin *S. brunnea*
- 3b. Lateral and distal margins of pleotelson not as above 4
- 4a. Cephalon with deep medial notch; pleotelson tapering to very narrow, emarginate apex *S. marmorata*
- 4b. Cephalon without deep medial notch, faintly emarginate at most; pleotelson not tapering to narrow apex 5
- 5a. Antennal flagellum with 13–20 articles; body length of mature male ca. 12.5 mm; appendix masculina of male not extending beyond apex of endopod of pleopod 2 *S. marplatensis*
- 5b. Antennal flagellum with 7–8 articles; body length of mature male ca. 4.2 mm; appendix masculina extending beyond apex of endopod of pleopod 2 *S. fosteri* n.sp.

Synidotea fosteri, n. sp.

Figs. 1, 2

Synidotea sp. Clark & Robertson, 1982:46 (key), 49–50 (Table & Text), 57 (Fig. 5); Rakocinski, et al. 1996:351 (Table).

Material examined.—Holotype male USNM 1022910, TL 6.5 mm, from sea grass clumps (origin unknown) in surf/swash zone, “Bid-a-wee” Beach, Panama City Beach, Florida, 30°12.2'N, 085°52.5'W, sal. 34 ppt., coll. R. Heard and J. Foster, 23 Nov 1996; Allotype female USNM 1022911, TL 6.0 mm, same data. Paratypes: 7 males, 6 ovig. females, 53 females, 1 juv., USNM 1022912, same locality data.

Other material: 1 male, 7 ovig. females, 2 females, 2 juvs., open gulf off Santa Rosa Beach, northwest Florida, 1–1.5 m, coarse sand with detritus, *Sargassum* and algae, coll. R. Heard, 15 July 1991.

Description.—Male: body length 2.7

times greatest width (at pereonite 3) with minutely spinulose integument (Figs. 3C, D) and faint dorsolateral sculpturing on all tergites. Cephalon with faint curved anterior groove above slight dome and faint lateral grooves, transverse posterior groove deeper; anterior margin of cephalon straight, sometimes with minute medial emargination. Width of head to width of pereonite 4 ratio 0.79. Eyes prominent. Lateral angles of first pereonite nearly straight; lateral angles of pereonites 2–4 convex and 5–7 nearly straight, making continuous margin. Lunette on pereonites 2–4 with broadly rounded posterior margin. Coxal plates not discernible dorsally. Sutures separating tergites from coxae faintly visible on tergites 2–4. Pleotelson length to width ratio 1.29; length of pleotelson 0.32 times body length, lateral margins tapering slightly to broad apex with straight or very slightly emarginate posterior margin. Uropodal peduncle with single, oblique ridge; length to width ratio of exopod 0.94, with curve between lateral margin and truncate apex.

Antenna 1 with 4 articles, terminal article bearing aesthetascs; antenna 2, single distal plumose seta on 5th peduncle article; flagellum with 8 articles. Mouthparts typical of genus, with secondary tooth noted on lacinia mobilis of mandible.

Pereopod 1, palmate propodus bearing many pectinate spine-like setae; end of dactyl reaching carpus-merus suture. Pereopods 2–4 similar with posterior margins of propodi, carpi, and meri bearing several long and short simple setae. Pereopod 7 with spine-like setae, some pectinate on anterodistal margins of propodus, carpus and merus. Pereopods lacking dense pads of setae.

Pleopod 1, peduncle with 5 coupling hooks, 23 and 25 plumose marginal setae on endopod and exopod, respectively. Pleopod 2, appendix masculina parallel-sided through 90% of its length, tapering to nearly acute apex, curving laterad, extending slightly beyond apex of endopod; endopod

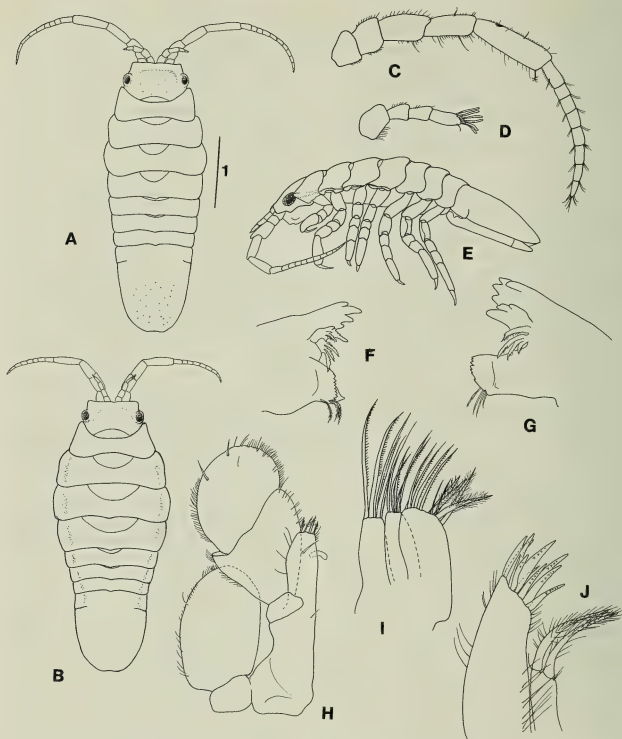


Fig. 1. A, male habitus; B, female habitus; C, antenna; D, antennule; E, lateral aspect of male; F, right mandible; G, left mandible; H, maxilliped; I, second maxilla; J, first maxilla. Scale = 1 mm.

bearing 9 plumose marginal setae, exopod bearing 22. Pleopods 3–5 with partial suture on exterior margin of exopod; exopods bearing few setae, endopods none. Fused penial plate weakly waisted, widening

somewhat distally with apex evenly, broadly rounded.

Ovigerous female.—As in male except for sexual characters and length/width proportions. Length of body 2.3 times width.

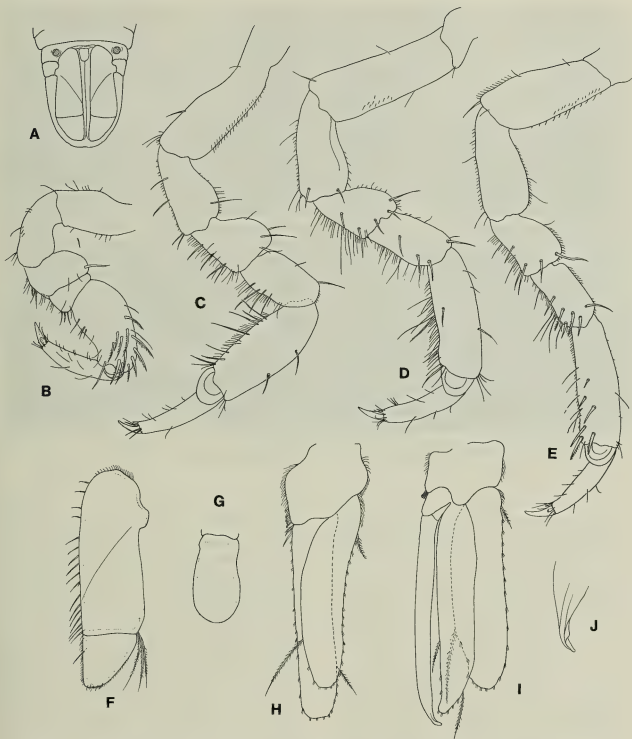


Fig. 2. A, ventral pleon; B, pereopod 1; C, pereopod 2; D, pereopod 4; E, pereopod 7; F, uropod; G, penial papilla; H, pleopod 1; I, pleopod 2 of male; J, apex of appendix masculina.

Length of pleotelson 0.29 times body length. Length to width ratio of pleotelson 1.32.

Color.—Specimens in preservation a light red-brown color, pigmentation subtly reticulated overall.

Etymology.—The species is named for Mr. John M. Foster of Gulf Coast Laboratory, who collected the new species in the company of the second author.

Remarks.—The *Synidotea* species *S. hirtipes* H. Milne Edwards, 1940, *S. brunnea*

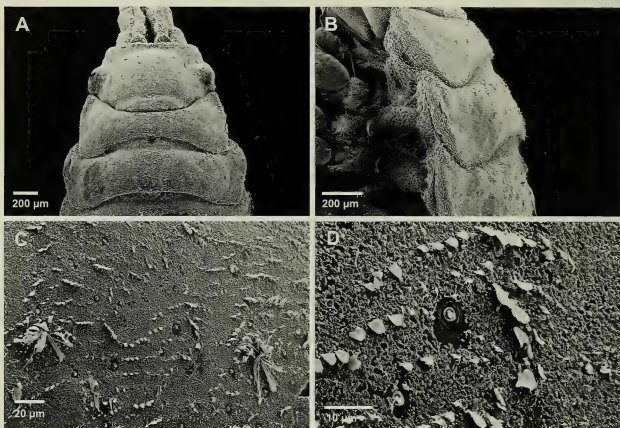


Fig. 3. Scanning Electron Micrographs: A, dorsal view of cephalon, pereonites 1 and 2; B, lateral margins of pereonites 1-3; C, integument of dorsal pereonite; D, close-up of integument.

Pires & Moreira, 1975, *S. marplatensis* Giambiagi, 1922, *S. laticauda* Benedict, 1897, *S. harfordi* Benedict, 1897, *S. laevidorsalis* Miers, 1881, *S. keablei* Poore and Lew Ton 1993, and *S. fosteri* n. sp. resemble each other closely. Based on morphological differences, Poore, 1996 concluded that *S. hirtipes*, *S. laticauda* and *S. laevidorsalis*, all from Indo-Pacific coasts, are valid and separate species, not synonyms of the earliest described member of the group (*S. laevidorsalis*), and do not represent a global invasion thereof, as suggested by Chapman and Carlton, 1991. Poore and Lew Ton, 1993 described *S. keablei* from Australia, which also superficially resembles *S. laevidorsalis*. But consistently different character states again allowed these authors to call into question the conclusion of Chapman and Carlton and their resulting synonymies.

Of the western Atlantic species, *S. fosteri*

most resembles *S. marplatensis* and *S. brunnea*, neither of which were available for direct observation. *S. marplatensis* and *S. fosteri* can be separated by the number of articles in the antennal flagellum (7-8 in *S. fosteri*, 13-20 in *S. marplatensis*); relative length of the appendix masculina (extending beyond apex of pleopodal endopod in *S. fosteri*, shorter than the apex in *S. marplatensis*); and the larger size of mature male specimens, e.g., 12.5 mm in the latter vs. 6.5 mm in the new species. Chief differences separating *S. brunnea* from *S. fosteri* include 13 articles in the antennal flagellum (7-8 in *S. fosteri*), convex margin of pereonite 1 lateral margin (nearly straight in the new species) and distinct difference in shape of the pleotelson. In *S. brunnea* these lateral margins are nearly straight then angled medially in the distal third, joined by a broad but shallowly emarginate apex on the distal margin. In *S. fosteri* the pleo-

Table 1.—Comparison of two additional *Synidotea* species from North America, as addendum to Poore, 1996. Data from our own observations.

	<i>S. fosteri</i>	<i>S. harfordi</i>
Maximum length of ovigerous female	6.0 mm	—
Maximum length of adult male	6.5 mm	17.0 mm
Color in alcohol	red-brown, reticulated	blotchy yellow-brown; darker medial stripe on pereon
Pleotelson length: width in males (number of specimens)	1.29 (6)	1.21 (1)
Pereon margin	pereonite 1 nearly straight; 2 and 3 convex, 4–7 straight	pereonite 1 with subtle curved angle; 2–7 making continuous line
Frontal margin of cephalon; dorsal sculpture	straight; weak depression in front of eyes	straight; obvious depression in front of eyes
Head width: pereonite 4 width	0.79	0.62
Pereopod 1 of male	palm of propodus concave; dactyl reaching carpus-merus suture	palm of propodus concave; dactyl reaching carpus-merus suture
Setation of ischium-propodus of pereopods of female	long and short setae along lower margins	—
Setation of ischium-propodus of pereopods of male	long and short setae along lower margins	dense pads of short setae
Fused penial plate	weakly waisted; length: width 1.85; broadly rounded apically	not waisted; length: width 2.14; rounded apically
Uropodal peduncle	1 oblique ridge	no oblique ridge
Uropodal exopod: length/width	curve between lateral margin lateral and truncate apex; 0.94	curve between lateral margin and truncate apex; 0.88

telson is broadly rounded apically with little or no emargination. The male of *S. brunnea* is as yet unknown.

S. fosteri can be distinguished from all others in this group by the combination of the nearly rectilinear lateral margins of the first pereonite, which are rounded or convex in most of the others. It is readily separated from *S. laevidorsalis* by the shape of the fused penial plate, and the longer, narrower pleon in the latter. Mature males of the new species measure 4.2 to 6.5 mm in length, whereas Miers' type specimens of *S. laevidorsalis* (also male) are longer than 25 mm. Table 1, patterned after Poore's 1996 comparison of five *Synidotea* species Indo-Pacific coasts, lists the same morphological data for *S. fosteri* and *S. harfordi* to help distinguish this group of similar animals.

Ecological notes.—*Synidotea fosteri* was collected on sand substrata at depths of 1–2 m. All of our records came from sites adjacent to high energy beaches facing the

open Gulf of Mexico. Specimens collected and observed during our study occurred between the beach and first or second seaward sand bar. The specimens were always found associated with unattached macro-plant detritus or algae. Other peracarids commonly found associated with *S. fosteri* included the amphipods *Micropotopus raneyi* Wigely and *Atylus urocarinatus* Mc Kinney.

Acknowledgments

We wish to thank John Foster, Sara LeCroy, and Jerry McClelland for making material available for study. Our sincere appreciation goes to Scott D. Whittaker, SEM Lab Manager in the Laboratories of Analytical Biology, National Museum of Natural History for technical assistance with the Scanning Electron Micrographs. We also thank Dr. Brian Kensley of the National Museum of Natural History and two anonymous reviewers for helpful comments on the manuscript.

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A new genus of the Clausidiidae (Copepoda: Poecilostomatoida) associated with a polychaete from Korea, with discussion of the taxonomic status of *Hersiliodes* Canu, 1888

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Abstract.—A new genus and new species of the Clausidiidae (Copepoda: Poecilostomatoida), *Hemadoma clavicrura*, is described based on the specimens obtained from the washings of the polychaete, *Dasybranchus caudatus* Grube, collected from Namhae-do Island in Korea. The new genus is characteristic in having (1) the 3rd segment of the antenna drawn out to form a sharp claw, (2) a 3-segmented maxilliped in female, and (3) an armature formula of II-4 on the third endopodal segment of leg 1. Phylogenetic analysis on the genera of the Clausidiidae shows that *Hersiliodes* can not be relegated to a synonym of *Hemicyclops* as proposed in the recent past. It is a sister-taxon with the new genus, *Hemadoma*, and separated from *Hemicyclops* in having a 6-segmented antennule, an armature formula of II,4 on the distal segment of the endopod of leg 1, and a medial protrusion on the proximal segment of the male maxilliped. Interestingly, the phylogenetic analysis shows also that the three genera (*Conchylurus*, *Leptinogaster*, and *Pholadicola*) living in bivalve mollusks are monophyletic.

Poecilostome copepods of the family Clausidiidae are known to live largely in symbiosis with various marine invertebrates, such as alcyonarians, polychaetes, mollusks, and callianassid crustaceans. Currently, the family comprises nearly 80 species in 9 genera. One of its genera, *Hersiliodes* Canu, 1888, living in association with polychaetes and bivalves, has been considered almost impossible to separate from *Hemicyclops* Boeck, 1872 by Bocquet et al. (1963) and Vervoort & Ramirez (1966). Furthermore, Gooding (1963) as well as Humes & Huys (1992) had even advocated the doubtfulness of keeping the genus *Hersiliodes* as a valid taxon in the Clausidiidae. Nevertheless, in his book on the copepods associated with the marine invertebrates of the British Isles, Gotto (1993) treated *Hersiliodes* as a valid genus of the

Clausidiidae and, furthermore, in their report on a new species of *Hersiliodes* from Korea, Kim & Stock (1996) alleged that the genus differs from *Hemicyclops* in bearing a 6-segmented (instead of 7-segmented) antennule and an armature formula of II,4 (instead of I,5) on the third endopodal segment of leg 1. However, it should be pointed out that the former character state is also found in one (out of 38) species of *Hemicyclops* and the latter, in all nine species of *Conchylurus*.

Recently, one of us (IHK) discovered, during his general survey of the symbiotic copepods on Namhae-do Island in Korea Strait, a new genus and species of clausidiid associated with a polychaete. The new form carries, interestingly, some characteristic features of both *Conchylurus* and *Hersiliodes*. Thus, in this paper, in addition to de-

scribing this new clausidiid, a phylogenetic analysis of the ten genera of the Clausidiidae will be conducted to investigate the taxonomic status of the genus *Hersiliodes*.

Materials and Methods

The polychaetes, *Dasybranchus caudatus* Grube (Capitellidae), were dug out from the mud flat and were placed in a plastic bag and fixed with 70% ethanol. Back at the laboratory, water was added into the bag containing the worm fixed in alcohol and then shaken hard to dislodge the copepods. The water together with the sediment and debris were examined under a dissection microscope for associated copepods. The copepods were removed and preserved in 70% ethanol. In studying the preserved copepods, the specimens were cleared in lactic acid, dissected on a wooden slide (Humes & Gooding 1964), and examined under a compound microscope. All drawings were made with the aid of a *camera lucida*. For formula of armature, "A" represents aesthete; Roman numeral, spine; and Arabic numeral, seta.

Seven genera were recognized by Humes & Huys (1996) in the family Clausidiidae. They are *Hemicyclops* Boeck, 1873; *Clausidium* Kossmann, 1874; *Hippomolgus* G. O. Sars, 1917; *Leptinogaster* Pelseneer, 1929; *Conchylurus* Bocquet & Stock, 1957; *Doviella* Rocha, 1986; and *Hyphalion* Humes, 1987. However, several changes have been made since then; two new genera (*Folliomolgus* Kim and *Pholadicola* Ho & Wardle) were added, respectively, by Kim (2001) and Ho & Wardle (1992), *Hersiliodes* Canu, 1888 was suggested to be resurrected by Kim & Stock (1996), and *Doviella* was relegated to a synonym of a clausiid genus by Ho & Kim (in press). Thus, including a new genus to be described below, there are now 10 genera in the Clausidiidae to be considered.

The data used in the character analysis to prepare for construction of a matrix were taken from the type species of each of the

10 clausidiid genera. Since Ho's (1992) phylogenetic analysis of the Poecilostomatoida shows that Erebonasteridae Humes, 1987 occurs in sister-taxa relationship with a monophyletic clade comprising Clausidiidae + (Oncaeidae + Paralubbockidae), Erebonasteridae was accordingly employed as an outgroup to polarize the 14 characters selected and also to root the cladogram(s) in reconstruction of the phylogeny. Although *Centobnaster* Huys & Boxshall, 1990 is generally considered the most primitive erebonasterid copepod (Huys & Boxshall 1990), some features in *Tychidion* Humes, 1973 were found to be even more primitive. Therefore, both *Centobnaster* and *Tychidion* were used as outgroup in the polarization of the selected characters shown in Appendix A. Also, in coding multistate characters, when a transformation series containing a single basal bifurcation (dichotomous transformation) was encountered, the method of "internal rooting" proposed by O'Grady & Deets (1987) was employed. In this case, as shown in Characters 3, 4 and 8 in Appendix B, the coding of "0" indicates apomorphy, not plesiomorphy.

The computer program HENNIG86 Version 1.5 (Farris 1988) was employed to analyze the phylogenetic relationships among the genera of the Clausidiidae. The command "ie*" (implicit enumeration) was used to produce multiple, shortest trees through performance of exhaustive search and use all available tree space to find all shortest trees. In order to avoid predetermination of the topology of the resultant cladogram(s), all multistate characters were changed to nonadditive (unordered) before employing the command to reconstruct the phylogeny.

Description

Order Poecilostomatoida Thorell, 1859

Family Clausidiidae Embleton, 1901

Hemadona, new genus

Diagnosis.—Body elongate, 9-segmented in female and 10-segmented in male.

First pediger fused to cephalosome. Antennule short, 6-segmented, with 2nd and 3rd segments incompletely separated. Antenna 4-segmented, with 3rd segment (middle segment of endopod) drawn out into a large claw, distal segment tipped with 7 elements. Labrum well-developed. Mandible tipped with 2 large spiniform elements and 2 setae. Paragnath a lobe with spinules. Maxillule bilobate distally, both lobes tipped with setae. Maxilla 2-segmented, with armature formula of 2, 4. Maxilliped 3-segmented in female and 4-segmented in male; proximal segment in male with medial outgrowth. Legs 1–4 biramous with 3-segmented rami; armature formulae generally as in *Hemicyclops*, except 3rd segment of leg 1 endopod with II,4 and 3rd segment of leg 4 exopod with III,I,5. Leg 5 2-segmented, armature formula as in *Hemicyclops*. Basal segment of leg 5 in male fused to pediger. Leg 6 in male a single seta on genital operculum. Caudal ramus with usual 6 elements. Egg sac elongate, multiseriate.

Etymology.—The generic name *Hemadona* is an anagram of the island Namhaedo located in the Korean Strait from where the new genus was discovered. Gender feminine.

Type species.—*Hemadona clavicurra* new species.

***Hemadona clavicurra*, new species**

Figs. 1–3

Material examined.—3 ♀♀ and 7 ♂♂ collected from washings of *Dasybranchus caudatus* Grube collected from intertidal mud flat on Namhae-do Island (34°49'N 128°03'E) in Korea Strait on 22 July 2001. Holotype ♀ (USNM 1013731), allotype ♂ (USNM 1013732), and 6 paratypes (USNM 1013733, including 1 ♀ and 5 ♂♂) are deposited in the U.S. National Museum of Natural History in Washington, D.C. Dissected paratypes (1 ♀ and 1 ♂) are kept in the author's (IHK) collection.

Female.—Body (Fig. 1A) elongate, 6.34 mm long (excluding setae on caudal rami).

Cephalothorax semicircular and containing 1st pediger. Second pediger widest of body, 1.04 mm; width of 3rd and 4th pedigers decreasing only slightly from that of 2nd pediger. Urosome 5-segmented, 2.37 times longer than prosome. Genital double somite longer than wide, $877 \times 693 \mu\text{m}$, with aliform dorsolateral protrusion in anterior half of somite covering area of egg sac attachment (Fig. 1A). Abdomen 3-segmented, with all segments longer than wide, $833 \times 553 \mu\text{m}$, $798 \times 508 \mu\text{m}$, and $880 \times 430 \mu\text{m}$. Caudal ramus (Fig. 1C) 4.44 times longer than wide ($720 \times 162 \mu\text{m}$), armed with 1 short, outer seta at about midlength of lateral margin, 1 short, medial, subterminal seta, and 2 short and 2 long terminal setae; longest terminal seta ($830 \mu\text{m}$) 1.15 times as long as ramus. Egg sac greatly elongated (7.05 mm), longer than body and cylindrical.

Rostrum subquadrate in dorsal view, produced forward, and well demarcated from cephalothorax (Fig. 1A). Antennule (Fig. 1B) short and robust, 6-segmented; formula of armature: 5, 16, 10, 4, 2 + A, and 7 + A. Antenna (Fig. 1C) 4-segmented; first segment (coxobasis) longer than wide, with long outer-distal seta; second segment (1st endopodal segment) shorter than proximal segment, with small subterminal seta; third segment (2nd endopodal segments) drawn out into a large uncinatate claw, with basal patch of spinules on outer surface and 2 unequal setae plus 1 blunt tip, bent, spiniform seta bearing terminal row of spinules on medial margin; terminal segment 2.75 times longer than wide, tipped with 3 unequal setae and 4 spiniform setae structured as that one on 3rd segment. Labrum (Fig. 1D) well-developed, with submarginal, inner, central process, and 2 disjunct, marginal rows of spinules on either side of this process. Gnathobase of mandible (Fig. 1E) armed terminally with 1 stout, pinnate element, 1 stout, spinulose element, and 1 pinnate and 1 naked setae. Paragnath (Fig. 1F) an obtuse lobe fringed with spinules on distal margin. Maxillule (Fig. 1G) bilobate,

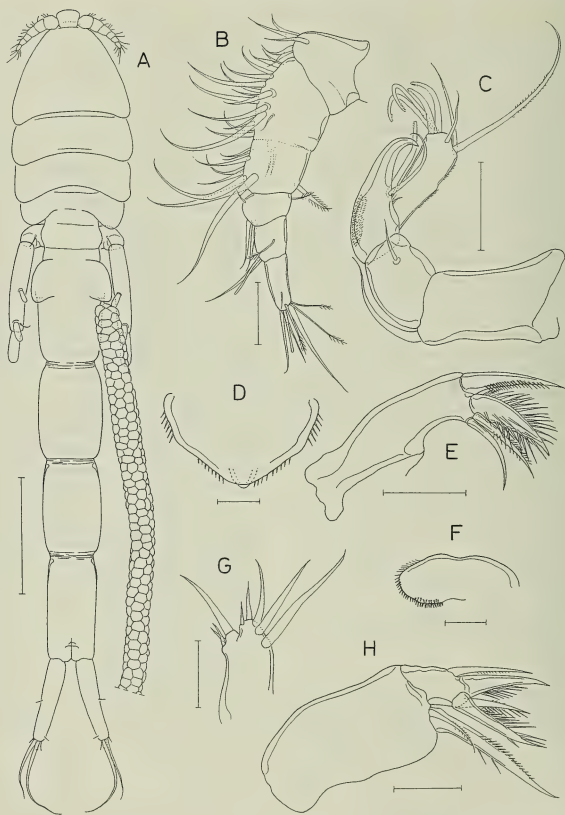


Fig. 1. *Hemadona clavicura*, new genus, new species, female. A, habitus, dorsal; B, antennule; C, antenna; D, labrum; E, mandible; F, paragnath; G, maxillule; H, maxilla. Scale bars: A, 1 mm; B, C, 0.02 mm; D, F 0.02 mm; E, G, H, 0.05 mm.

small outer lobe tipped with 1 long and 2 short setae and larger inner lobe with 5 unequal setae. Maxilla (Fig. 1H) 2-segmented; robust proximal segment (syncoxa) armed with 1 large spiniform and 1 small pinnate setae; distal segment (allobasis) tipped with 2 spiniform elements bearing spinules on one side and 2 pinnate setae. Maxilliped (Fig. 2A) 3-segmented; proximal segment (syncoxa) with 2 unequal medial setae; middle segment (basis) greatly expanded laterally and carrying 2 unequal medial setae; terminal segment (endopod) tiny, bearing 1 spiniform and 2 setiform elements.

Legs 1-4 (Figs. 2B-D, 3A) biramous, with 3-segmented rami. Formula of spines and setae as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-1	1-I	I-0; I-1; III,I,4	0-1; 0-1; II,4
Leg 2	0-I	1-0	I-0; I-1; III,I,5	0-1; 0-2; II,I,3
Leg 3	0-I	1-0	I-0; I-1; III,I,5	0-1; 0-2; II,II,2
Leg 4	0-1	1-0	I-0; I-1; III,I,5	0-1; 0-2; II,II,1

Outer surface of all segments on rami fringed with spinules. Outer spines on all legs club-shaped, with swollen tip covered with fine denticles. Leg 5 (Fig. 3B) 2-segmented; proximal segment small, carrying simple, outer seta; distal segment elongate, about 4 times longer than wide ($750 \times 187 \mu\text{m}$), armed with 3 club-like spines and 1 thin, simple seta.

Male.—Body (Fig. 3C) elongate as in female, 3.40 mm long (excluding setae on caudal rami). Cephalothorax semi-ellipsoid shaped and containing 1st pediger. Second pediger widest of body, $532 \mu\text{m}$ wide; width of 3rd and 4th pedigers decreasing only slightly from that of 2nd pediger. Urosome 6-segmented, 1.51 times longer than prosome. Ventrally, proximal segment of leg 5 indistinctly separated from its pediger (Fig. 3D). Genital somite slightly longer than wide, $310 \times 300 \mu\text{m}$; genital operculum (Fig. 3D) small. Abdomen 4-segment-

ed, with following measurements (proceeding from anterior to posterior): $295 \times 282 \mu\text{m}$, $366 \times 275 \mu\text{m}$, $317 \times 254 \mu\text{m}$, and $423 \times 246 \mu\text{m}$. Caudal ramus 4.08 times longer than wide ($408 \times 100 \mu\text{m}$) and armed as in female. Maxilliped (Fig. 3E) 4-segmented; proximal segment (syncoxa) with large, medial protrusion tipped with 3 sharp tines; second segment (basis) largest, armed with small patch of subterminal denticles on lateral surface, a seta in distomedial corner followed by a row of spinules on medial margin; third segment (1st endopodal segment) smallest and naked; distal segment (2nd endopodal segment) drawn out into a long claw with accessory tine and 2 simple setae on medial surface of basal region.

Etymology.—The species name is a combination of Latin, *clava* (= a club) and *crus* or *cruris* (= leg), alluding to the club-shaped outer and terminal spines on all five pairs of legs.

Remarks.—The general appearance of *Hemadona clavicurra* resembles the species of *Conchylurus* in having an elongated (non-cycloform) body. They are further alike in having a 6-segmented antennule, an armature formula of II,4 on the terminal segment of the endopod of leg 1, and a prominent medial, basal protuberance on the proximal segment (syncoxa) of the male maxilliped. These four features are also shared with *Hersiliodes*. However, *H. clavicurra* cannot be placed in *Conchylurus* due to the presence of the following character states: (1) the hook on the 3rd segment of the antenna is completely fused to its segment proper, (2) the gnathobase of the mandible carries four (instead of three) terminal elements, (3) the proximal segment (syncoxa) of the maxilla bearing two (instead of none) elements at outer-distal corner, and (4) the maxilliped in female is 3-segmented (instead of 2-segmented). Moreover, 10 species of *Conchylurus* are known and, unlike *H. clavicurra* living in association with polychaetes, they were all

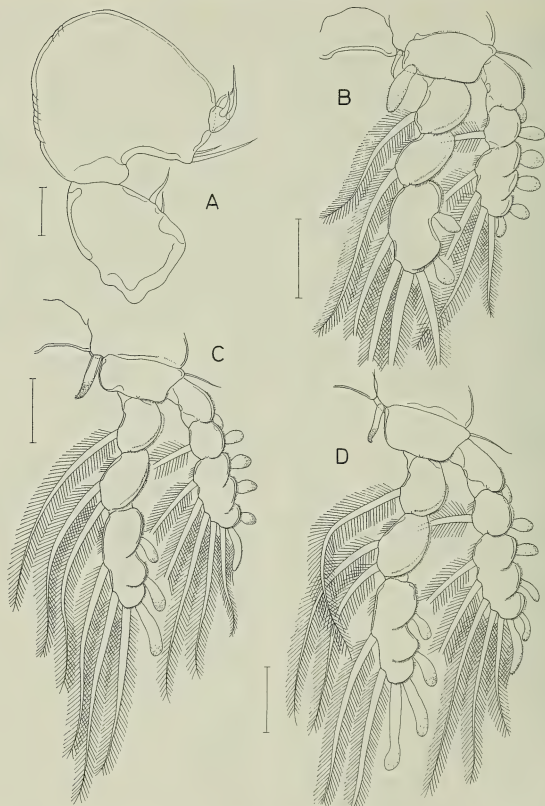


Fig. 2. *Hemadona clavicurva*, new genus, new species, female. A, maxilliped; B, leg 1; C, leg 2; D, leg 3. Scale bars: A, 0.05 mm; B-D, 0.2 mm.

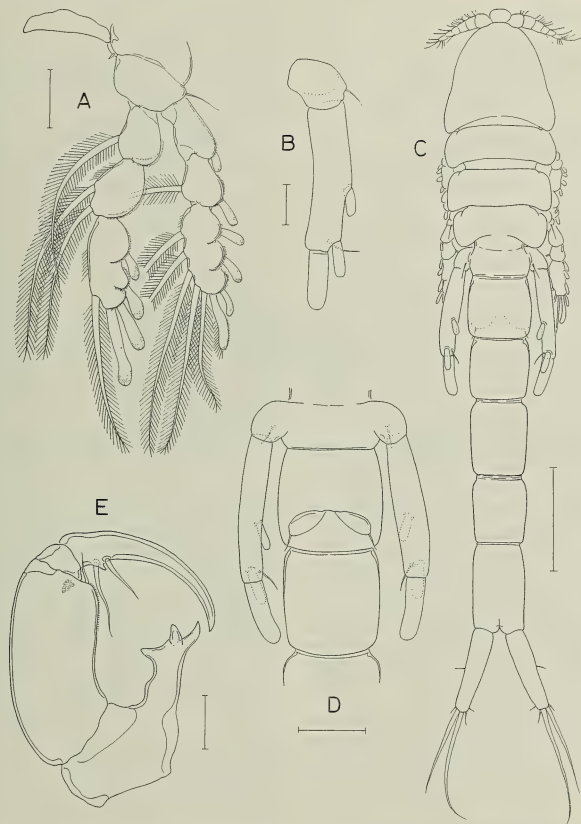
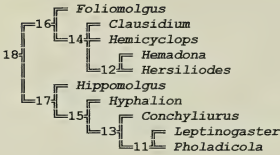
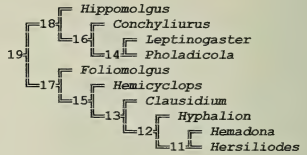


Fig. 3. *Hemadona clavicura*, new genus, new species. Female: A, leg 4; B, leg 5. Male: C, habitus, dorsal; D, first three somites of urosome, ventral; E, maxilliped. Scale bars: A, B, D, 0.2 mm; C, 0.5 mm; E, 0.05 mm.

Tree 1



Tree 7



Tree 9

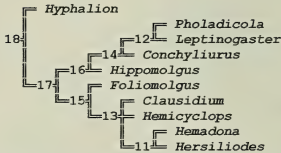


Fig. 4. Clausidiid phylogeny produced through analysis of nonadditive (unordered) coding. Showing three representatives from three patterns of phylograms. (Other 15 phylograms are available from JSH upon request.)

reported from the mantle cavities of the bivalve mollusks.

Of the four differences mentioned above between *H. clavicurva* and *Conchyliliurus*, only items (1) and (4) also apply to the distinction between it and *Hersiliodes*. So far two species of *Hersiliodes* are known from either a polychaete (Bocquet et al. 1963) or a bivalve (Kim & Stock 1996). Thus, it seems *Hemadona* is closer to *Hersiliodes* than to *Conchyliliurus*.

In general, *H. clavicurva* is most characteristic in having an unusually long urosome (2.37 times longer than its prosome) and club-shaped outer and/or terminal spines on all five pairs of legs.

Phylogenetic Analysis

A total of 18 equally parsimonious trees (cladograms, phylograms) were obtained with a length of 37 steps, a consistency index (CI) of 64 and a retention index of 62.

A close comparison of these 18 trees shows that there are three patterns of tree according to the grouping of the 10 genera. In Pattern I, as Tree 1 in Fig. 4, the 10 genera are separated into two clades, with one clade (Clade 16) containing *Clausidium*, *Foliomolgus*, *Hemadona*, *Hemicyclops*, and *Hersiliodes* and the other clade (Clade 17), *Conchyliliurus*, *Hippomolgus*, *Hyphalion*, *Leptinogaster*, and *Pholadicola*. There are 10 phylograms belonging to this category—Tree 1, 2, 3, 4, 5, 6, 11, 12, 13 and 14 (authors' enumeration; unpublished data). Phylograms in Pattern II, as Tree 9 in Fig. 4, have *Hyphalion* set aside on a clade of its own and the remaining nine genera divided into two groups, with *Clausidium*, *Foliomolgus*, *Hemadona*, *Hemicyclops*, and *Hersiliodes* in one clade (Clade 15) and *Conchyliliurus*, *Hippomolgus*, *Leptinogaster*, and *Pholadicola* in the other clade (Clade 16). There are six phylograms belonging to

this category—Tree 8, 9, 10, 16, 17 and 18 (authors' enumeration; unpublished data). One of the two remaining phylograms, Tree 7, belonging to Pattern III, is shown in Fig. 4. It has the 10 clausidiid genera divided into two groups, with one comprising *Conchylurus*, *Hippomolgus*, *Leptinogaster*, and *Pholadicola* and another one, *Clausidium*, *Foliomolgus*, *Hemadona*, *Hemicyclops*, *Hyphalion* and *Hersiliodes*.

The difference among the three patterns mentioned above is chiefly due to the inconsistent positions of *Hyphalion*. In Pattern I (see Tree 1 in Fig. 4), it is a member of the group comprising *Conchylurus*, *Hippomolgus*, *Leptinogaster*, and *Pholadicola*; in Pattern II (see Tree 9 in Fig. 4) it is by itself; and in Pattern III (see Tree 7 in Fig. 4) it is a member of the group comprising *Clausidium*, *Foliomolgus*, *Hemadona*, *Hemicyclops*, *Hyphalion* and *Hersiliodes*, which is entirely different from the one that it is affiliated with in Pattern I.

There are two monophyletic taxa that maintain identical relationships in all 18 phylograms. They are *Hemadona* + *Hersiliodes* and *Conchylurus* + (*Pholadicola* + *Leptinogaster*). The former two genera are held together by sharing characters 1 (with 6-segmented antennule), 12 (proximal segment of male maxilliped with medial protrusion) and 13 (with an armature formula of II,4 on distal segment of leg 1 endopod), and the latter three genera, by sharing characters 3 (with 2 elements on 3rd segment of antenna), 5 (mandible tipped with 3 elements) and 10 (with 3-segmented maxilliped in female). It is noteworthy that both *Hemadona* and *Hersiliodes* are characteristic in having a 6-segmented antennule (Character 1). They were not placed in the same group (clade) with *Conchylurus* + *Leptinogaster* + *Pholadicola* on any of the 18 phylograms. In other words, the two constant monophyletic taxa are remotely related. It is interesting to point out that the latter three genera comprise parasites of bivalve mollusks, while species of *Pholadicola* inhabit in the host's intestine, and

those of *Conchylurus* and *Leptinogaster* are found in the host's mantle cavities.

Five of the 18 obtained phylograms contain a clade with trichotomy, three of these phylograms (Trees 1, 5 and 12) are in Category I and the other two (Trees 9 and 17), in Category II. *Hemicyclops* appears as one of the three terminal clades in all five phylograms showing trichotomy. In four of these five phylograms, i.e., Trees 1, 5, 12 and 9, the branch embracing *Hemadona* + *Hersiliodes* appears as another terminal clade, with either *Clausidium* or *Foliomolgus* as the third terminal clade. In addition, Trees 2 and 13 in Category I have a topology showing *Hemicyclops* in a sister-taxon relationship with *Hemadona* + *Hersiliodes*. These six phylograms indicate that both *Hemadona* and *Hersiliodes* are closely affiliated with *Hemicyclops*. However, since none of the 18 phylogram shows *Hersiliodes* in a sister-taxon relationship with *Hemicyclops*, the former, accordingly, cannot be relegated to a synonym of the latter. Thus, the present phylogenetic analysis supports Kim and Stock's (1996) notion that *Hersiliodes* is a valid genus in the Clausidiidae and cannot be synonymized with *Hemicyclops*.

Key to the Genera of the Clausidiidae

A key to the genera of the Clausidiidae was provided by Humes and Huys (1992). Since only six of the ten genera currently recognized were dealt with in that key, a new key is provided below.

1. Formula of armature on terminal segment of leg 1 endopod I,5 2
 - Formula of armature on terminal segment of leg 1 endopod otherwise 5
2. Antenna 3-segmented *Hyphalion*
 - Antenna 4-segmented 3
3. Maxilliped in female 4-segmented *Hemicyclops*
 - Maxilliped in female reduced or absent 4
4. Antennule 7-segmented; 3rd segment of antenna with 4 elements *Foliomolgus*
 - Antennule 6-segmented; 3rd segment of antenna with 2 elements *Leptinogaster*

- 5. Endopods of legs 1–4 with sucking discs; middle exopodal segment of leg 1 without inner seta *Clausidium*
- No sucking discs on legs; middle exopodal segment of leg 1 with inner seta 6
- 6. Proximal segment of maxilla armed with setae 7
- Proximal segment of maxilla unarmed 8
- 7. Maxilliped in female 4-segmented and well-developed; armature formula for terminal segment of leg 1 exopod II,1,5 *Hersiliodes*
- Maxilliped in female 3-segmented and reduced; armature formula for terminal segment of leg 1 exopod III,1,5 *Hemadona*
- 8. Armature formula for terminal segment of female leg 1 endopod II,4 *Conchylurus*
- Armature formula for terminal segment of female leg 1 endopod otherwise 9
- 9. Maxilliped in female rudimentary *Pholadicola*
- Maxilliped in female well developed, at least 3-segmented *Hippomolgus*

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Appendix 1.—Characters and character states used in the phylogenetic analysis of the Clausidiidae. Numbers in parentheses denote the numerical coding of the character states. Coding in Characters 3, 4, and 8 employed "internal rooting" proposed by O'Grady & Deets (1987). *Centobnaster* and *Tychidion* were utilized as the outgroup in polarization of the character state transformations.

01	3rd and 4th segments of antennule separated (0) or fused (1)
02	Aesthetasc on antepenultimate segment of antennule absent (0) or present (1)
03	3rd segment of antenna with 3 elements (1), 4 elements (0) or 2 elements (2)
04	Terminal segment of antenna with 6 elements (1), 7 elements (0), 5 elements (2) or 4 elements (3)
05	Mandible tipped with 4 elements (0) or 3 elements (1)
06	Inner lobe of maxillule carrying 2 elements (0) or 3 elements (1)
07	Outer lobe of maxillule carrying 3 elements (0) or 4 elements (1)
08	Proximal segment of maxilla without seta (0), with 1 seta (1), 2 setae (2) or 3 setae (3)
09	Distal segment of maxilla with 4 elements (0), 3 elements (1), 2 elements (2) or 1 element (3)
10	Maxilliped in female 4-segmented (0), 3-segmented (1), 2-segmented (2) or absent (3)
11	Proximal segment of female maxilliped with 2 setae (0), 1 seta (1) or none (2)
12	Proximal segment of male maxilliped without protrusion (0) or with medial protrusion (1)
13	Distal segment of endopod on leg 1 with an armature formula of I, 5 (0) or II, 4 (1)
14	Distal segment of exopod on leg 4 with an armature formula of II, I, 5 (0) or III, I, 5 (1)

Appendix 2.—Data matrix of 14 characters and their states in ten genera of Clausidiidae as used in the cladistic (phylogenetic) analysis. The question mark "?" indicates an unknown state. Due to the application of "internal rooting" (O'Grady & Deets, 1987) those characters coded with "1" in the outgroup are treated as plesiomorphic and "0" in the ingroup, apomorphic.

Genus (OTU)	Characters													
	1		5				10				14			
Outgroup	0	0	1	1	0	0	0	1	0	0	0	0	0	0
<i>Clausidium</i>	0	0	0	0	1	1	1	3	0	0	0	0	?	0
<i>Conchylurus</i>	1	1	2	0	1	1	1	0	0	2	1	1	1	1
<i>Foliomolgus</i>	0	1	0	0	0	1	1	1	1	3	?	0	0	0
<i>Hemadona</i>	1	0	0	0	0	1	1	2	0	1	0	1	1	1
<i>Hemicyclops</i>	0	1	0	0	0	1	1	2	0	0	0	0	0	0
<i>Hersiliodes</i>	1	1	0	0	0	1	1	2	0	0	0	1	1	0
<i>Hippomolgus</i>	1	1	1	0	0	1	1	0	0	0	1	?	0	0
<i>Hyphalion</i>	1	0	?	?	0	?	?	1	0	2	2	0	0	0
<i>Leptinogaster</i>	1	1	2	2	1	0	0	0	2	3	?	0	0	0
<i>Pholadicola</i>	1	0	2	3	1	0	0	0	3	3	?	0	?	?

***Vesicomycicola trifurcatus*, a new genus and species of commensal polychaete (Annelida: Polychaeta: Nautiliniellidae) found in deep-sea clams from the Blake Ridge cold seep**

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Abstract.—A new genus and species of deep-sea polychaete belonging to the family Nautiliniellidae is described from the Blake Ridge cold seep off the coast of South Carolina at a depth of 2155 m. This species is commensal within the mantle cavity of ~60% of the vesicomimid clams collected at the seep site. *Vesicomycicola trifurcatus* is distinguished from previously described nautiliniellid genera and species by the presence of two pairs of tentacular cirri and up to seven trifurcate hooked chaetae on the posterior parapodia. The new species resembles *Itheyomytilidicola tridentatus* in having trifurcate hooks, but the arrangement and number of chaetae differs. Only two types of chaetae are present in *V. trifurcatus*: four to seven stout, simple hooks anteriorly to mid-body, and up to seven trifurcate hooks posteriorly. In contrast, there are three types of chaetae in *I. tridentatus*: up to five stout hooks per parapodium, each with a minute projection on cutting edge of the main fang, 10–20 simple, slender tridentate chaetae, and numerous minute mucronate chaetae. A key to species of Nautiliniellidae is included.

The Nautiliniellidae is a small group of deep-sea polychaetes that live in the mantle cavity of a clam or mussel host. Nautiliniellids have been collected from chemosynthetically based deep-sea habitats, including cold seeps and hydrothermal vents. Since nautiliniellids were first reported by Miura & Laubier (1989), 10 genera and 14 species have been described (Table 1). Two undescribed species have also been reported, one from a cold seep at Barbados Trench (4960 m; Olu et al. 1996) and one off the Pacific coast of Mexico (3221 m; Olu, pers. comm.).

An additional genus, *Santelma*, has been assigned to the family Nautiliniellidae (Blake 1993, Glasby 1993), but its affiliation with the Nautiliniellidae remains questionable. The only known species, *Santelma*

miraseta (Fauchald, 1972), was first placed in the family Pilargidae and the genus *Pilargis*. Blake (1993) redescribed the species and assigned it to *Santelma*, a new nautiliniellid genus, based on chaetal similarities. Unlike nautiliniellids, *S. miraseta* has extruded neuroaciculae, a median antenna (or its trace), and it lacks neuropodial hooks and parapodial cirri. Based on these features, *S. miraseta* fits better within the original family Pilargidae (Salazar-Vallejo, pers. comm.). We follow the precedent of Miura & Hashimoto (1996) and exclude *S. miraseta* from the Nautiliniellidae.

Nautiliniellids have reduced and simplified body structures that are associated with a commensal or parasitic life. These modifications include a less developed anterior region, the presence of only simple hooked

Table 1.—Family Nautiliniellidae: list of genera and species, host bivalve genus and family, collection depth of type specimen, location where type specimen was collected and author reference.

Genus and species	Host bivalve Genus (Family)	Depth (m)	Location	Reference
1 <i>Flascarpia alvinae</i>	Unknown	3303	Florida Escarpment	Blake (1993)
2 <i>Itheyomytilidicola tridentatus</i>	<i>Bathymodiolus</i> (Mytilidae)	1395	Okinawa Trough	Miura & Hashimoto (1996)
3 <i>Lautierius mucronatus</i>	(Mytilidae)	3243	Florida Escarpment	Blake (1993)
4 <i>Miura spinosa</i>	Unknown	565	Santa Maria Basin	Blake (1993)
5 <i>Mytilidiphila enseiensis</i>	near <i>Adula</i> (Mytilidae)	625	Okinawa Trough	Miura & Hashimoto (1993)
6 <i>Mytilidiphila okinawaensis</i>	<i>Bathymodiolus</i> (Mytilidae)	701	Okinawa Trough	Miura & Hashimoto (1993)
7 <i>Natsushima bifurcata</i>	<i>Solemya</i> (Solemyidae)	1114	Sagami Bay	Miura & Laubier (1990)
8 <i>Natsushima graciliceps</i>	<i>Solemya</i> (Solemyidae)	98	Kagoshima Bay	Miura & Hashimoto (1996)
9 <i>Nautiliniella calyptogenticola</i>	<i>Calyptogena</i> (Vesicomomyidae)	5650	Japan Trench	Miura & Laubier (1989)
10 <i>Petrecca thyasira</i>	<i>Thyasira</i> (Thyasiridae)	3700	Laurentian Fan	Blake (1990)
11 <i>Shinkai longipedata</i>	<i>Calyptogena</i> (Vesicomomyidae)	1400	Okinawa Trough	Miura & Ohra (1991)
12 <i>Shinkai sagamiensis</i>	<i>Calyptogena</i> (Vesicomomyidae)	1170	Sagami Bay	Miura & Laubier (1990)
13 <i>Shinkai semilonga</i>	<i>Calyptogena</i> (Vesicomomyidae)	625	Okinawa Trough	Miura & Hashimoto (1996)
14 <i>Thyasiridicola branchiatus</i>	<i>Conchocle</i> (Thyasiridae)	1160	Sagami Bay	Miura & Hashimoto (1996)
15 <i>Vesicomomyicola trifurcatus</i>	<i>Vesicomomya</i> (Vesicomomyidae)	2155	Blake Ridge Diapir	Present study

chaetae modified to grasp host tissue, and the absence of anal cirri on the pygidium. Diagnostic characters of the family include the number of prostomial appendages, number of tentacular cirri, and chaetal morphology and number. These characters are specific to each genus but are useful for species identifications since seven of the ten nautiliniellid genera are monospecific. Based on these morphological characters, we determined that the specimens collected from the Blake Ridge cold seep belong to a new genus and species described herein.

Material and Methods

Biological samples were collected at the Blake Ridge Diapir site (ODP Site 996; 32°30'N, 76°11'W; 2155 m) on 25 to 28 Sep 2001, using the DSV *Alvin*. A description of the study site can be found in Van Dover et al. (2003). Although geological and chemical properties of this site have been explored during the past decade, the *Alvin* 2001 samples represent the first collections of megafauna and macrofauna from this area.

Host clams were collected using a suction sampler. The clams were identified as a new genus and species in the Family Vesicomomyidae, based on morphological characters, molecular differences in comparison to described species, and geographic and bathymetric location (E. Kryolora, pers. comm.). Clams were dissected and nautiliniellids were removed and placed into either 10% buffered formalin or 3% glutaraldehyde and 0.1 M phosphate buffer with 0.25 M sucrose (pH 7.4). After 24 hours, formalin-fixed nautiliniellids were rinsed and stored in 70% ethanol.

Photographs of the external morphology were taken with a compound light microscope (LM) and a scanning electron microscope (SEM). Specimens for LM were mounted in glycerol and ethanol and observed with a Zeiss Axioskop 2 binocular compound microscope. Specimens for SEM were dehydrated through a graded series of

ethanol, terminating with 100% ethanol. Samples were then critical-point dried, gold sputter coated (20 nm thick), and observed with an Amray SEM 1810. Images were captured using a Spot camera (Diagnostic Instruments) or a DP11 digital camera (Olympus). Line illustrations were prepared using a camera lucida attached to a Wild Heerbrugg compound microscope.

Systematics

Family Nautiliniellidae Miura & Laubier,
1989

Vesicomycicola, new genus

Type species.—*Vesicomycicola trifurcatus*, new species, by present designation.

Diagnosis.—Body with strong dorsal arch, ventrally flattened. Prostomium with one pair of palps, without eyes. Tentacular segment fused with prostomium, with dorsal and ventral cirri, neuroacicula, and neuropodial hooked chaetae. Parapodia sub-biramous, with dorsal and ventral cirri. Notopodia and neuropodia each with one embedded acicula. Chaetae absent on notopodia. Two types of chaetae present on neuropodia: simple hooked chaetae on anterior segments (some with single subapical tooth present on anterior to mid-body segments), and tricurcate hooked chaetae on posterior segments. Pygidium cylindrical, without anal cirri.

Gender.—Masculine.

Etymology.—The generic name is derived from the name of the host vesicomycid clams these polychaetes inhabit.

Vesicomycicola trifurcatus, new species (Figs. 1–4)

Type material.—Holotype (ODP Site 996; 32°30'N, 76°11'W; 2155 m, 28 Sep 2001, Alvin Dive 3712; USNM 1016220) and five paratypes (USNM 1016221) from same dive and date were deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia. An ad-

ditional five paratypes, each from the same dive and date, were deposited in the Museum National d'Histoire Naturelle, Paris (MNHN POLY TYPE 1405) and the National Science Museum, Tokyo (NSMT—Pol P 458).

Additional material.—Voucher specimens were retained in the collection of CLVD in the Department of Biology at The College of William and Mary.

Description.—Holotype female, ovigerous, measuring 8.4 mm long, 1.3 mm wide, including parapodia, with 37 segments. Paratypes ranging from 4.4–12.7 mm long, 0.8–1.6 mm wide, including parapodia, and with 28–41 segments. Body flattened ventrally, arched dorsally. Some live specimens with green pigment in parapodia, others with pale pink color; preserved specimens in alcohol pink to white in color. Some preserved females pale green; internal oocytes evident through transparent parapodial epidermis. Preserved holotype and paratypes curled (Fig. 1A).

Prostomium rounded, with palps (Fig. 2A–C). Eyes absent. Tentacular segment fused with prostomium, with one pair of dorsal and ventral cirri, neuroacicula, and neuropodial hooked chaetae (Fig. 2C). Foregut with well-developed muscular region (Fig. 2A–C). Pygidium rounded, without anal cirri (Fig. 2D).

Parapodia subbiramous, with dorsal and ventral cirri. Dorsal cirri with inflated base and tapering tip, twice as long as ventral cirri. Notopodia with single embedded acicula, lacking chaetae (Fig. 3A). Neuropodia with a single bent acicula and hooked chaetae (Fig. 3B).

Neuropodial hooks of two types. Anterior neuropodia with simple stout hooks with recurved tips, four to seven on each parapodium (Fig. 4A, B), some anterior to mid-body chaetae with single small apical tooth near tip, appearing slightly bifid (Fig. 4C). Posterior neuropodia with thinner, simple hooks with trifurcate tips, up to seven per neuropodium (Fig. 4D, E).

Etymology.—The specific name comes

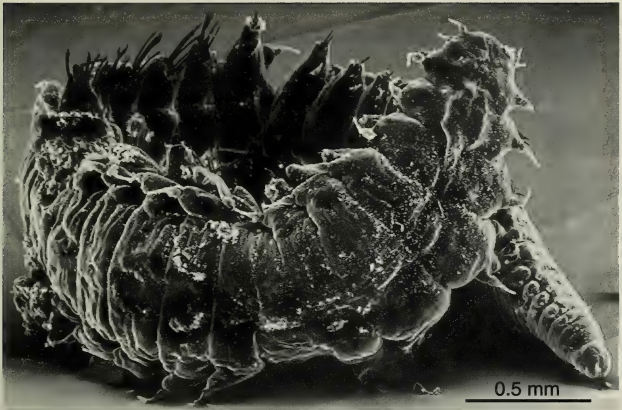


Fig. 1. *Vesicomycicola trifurcatus* new genus, new species. Scanning electron micrograph (SEM) of whole body.

from *tri-* = three times, + *furcatus* = forked, in reference to the trifurcate chaetae present on the posterior segments.

Biology.—The mantle cavities of ~60% of the Blake Ridge clams sampled contained one to five nautiliniellid polychaetes. Carbon and nitrogen stable isotope compositions of worm and clam tissues were consistent with a parasitic life-style for the worm, but the sulfur isotope composition of the worms was so distinct from that of the clams that an alternative diet must be inferred (Van Dover et al. 2003). Van Dover et al. (2003) proposed a feeding strategy whereby ciliary activity of the clam gills moves sufficient volumes of seawater to allow the polychaetes to collect and consume suspended organic particles either from gill mucus or from a worm-generated mucus net.

Discussion

Vesicomycicola trifurcatus resembles species in the genera *Nautiliniella*, *Natsushi-*

ma, *Shinkai*, and *Thyasiridicola*, based on shared characters of the tentacular segment, which in these four genera includes dorsal and ventral cirri and neurochaetae (with the exception of the genus *Thyasiridicola*, which lacks neurochaetae). The genus *Vesicomycicola* differs from these four genera in the number and morphology of the neuropodial chaetae.

Vesicomycicola trifurcatus resembles *Iheyomytilidicola tridentatus* Miura & Hashimoto, 1996 based on the trifurcate chaetal morphology, but the arrangement and number of chaetae on the parapodia differs. There are only two types of chaetae present in *V. trifurcatus*: stout, simple hooks (four to seven; sometimes bifid) on the anterior to mid-body parapodia, and trifurcate hooks (up to seven) on the posterior parapodia. In contrast, there are three types of chaetae in *I. tridentatus*: stout hooks (up to five), each with a minute projection on the cutting edge of the main fang; simple,

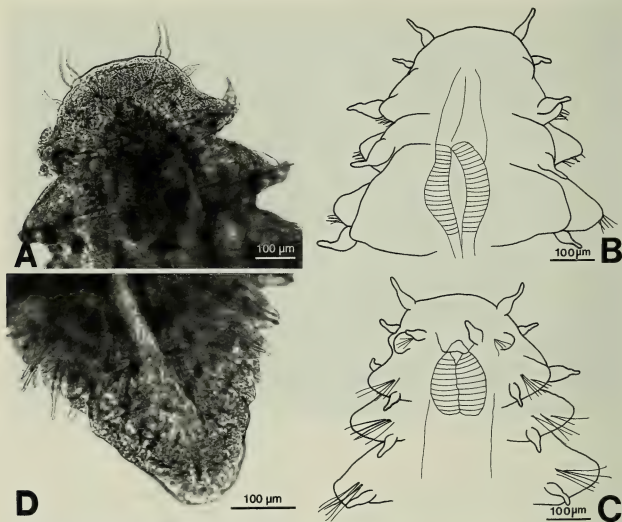


Fig. 2. *Vesicomycicola trifurcatus* new genus, new species. A. Light micrograph (LM) of anterior end, dorsal view. B. Drawing of anterior end, dorsal view. C. Drawing of anterior end, ventral view. D. LM of pygidium, dorsal view.

slender tridentate chaetae (10–20); and numerous minute chaetae with mucronate tips (Miura & Hashimoto 1996).

Based on its unique set of morphological characters, we consider *V. trifurcatus* to be a new genus and species. A key to nautiliniellid species is provided to aid in identification; most species are location and host specific.

The terminology and interpretation of prostomial appendages in this family is the subject of some debate (Blake 1993, Miura & Hashimoto 1996), suggesting the need for a re-evaluation and revision of this family and its genera once a consistent diagnosis of prostomial appendages can be applied.

Color dimorphism was a distinctive character of live *V. trifurcatus*, but on preservation the color variation was lost. Polychaetes with green parapodia in new collections (2003) were all gravid females. In other nautiliniellid species, color dimorphism corresponds to sexual dimorphism (Miura & Hashimoto 1996, Miura 1998). We have yet to confirm that the pale colored specimens are males. With the discovery of each new species in the Nautiliniellidae, we learn more about the ecology of these worms and their relationship with their host bivalves; we still know little about the internal anatomy, reproductive biology and larval characteristics, or the trophic ecology of this polychaete family.

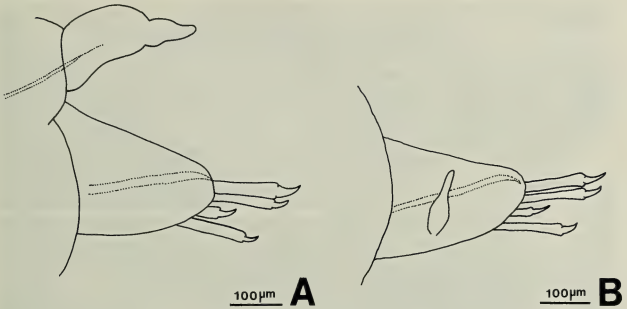


Fig. 3. *Vesicomycicola trifurcatus* new genus, new species. A. Drawing of mid-body parapodium with embedded aciculum and dorsal cirrus; lateral view. B. Drawing of mid-body neuropodium and ventral cirrus; ventral view.

Key to the species of Nautiliniellidae

- 1a. Prostomial appendages (palps or antennae) absent *Miura spinosa* Blake, 1993
- 1b. One or two pairs of prostomial appendages present 2
- 2a. Tentacular segment with only one pair of cirri 3
- 2b. Tentacular segment with one pair of dorsal and ventral cirri 7
- 3a. Tentacular segment with or without neurochaetae; all neuropodial hooks slender 4
- 3b. Tentacular segment without neurochaetae; some neuropodial hooks stout 5
- 4a. Neurochaetae ≥ 20 (up to 35) per parapodium; neurochaetae with inflated, subdistal stems and slightly curved, pointed distal ends *Mytilidiphila enseisensis* Miura & Hashimoto, 1993
- 4b. Neurochaetae ≤ 20 per parapodium; neurochaetae with rounded tips and slightly curved, distal ends *Mytilidiphila okinawaensis* Miura & Hashimoto, 1993
- 5a. Only one type of neurochaeta present: large, stout hooks 6
- 5b. Two types of neurochaetae present: One to two large, stout hooks and 15–20 small, mucronate tipped chaetae (in crows of 2) *Laubierus mucronatus* Blake, 1993
- 5c. Three types of neurochaetae present: \leq five stout hooks with minute projection on cutting fang, 10–20 tridentate chaetae, and numerous minute, slender chaetae with single mucronate spin *Theyomytilidicola tridentatus* Miura & Hashimoto, 1996
- 6a. Maximum of one to two stout hooks per parapodium *Petrecca thyasira* Blake, 1990
- 6b. Maximum of seven to eight stout hooks per parapodium *Flascarpia alvinae* Blake, 1993
- 7a. One type of neurochaetae present ... 8
- 7b. Two types of neurochaetae present .. 9
- 8a. One large, stout hook per parapodium *Nautiliniella calyptogenicola* Miura & Laubier, 1989
- 8b. Maximum of four stout hooks per parapodium, and branchiae-like notopodial projections present *Thyasiridicola branchiatus* Miura & Hashimoto, 1996
- 8c. Number of anterior stout hooks variable (2–25) and notopodial branchiae-like projections absent 10

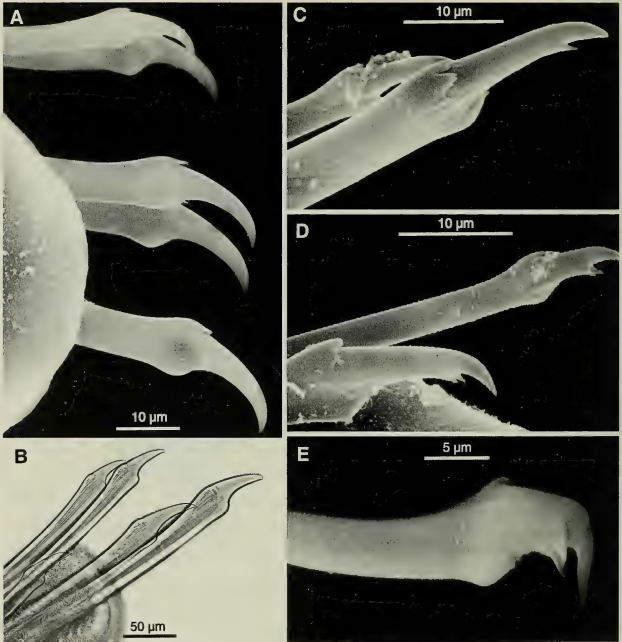


Fig. 4. *Vesicomycicola trifurcatus* new genus, new species. A. SEM of simple anterior neuropodial hooks. B. LM of anterior neuropodial hooks. C. SEM of mid-body chaetae with small apical tooth near tip, appearing slightly bifid. D, E. SEM of posterior trifurcate chaetae.

- 9a. Neurochaetae with two to three stout hooks and numerous bifurcate simple chaetae 11
- 9b. Neurochaetae with four to seven stout hooks per parapodium present anteriorly and five to seven trifurcate hooks posteriorly . . . *Vesicomycicola trifurcatus*, new genus and species
- 10a. Notopodia in middle regions especially elongate; middle to posterior

- neuropodia with a single hook with strongly curved distal fang . . . *Shinkai longipedata* Miura & Ohta, 1991
- 10b. Notopodia not elongate in any regions; middle to posterior neuropodia with a single hook, strongly curved on distal end with knob on tip *Shinkai sagamiensis* Miura & Laubier, 1990
- 10c. Notopodia in middle regions slightly

elongated; middle to posterior neuropodia with \geq five, slightly curved hooks *Shinkai semilonga*
Miura & Hashimoto, 1996

11a. Short, conical notopodia on middle segments *Natsushima bifurcata*
Miura & Laubier, 1990

11b. Elongate notopodia on middle segments *Natsushima graciliceps*
Miura & Hashimoto, 1996

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Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa). Part 4: The genus *Paracalyptophora* Kinoshita, 1908

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Abstract.—Previously undocumented from the western Atlantic, three new species of *Paracalyptophora* are described from this region. In order to facilitate comparisons, all six species in the genus are diagnosed, illustrated, included in a dichotomous key, and compared in a table of distinguishing characteristics. *P. kerberti* is herein designated the type species of *Paracalyptophora*. Additional specimens are reported of all six species. *Paracalyptophora* is now known to occur in the central and South Pacific and both sides of the North Atlantic at depths of 150–1480 m.

Kinoshita (1908:58), in his report on Primnoidae from Japanese waters, recognized the sharp distinction between species of *Calyptophora* having the large sclerites of the body of the polyp inseparably fused to form solid rings, as in the type species *C. japonica* Gray, and those in which the large sclerites encircling the body of the polyp remain separable and unfused. For the latter he established the subgenus *Paracalyptophora* including *Calyptophora kerberti* Versluys, *C. mariae* Versluys, and *C. josephinae* (Lindström). This subgenus was not recognized by subsequent authors until it was elevated to generic status in keys but without further description (Bayer 1981:937; Bayer & Stefani 1989:455).

Dredging and trawling in the western Atlantic by several research vessels, including the USFC steamer *Albatross* and R/V *Gerda*, obtained many specimens referable to three species of *Paracalyptophora*, which are described herein.

Material and Methods

Most of the specimens reported in this paper were collected by the R/V *Gerda*, a vessel operated by the University of Miami, the specimens later deposited at the USNM.

Other specimens were collected by the: *Albatross*, *Oregon*, *Silver Bay*, *Chalcal II* (MNHN), and *Atlantis* (MCZ).

Designation of polyp scales follows the terminology used by Versluys (1906) as amplified by Bayer et al. (1983). Synonymies are purported to be complete. The SEM photomicrographs were taken by the authors on a variety of instruments in the SEM Lab at the NMNH.

The following abbreviations are used: *Alb*—USFWS *Albatross*; *G*—R/V *Gerda*; *H:W*—height to maximum width of an opercular scale; *IL*—inner-lateral opercular scale; *JSL-I*—*Johnson Sea-Link-I*; *MCZ*—Museum of Comparative Zoology, Harvard, Cambridge; *MNHN*—Muséum national d'Histoire naturelle, Paris; *MOM*—Musée Océanographique, Monaco; *NMNH*—National Museum of Natural History, Smithsonian, Washington, D.C.; *O*—R/V *Oregon*; *SB*—R/V *Silver Bay*; *OL*—outer-lateral opercular scale; *SEM*—Scanning Electron Microscope stub number (unprefaced number in Bayer series, Cairns series prefaced with a C); *USNM*—United States National Museum (now the NMNH); *ZMA*—Zöologisch Museum, Amsterdam; *ZMB*—Zoologisches Museum, Berlin.

Subclass Octocorallia

Order Alcyonacea

Suborder Calcaxonina

Family Primnoidae Gray, 1858

Genus *Paracalyptrophora* Kinoshita, 1908

Calyptrophora.—Versluys, 1906:104 (part).—Kükenthal, 1919:468 (part); 1924:317 (part).—Aurivillius, 1931:301 (part).—Deichmann, 1936:171 (part).—Bayer, 1956: F221 (part).—Tixier-Durivault, 1987:171 (part).

Calyptrophora (Paracalyptrophora) Kinoshita, 1908:58.

Paracalyptrophora Bayer, 1981:937, 946.—Bayer & Stefani, 1989:455 (in key only).—Bayer, 2001:367.

Type species.—*Calyptrophora kerberti* Versluys, 1906, here designated.

Diagnosis.—Primnoidae with verticillate polyps directed downward, enclosed in two pairs of large abaxial scales (i.e., basal and buccal) extending around body to form rings, a pair of smaller infrabasals, and in one species a variable number of small adaxial buccals. The two pairs of large body wall scales are never inseparably fused, sometimes not even meeting at adaxial side of body. When present, sclerites of tentacles are few and small, but usually absent entirely. Branching dichotomous, in one or two fans.

Description.—Colonies are dichotomously branched in one plane or in two parallel fan-shaped planes, with polyps always arranged in whorls and directed downward. The polyps are armed with two pairs of large abaxial scales that nearly or completely encircle the body. They may be so firmly wedged together by the complex sculpture along the abaxial midline that a few pairs may remain joined through cleaning and preparation, but they are not inseparably fused abaxially or adaxially to form solid rings; in many cases the members of the buccal pair do not even meet adaxially. One pair of curved infrabasal scales lies between the large basal scales and the sclerites of the coenenchyme. Eight roughly tri-

angular scales/plates fold over the retracted tentacles to form an operculum covering the retracted tentacles and closing the buccal aperture. In one species, small adaxial buccal scales may be developed below the adaxial opercular scales. The tentacles are either without sclerites, or have extremely small scales in such small numbers as to be easily overlooked. The axis is stiff, brittle, heavily calcified, weakly grooved longitudinally, brownish or blackish and sometimes with metallic luster; the holdfast is calcareous, irregularly discoidal, attached to solid substrate.

Distribution.—Southwestern Pacific (Timor Sea, Norfolk Ridge), Japan, Hawaii, and the North Atlantic; 150–1480 m.

Remarks.—So far as known, the correlation of downward facing polyps and two pairs of large, unfused body scales is unique for this genus. Although the members of basal and buccal abaxial body scale pairs are separate and unfused, they sometimes are so tightly interlocked by the complex tubercular sculpture of the margins that meet along the abaxial suture that they remain attached even after maceration in sodium hypochlorite solution. The adaxial processes of the basal pair may meet but are not permanently united, and the abaxial symphysis usually separates during manipulation for mounting.

The following key begins with a determination of the gross colony form; however, if only branch fragments are available, this can be problematic. In that case, the tabular key (Table 1) can be used to distinguish all six species. In fact, the shape, size, and ornamentation of the buccal scales alone are probably adequate to distinguish the six species.

Key to the Six Species of
Paracalyptrophora
(Atlantic species in bold face)

1. Colonies in the shape of a single large fan; mature colonies over 40 cm in height 2
- 1'. Colonies in the shape of two rounded,

- parallel fans; mature colonies usually less than 30 cm in height 3
- 2. Distal margin of buccal scales only slightly flared, revealing most of the opercular scales in abaxial view; dorso-lateral edge of buccal scales ridged *P. josephinae* (Lindström, 1877)
- 2'. Distal margin of buccal scales strongly flared, obstructing view of most of the underlying opercular scales; dorso-lateral margin of buccal scales not ridged *P. simplex*, n. sp.
- 3. Dorso-lateral margin of buccal scales ridged; coenenchymal scales also ridged 4
- 3'. Dorso-lateral margin of buccal scales granular or smooth, but not ridged; coenenchymal scales granular, but not ridged 5
- 4. Dorso-lateral margin of basal scales not ridged; dorso-lateral margin of buccal scales with one low ridge; tentacular sclerites present *P. carinata*, n. sp.
- 4'. Dorso-lateral margin of basal scales having 3 or 4 prominent ridges; dorso-lateral margin of buccal scales with 4 or 5 prominent ridges; tentacular scales absent *P. mariae* (Versluys, 1906)
- 5. Polyps small (1.0–1.2 mm in length); adaxial buccals absent; sclerites uniformly granular; tentacular sclerites absent *P. duplex*, n. sp.
- 5'. Polyps large (over 2 mm); 1–5 adaxial buccals usually present; sclerites smooth with only slight indication of granularity; tentacular sclerites present *P. kerberti* (Versluys, 1906)

***Paracalyptophora duplex*, new species**
 Figs. 1A–D, 2A–D, 3, 4 A–K

Primnoa regularis Duchassaing & Michelotti, 1860:17, pl. 1, figs. 12–13 (see Remarks herein).

Material examined/Types.—Straits of Florida off Cape Canaveral: 28°08'N, 80°04'W, 49 m (depth suspect), O-5191, 14 Jan 1965, one small colony lacking holdfast and most of main stem, USNM 52755, paratype.

Northwest of Little Bahama Bank: 27°37.65'N, 78°58.74'W, 404 m, JSL-I-

3572, 10 Aug 1993, one large colony lacking holdfast, USNM 93960, paratype.

North of Little Bahama Bank: 27°29.5'N, 78°37.5'W, 485–496 m, G-252, 5 Feb 1964, one dry specimen with commensal galatheid crab, USNM 52747 (SEM 1744), paratype.

West of Little Bahama Bank: 27°21'N, 79°15'W, 439–503 m, SB-440, 29 Dec 1958, 3 damaged colonies, and detached branches, USNM 51264 (SEM C1045), paratypes.

Off Southwest Point, Grand Bahama: 26°35'N, 78°25'W, 329–421 m, G-692, 21 Jul 1965, one branch, USNM 52748; one nearly complete small colony lacking holdfast, USNM 52749; one colony, USNM 52752; 3+ broken branches, USNM 52753, paratypes.

Off Southwest Point, Grand Bahama: 26°29'N, 78°39'W, 247–374 m, G-697, 22 Jul 1965, one nearly complete small colony with part of holdfast, USNM 52745, paratype.

Off Southwest Point, Grand Bahama: 26°28'N, 78°37'W, 555–575 m, G-695, 22 Jul 1965, one branch, USNM 52756, paratype.

Off Southwest Point, Grand Bahama: 26°27'N, 78°43'W, 522–489 m, G-706, 22 Jul 1965, one young colony lacking holdfast, USNM 52746 (SEM 1752); 3 more or less complete colonies and detached branches, USNM 52754 (SEM 263, 1755, 1756), paratypes.

Off Southwest Point, Grand Bahama: 26°27'N, 78°43'W, 384–403 m, G-533, 4 Mar 1965, one colony, USNM 52751 (SEM C1046–47), holotype; 2 damaged colonies, one denuded incomplete axis, and detached branches, USNM 52750 (SEM 1753, 1754, C1042); one young colony, USNM 100773, paratypes.

Off Havana: 23°10'39"N, 82°20'21"W, 389 m, Alb-2350, 20 Jan 1885, one intact colony and many damaged branches, USNM 17314, paratype.

South of Great Inagua Island: 20°43'N, 73°29'W, 448 m, O-5416 24 May 1965, one

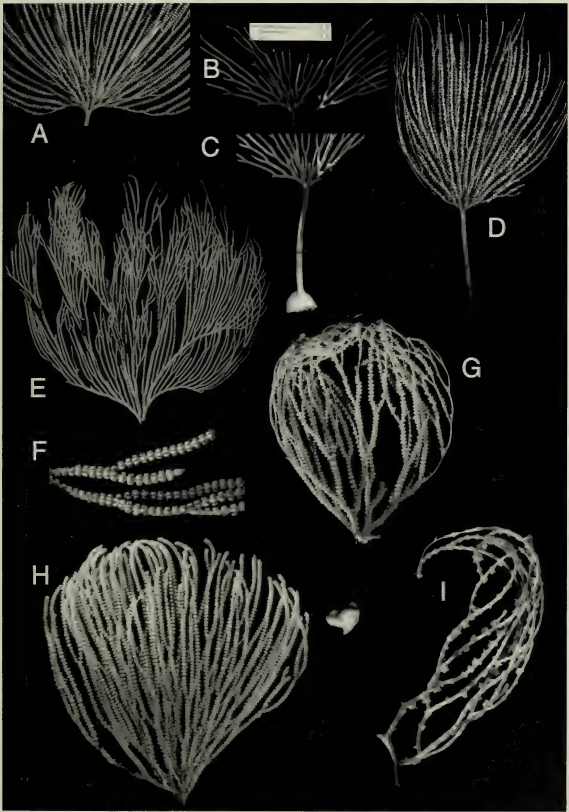


Fig. 1. A-D, *Paracalyptophora duplex* (A, paratype from G-252, USNM 52747; B, C, holotype of *Primnoa regularis*, Turin Coel. 275; D, holotype, USNM 52751): A, base of double fan showing enclosed galatheid crab, $\times 0.36$; B, upper part of colony with broken branch in place, $\times 0.25$; C, lower part of colony showing calcified holdfast, $\times 0.25$; D, complete holotype, $\times 0.31$. E, *P. simplex*, holotype USNM 52767, $\times 0.15$. F, *P. josephinae*, Atlantis 23-152, USNM 100788, branch fragment, $\times 1.0$. G, *P. carinata*, holotype, USNM 49948, complete colony and holdfast, $\times 0.33$. H, *P. mariae*, Chalcal II, CP25 (MNHNP), colony, $\times 0.25$. I, *P. kerberti*, Alb-5093, USNM 30105, $\times 1.0$.

colony without holdfast (dry), USNM 1008871, paratype.

Holotype of *Primnoa regularis*, Guadeloupe, Museo Regionale di Scienze Naturali, Turin, Coel. 275 (ex. 175), 1 complete dry colony and several broken branches, all polyps lost (SEM C1043-44).

Type locality.—26°27'N, 78°43'W (off Southwest Point, Grand Bahama), 384-403 m.

Description.—Colonies consist of a robust, vertical main stem and a pair of parallel, dichotomously branching fans. The stem is anchored in a dense, white, calcareous, semi-hemispherical holdfast, the largest known 32 mm in diameter. Most damaged specimens are broken above the holdfast; only four of the specimens reported herein are complete in this regard. The main stem is inflexible, 7-10 cm in height, up to 8 mm in diameter, and usually round in cross section, although in large specimens the stem is slightly compressed in a direction perpendicular to the fan. In large colonies, the main stem constitutes about 35% of the height of the colony. The underlying stem axis is golden or black-brown, faintly longitudinally striate, and, when dried, often splits longitudinally to reveal a lighter colored central core. The first bifurcation of the main stem, which results in two branches, is in the plane of the eventual fans; the second series of bifurcations, which results in four branches, is perpendicular to the fans; and the third and all remaining bifurcations are in the plane of the fans. The length of the internode between the first and second bifurcations is quite short (e.g., 1.5 mm) and in most colonies, except for small ones, this internode is subsumed into the second internode, such that it would appear as though the first division of the main stem is into four robust branches that are oriented perpendicular to the fans. All higher order branching is dichotomous and equal such that both branches are of the same diameter, neither one seeming to dominate (and thus not lyriiform). In some cases, one half of a dichot-

omy remains simple or divides at a much wider interval than usual so that adjacent branches do not interfere with one another, but in general, most of the branching occurs within 5 cm of the top of the main stem, resulting in many elongate, unbranched terminal branches up to 11-13 cm in length. Rarely are there more than 7 nodes leading to a terminal branch, the most highly divided branches being those on the margin of the colony fans. A large colony might have 23-30 terminal branches per fan, or 46-60 terminal branches in the colony. The distance between adjacent branches of a fan is usually only 2-4 mm, whereas the distance between the two parallel fans is 12-15 mm. A fully developed fan is usually wider than tall, large fans measuring 21-25 cm across and 15-16 cm tall, thus occupying the top $\frac{2}{3}$ of the colony height. The holotype is 23.5 cm tall and 14 cm wide, with a main stem length (broken) of 7.6 cm, but the largest known specimen (holotype of *P. regularis*) is 27 cm tall, 25 cm wide, with a complete main stem length of 10 cm.

Polyps are arranged in regular whorls and directed downward. Usually the whorls are composed of three polyps, but whorls of 4 or 5 may occur on the proximal part of the branches; in some colonies, whorls of 4 or even 5 predominate; 14-20 whorls occupy 3 cm of axial length, but the variation in any one colony is not usually so great. In general, polyps are well spaced, in that polyps within a whorl do not touch one another and there is a distance of 0.40-0.45 mm between adjacent whorls. Polyps are present on the stalk in small colonies, but in large specimens they are absent from both stalk and the lower part of major branches; polyps are also often missing from the side of the branches that face the opposite fan. Polyps are 1.0-1.2 mm in length and 0.65-0.80 mm in width.

Each polyp is protected by two pairs of large abaxial body scales and a smaller pair of infrabasals. The infrabasals are the smallest of the body wall sclerites, only about 0.20 mm in maximum height, cres-

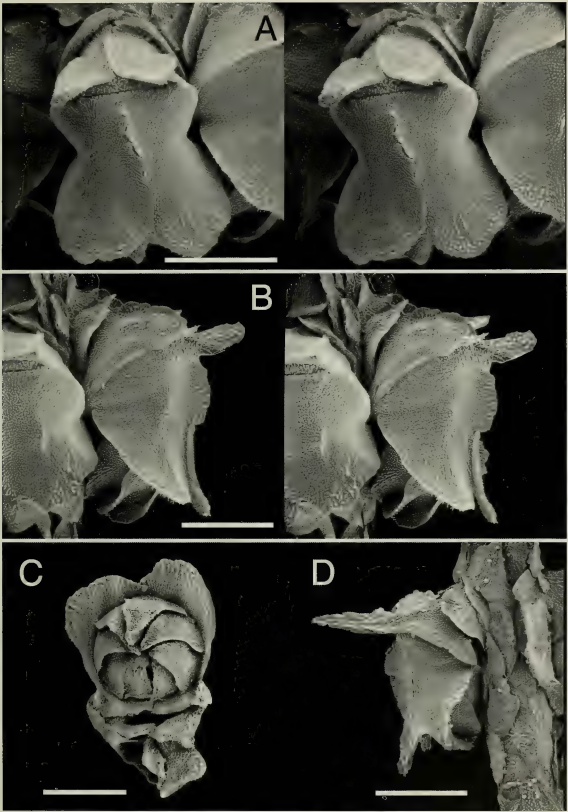


Fig. 2. *Paracalyptrophora duplex* (A, B, D, paratype from G-706, USNM 52754; C, holotype, USNM 52751): A, abaxial stereo view of polyp; B, lateral stereo view of polyps; C, opercular view of a polyp; D, lateral view of a polyp with jagged-edged buccal scales. Scale bars 0.5 mm.

cent-shaped, and anchor the polyp to the branch coenenchyme. The basal scales are much larger, up to 1.1 mm, and project perpendicular to the branch. Each basal bears a serrate, projecting spine at its dorso-lateral margin, the spine variable in shape ranging from short and broad to tall and slender, the latter constituting slightly over half the height of the scale. These spines usually bear one finely serrate ridge on their outer side, which is continuous with a ridge on the dorso-lateral margin of the basal scale and which extends only about half way to the base of the basal scale. Tall, slender basal spines also have three more ridges separated by 90°, whereas broad basal spines have 8–10 small parallel ridges on their inner face. The upper, inner face of the basals has a small ridge that hinges with the straight proximal margin of the adjacent buccal scale. The buccal scales are slightly shorter (0.9–1.0 mm) but much broader than the basals, and have a free, flared distal margin (0.15–0.25 mm) that encloses the opercular scales and obstructs a view of the operculars from the adaxial side. The projecting buccal margin, which is translucent due to a thinning of the scale as well as a replacement of the inner tubercles with short spines, may be evenly rounded, produced as a broad lobe on each side (Figs. 2A–C), or divided into 2 or 3 more or less acute, flat lobes, the latter condition more common in young colonies (Fig. 2D). This character varies to a considerable extent even in a single specimen. Whereas the abaxial margins of the basal scales meet as a sharp, raised crest along the abaxial suture, the buccal scales overlap one another at the abaxial midline, often in one direction along half the length, and in the opposite direction along the other half (Fig. 2A). The dorso-lateral margins of the buccals are evenly rounded, not ridged. The outer surfaces of the body scales and operculars are uniformly covered with small (8–10 μ m diameter), rounded to sharp granules, and their inner surfaces by crowded, complexly ornamented tubercles also 8–10 μ m in di-

ameter. The opercular scales are triangular in shape, decreasing in size from the abaxials (length = 0.48 mm, H:W 1.55) to the adaxials (length = 0.29 mm, H:W = 1.1). As is typical for many primnoids, the ad- and abaxials are symmetrical in shape, whereas the outer- and inner-laterals are asymmetrical, each class of operculars being more developed on their abaxial margin and thus having an off-centered keel. All operculars bear a prominent keel on their distal, inner surface as well as a field of crowded tubercles that concentrate on the central and basal regions. The lateral regions under the opercular scales are bare or covered with short spines and opercular margins are usually finely dentate, each equilateral triangular tooth being about 3 μ m in height (Fig. 4E). The upper surface of the operculars is covered with smooth granules like the body wall scales. The tentacles appear to be devoid of sclerites.

Coenenchymal scales are polygonal to elongate in shape, ranging from 0.15 to 0.80 mm in length, but on average about 0.4 mm. Those on the main stem occur as two layers, a lower layer of flattened sclerites, and an upper layer of thicker (0.06–0.10 mm), rotund scales that are fitted in a closely abutted, mosaic pattern (Fig. 4G–H). The coenenchymal scales of the branches occur in one layer and are flattened (0.02 mm thick), with slightly overlapping margins. Both types of coenenchymal scales are covered exteriorly with small (10–12 μ m diameter) granules, most of which are independent but occasionally are linked in short rows that appear to radiate outward from near the center of the scale, but ridges are never present. Their inner surfaces are covered with complex tubercles 8–12 μ m in diameter. Coenenchymal scales also cover the basal holdfast. The black axial background gives the translucent coenenchymal scales a milky white color.

Etymology.—Latin *duplex* = double or twofold, an allusion to the double fan-shape of the colonies.

Comparisons.—*Paracalyptophora du-*



Fig. 3. Distribution of *Paracalyptophora duplex*.

plex is compared to *P. simplex* in the account of that species and to other congenetics in Table 1.

Distribution.—Straits of Florida from off Cape Canaveral to Havana; Bahamas (Grand Bahama Island and south of Inagua); Lesser Antilles (Guadeloupe) (Fig. 3); 374–555 m.

Remarks.—The convex space between the two parallel fans appears to provide an ideal niche for galatheid crabs, one of which in each colony may place its abdomen in the region of dense branching at the top of the main stem, and orient its claws along the branching orientation of the fans (Fig. 1A). Coral and crab appear to be the same color.

Examination of the dry, somewhat damaged holotype (deposited at the Turin Museum) of *Primnoa regularis* Duchassaing & Michelotti, 1860 (Figs. 1B–C), which was

designated as the type species of the genus *Narella* by Gray (1870), shows it to be conspecific with *P. duplex*. Even though this specimen no longer retains any polyps or polyp sclerites, the branching of the colony and the coenenchymal sclerites are perfectly consistent with this species, and thus logically would have nomenclatural priority. However, following strict nomenclatural priority would cause widespread confusion within primnoid taxonomy. For instance, because *P. regularis* was chosen as the type of *Narella*, the three species heretofore placed in *Paracalyptophora* would now be placed in the genus *Narella*, and the 25 species heretofore placed in *Narella* would have to be transferred to the next available generic name, i.e., *Calypterinus* Studer, 1887. Furthermore, the morphological relationship implied by the names *Calyptrophora* and *Paracalyptrophora* would be

Table 1.—Distinguishing characteristics of the six species of *Paracalyptophora* (Atlantic species in bold face).

	<i>P. duplex</i> , n. sp.	<i>P. simplex</i> , n. sp.	<i>P. josephinae</i> (Lindström, 1877)	<i>P. carinata</i> , n. sp.	<i>P. mariae</i> (Verity, 1906)	<i>P. kerberti</i> (Verity, 1906)
Number of Fans	2	1	1	2	2	2
Maximum Colony Height (cm)	27	41	55	23	27.5	24
Maximum Main Stem Height (cm); % of total Height	10 (37%)	11 (22%)	20 (36%)	5 (22%)	5.5 (18%)	9 (37%)
Branching	Dichotomous (not lyrate)	Dichotomous (lyrate)	Dichotomous (not lyrate)	Dichotomous (not lyrate)	Dichotomous (not lyrate)	Dichotomous (not lyrate)
Polyp Length/Width (mm)	1.0–1.2/0.65–0.80	1.3–1.5/0.80–0.95	1.3–1.5/0.75–0.90	1.50–1.75/0.80–0.92	1.4–1.8/0.90	2.0–3.0/1.20–1.25
Separation of Adjacent Whorls (mm)	0.4–0.45	0.10–0.25	0.4–0.6	0.60–0.65	0.5–1.0	0.5–2.0
Polyps/Whorl	3–5	4–6–8	4–6–7	4–6–8	4–5–7	4–5–8
Whorls/3 cm	14–18–20	14–17–20	13–14–17	12–14–16	11–15	8–10–13
Dorso-lateral Edge of Basal Scale	Short ridge	Short ridge	Prominent ridge	Not ridged	3–4 prominent ridges	Smooth
Dorso-lateral Edge of Buccal Scale	Evenly rounded	Rounded, but with aligned granules	Multiple low ridges	Low ridge	4–5 prominent ridges	Smooth
Distal Edges of Buccal Scales	Flared; usually lobate, sometimes divided	Flared; lobate or divided	Slightly flared; evenly rounded	Not flared; straight; serrate	Slightly flared; curved outward	Slightly flared; even to spinose
Abaxial Buccal Scales	0	0	0	0	0	0–5
Max. Length of Abaxial Opercular Scales	0.48 mm	0.56 mm	0.57 mm	0.85 mm	0.83 mm	1.10 mm
Branch Coenenchyme Scales	Granular, not ridged	Granular, not ridged	Granular, not ridged	Granular and prominent ridges	Granular and prominent ridges	Granular, not ridged
Max. Length of Tentacular Sclerites	None noted	None noted	None noted	82 μ m	None noted	92 μ m
Distribution	Straits of Florida, Bahamas, Lesser Antilles; 374–555 m	Insular side of Straits of Florida; 165–706 m	Eastern Atlantic; 214–1480 m	Lesser Antilles; 514 m	South Pacific; 418–520 m	Japan; 150–731 m

lost. To avoid this widespread changing of generic combinations and the confusion that it would cause, we will suggest to the ICZN that the type of *Primnoa regularis* be suppressed and a neotype be designated (ICZN, 1999: article 75.6, conservation of prevailing usage by a neotype), a specimen that is consistent with the current understanding of the genus *Narella* and with the species *N. regularis* as described by Cairns & Bayer (2003).

***Paracalyptrophora simplex*, new species**

Figs. 1E, 4L–T, 5A–C, 9

Material examined/Types.—North of Little Bahama Bank: 27°34.5'N, 78°49'W, 488–516 m, G-254, 6 Feb 1964, broken branches probably of a single colony, USNM 52769, paratype.

North of Little Bahama Bank: 27°29.5'N, 78°37.5'W, 485–496 m, G-252, 5 Feb 1964: one large dry colony (holotype), USNM 52767 (SEM 1757, 1758, C1049–51); 5 branches, USNM 52757; one colony, USNM 52763; one large dry colony, USNM 52764; one large dry colony, USNM 52765; one large dry colony, USNM 52766; four dry branches, USNM 52768, paratypes.

Off Settlement Point, Grand Bahama: 26°45'N, 79°05'W, 494–530 m, G-1125, 13 Jun 1969, 6 branches and fragments, USNM 52762 (SEM 265, 267, 1731), paratypes.

Straits of Florida: 26°38'N, 79°02'W, 516 m, G-1312, 31 Mar 1971, detached branches, USNM 57556, paratypes.

Off Southwest Point, Grand Bahama: 26°31'N, 78°51'W, 366 m, G-503, 4 Feb 1965, 3 dry colonies, USNM 52770 (SEM 1760, 1761, 1771), paratypes.

North of North Bimini, Bahamas: 25°59'N, 79°19'W, 439–458 m, G-633, 30 Jun 1965, 5 broken branches, USNM 52759 (SEM 1721, 1722, 1747), paratypes.

North of North Bimini, Bahamas: 25°56'N, 79°22'W, 402 m, G-798, 12 Sep

1966, 2 incomplete colonies, USNM 52760 (SEM C1048), paratypes.

Off Havana, Cuba: 23°09'10"N, 82°23'W, 706 m, Alb-2152, 30 Apr 1884, 2 branches, USNM 7166, paratypes.

Yucatan Channel: 20°59'N, 86°23'00"W, 305 m, bottom temp. 17.1°C, Alb-2353, 22 Jan 1885, 2 dichotomous branches in poor condition, USNM 50087, paratypes.

Arrowsmith Bank, Yucatan: 20°57'N, 86°34'W, 165–140 m, G-899, 10 Sep 1967, one colony, USNM 52761, paratype.

Type locality.—27°29.5'N, 78°37.5'W (north of Little Bahama Bank), 485–496 m.

Description.—Colonies consist of a robust, vertical main stem, which gives rise to a fan that is uniplanar and consists of dichotomously branching elements. The stem is anchored in a white calcareous holdfast, although only one specimen was collected with the base intact. The main stem is inflexible, up to 11 cm in height and 9.6 mm in basal diameter, in large specimens compressed in the branching plane. In large colonies, the main stem constitutes about 22% of the height of the colony. The stem axis is golden or dark brown with a slightly lighter colored core, and faintly longitudinally striate. All branching is dichotomous and equal, except for the two outermost branches of the fan of larger colonies, which are often twice the diameter of the inward branching stems as well as being straight, which confers a lyrate shape to the colony. Although long end branches up to 12 cm length occur, in general, branching occurs throughout the fan at intervals of about every 1.5 cm, sometimes resulting in terminal branching that have resulted from 15 previous bifurcations. The distance between adjacent branches is about 4–5 mm. The fan is roughly the same height as width. The largest colony (the holotype) is 41 cm tall, with a fan 38 cm in height and 34 cm in width, and a broken main stem only 3 cm long.

Polyps are arranged in regular whorls consisting of 4–8 polyps (usually 6); 14–20 whorls occur in 3 cm of axial length,

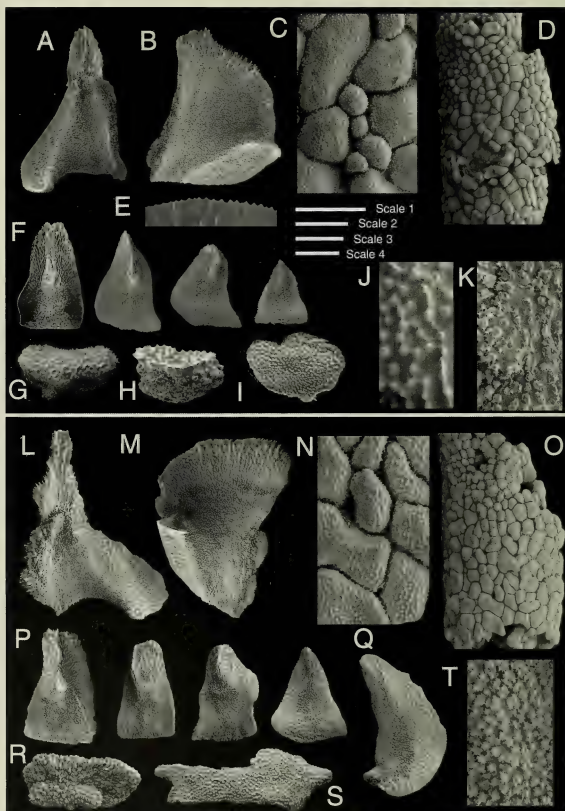


Fig. 4. A–K, *Paracalyptophora duplex* (A, B, E, F, holotype; C, D, paratype, SB-1440; G, J, K, paratype, G-533; H, I, holotype of *Primnoa regularis*, Turin Museum): A, basal scale; B, buccal scale; C, D, main stem coenenchymal scales in situ; E, distal margin of opercular scale; F, ad-, OL-, IL- and adaxial operculars; G, H, side views of coenenchymal scales from stalk; I, top of coenenchymal scale from branch; J, K, upper granular and lower warty sides of coenenchymal scales. L–T, *Paracalyptophora simplex* (L, M, P–T, holotype; N, O, paratype from G-798): L, basal scale; M, buccal scale; N, O, main stem coenenchymal scales in situ; P, ad-, OL-, IL-, and adaxial operculars; Q, infrabasal scale; R, S, lower and upper views of coenenchymal scales;

and although this range may be present within a single colony, 17 seems to be the predominant number. In general, polyps are closely spaced, i.e., adjacent polyps in a whorl are usually directly adjacent or even overlapping, and the distance between adjacent whorls is quite small (0.10–0.25 mm), such that the tip of the buccal scales of the polyps of one whorl almost touch the buccal spines of the polyp of an adjacent whorl. Polyps occur on the main stem of small colonies. Polyps are 1.3–1.5 mm in length and 0.8–0.95 mm in width.

Each polyp is protected by two pairs of large abaxial body scales and a pair of narrow, curved infrabasal scales situated between the coenenchymal sclerites and the basal pair. The body wall scales are virtually identical in shape and ornamentation to those described for *P. duplex*, differing primarily in size, those of *P. simplex* being slightly larger, i.e., the infrabasals are up to 0.33 mm in height, the basals up to 1.15 mm, and the buccals up to 1.05 mm, the latter with a flared distal margin 0.25 mm in extent, which, like that of *P. duplex*, may be produced as a single broad lobe (Figs. 4M, 5C) or divided into 2–4 acute teeth. Furthermore, the dorso-lateral margins of the basals bear only short ridges (Fig. 5B), whereas the dorso-lateral margins of the buccals often bear parallel, aligned rows of surface granules (Fig. 5A). The opercular scales are also similar in shape but slightly larger, the abaxial operculars up to 0.56 mm in length and the adaxials 0.34 mm in length, but all operculars having slightly serrate margins and a H:W ratio of 1.4–1.6, similar to that of *P. duplex*. The coenenchymal sclerites are also quite similar in size and shape to those of *P. duplex*; however, the surface granules are somewhat larger, up to 18 μ m in diameter.

Etymology.—Latin *simplex* = simple,

single, or onefold, an allusion to the colonies in the shape of a single fan.

Comparisons.—The shape of the polyps of *P. simplex* is virtually identical with those of *C. duplex*, differing primarily in having slightly larger (20–25%) sclerites and thus larger polyps. But, even though the polyps are larger, both species have the same range of polyps per cm, this because the distance between polyp whorls of *P. simplex* is shorter. In general, the polyps of *P. simplex* are more crowded, having more polyps per whorl as well as having more closely spaced whorls, these characters serving to distinguish isolated branches. Characters at the grosser (colonial) level that distinguish *P. simplex* from *P. duplex* are that it produces only one fan, it attains a larger colony size, branching occurs throughout the fan with as many as 15 nodes, and large colonies tend to have a lyrate branching pattern (Table 1).

Distribution.—Known only from the insular side of the Straits of Florida from the Yucatan Channel to north of Little Bahama Bank, Bahamas (Fig. 9); 165–706 m.

Paracalyptrophora josephinae

(Lindström, 1877)

Figs. 1F, 6A–C, 7A–G

Calyptrophora josephinae Lindström, 1877:6, pl. 1, figs. 1–3 (Josephine Bank).—Versluys, 1906:109 (re-examination of type and Studer's specimen).—Kükenthal, 1919:474 (diagnosis); 1924:319 (diagnosis and key).—Thomson, 1927:29 (Alice Bank).—Aurivillius, 1931:301, fig. 60, pl. 6, fig. 5 (re-description of type, key to species in genus).—Deichmann, 1936:172 (remarks).—Grasshoff & Zibrowius, 1983:119, pl. 1, figs. 5, 6 (Josephine Bank).—Carpine & Grasshoff, 1985:33 (MOM deposition).—

←

T, lower view of coenenchymal scale. Scale bar 1: R = 0.20 mm; 2: F, G, I, P, Q, S = 0.25 mm, H = 0.083 mm; 3: E, J, K, T = 0.05 mm; 4: A–C, L–N = 0.25 mm.

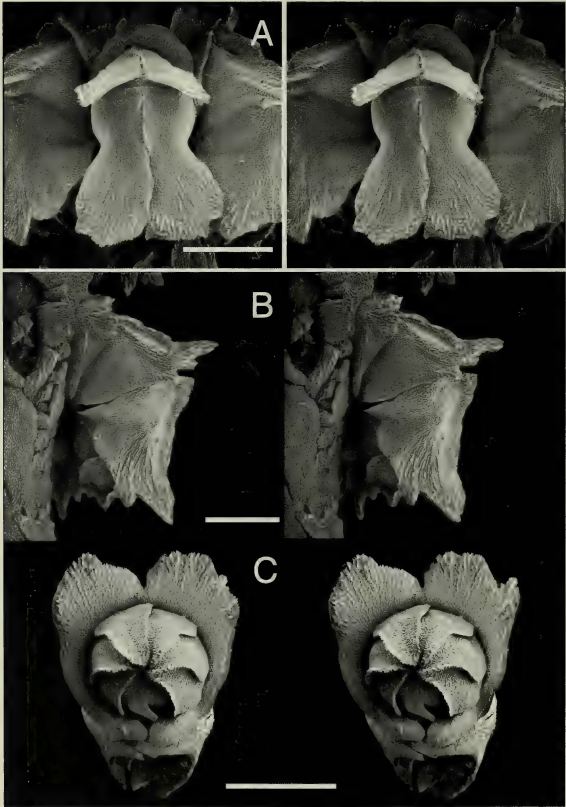


Fig. 5. *Paracalyptophora simplex* (A, C, holotype; B, paratype from G-633, USNM 52759): A, abaxial stereo view of a whorl; B, lateral stereo view of a polyp; C, opercular stereo view of a polyp. Scale bars 0.5 mm.

Grasshoff, 1985a:305 (*Talisman* specimens from Biskaya); 1985b:73 (Josephine and Great Meteor Banks); 1986:27 (remarks).

Stachyodes Josephinae.—Studer, 1901:41 (Azores).

Calyptraphora (Paracalyptraphora) josephinae.—Kinoshita, 1908:58 (taxonomic reassessment).

Paracalyptraphora josephinae.—Bayer, 1981:938, text-fig. 77 (new comb.).—Grasshoff, 1989:219 (listed).—Bayer, 2001:367 (mentioned).

Material examined.—Atlantis Seamount: 34°05'N, 30°15'W, 293 m, R/V *Atlantis* cruise 152, station 23, 26 Aug 1948, 2 dichotomous branches (MCZ, in alcohol; fragment USNM 100788) (SEM 1719).

Fragment of holotype (SEM C1052–54).

Types.—The holotype is deposited at the Swedish Museum of Natural History (1113). Type Locality: Josephine Bank (36°46'N, 14°07'W), 201–214 m, station 36n.

Diagnosis.—This species has been described three times before, the first being the detailed original description of Lindström, the second by Versluys (1906), and the third and by far the most detailed by Aurivillius (1931), all three based on the holotype or fragments of it. We have also examined a small fragment of the holotype but can add little to the previous descriptions except for what can be illustrated by SEM. Thus, only a diagnosis for this species is presented herein:

Colonies uniplanar, one of the largest (the holotype) 55 cm in height. Branching dichotomous, occurring throughout colony at intervals of 20–35 mm. Stem axis bronze to golden yellow. Polyp whorls consist of 4–7 polyps (the average being 6); 13–17 (usually 14) whorls occur over 3 cm axial length; adjacent whorls separated by 0.4–0.6 mm, depending on branch diameter. Polyps 1.3–1.5 mm in length (not 1.6 mm, as stated by Lindström) and 0.75–0.90 mm in width. Infrabasals typically crescent

shaped, 0.25–0.30 mm in height. Basals 0.75–0.90 mm in height, the distal 0.17–0.20 mm (20%) being a short, quite broad, blunt distal “spine”, which on the exposed interior face is covered with 10–12 parallel, serrate ridges (Figs. 7A–B). Each basal scale also bears one prominent ridge on its exterior dorso-lateral margin. Buccal scales up to 1.0 mm in length, having very slightly flared, evenly rounded distal margins that envelop only the proximal 0.07–0.09 mm of the opercular scales; however, the dorso-lateral margins of buccal scales usually bear 2–4 low ridges. Opercular scales typical in shape for the genus, the abaxial up to 0.57 mm, the outer- and inner laterals equal to or longer than the abaxials (0.54–0.69 mm), and adaxials up to 0.43 mm in length, all operculars having a H:W of 1.4–1.5. Coenenchymal sclerites irregular in shape, up to 0.76 mm in length, but mostly 0.4 mm in length. These scales, like those of the polyps, bear small (10 μ m diameter) blunt granules exteriorly, which are occasionally linked in short rows but never formed into ridges. Inner faces of coenenchymal scales as well as those of polyp scales bear complexly ornamented tubercles about 10 μ m in diameter. Tentacular sclerites not observed.

Comparisons.—*C. josephinae* is quite similar to *P. simplex*, as can be seen in the comparison of characters in Table 1, but differs from both *P. simplex* and *P. duplex* in having less flared and less projecting buccal scales (Figs. 6A–C), which allows a view of most of the opercular scales in abaxial view. *P. josephinae* also has fewer polyp whorls per cm because the average spacing between whorls is higher. The dorso-lateral ridges on the buccal and basal scales are more prominent than those of *P. simplex*. Finally, the short, broad basal “spines” of *P. josephinae* may be unique, these spines more accurately called a flattened lobe.

Remarks.—Apart from having “erect and regularly dichotomizing branches” (Lindström 1877:6), the form of Lindström's

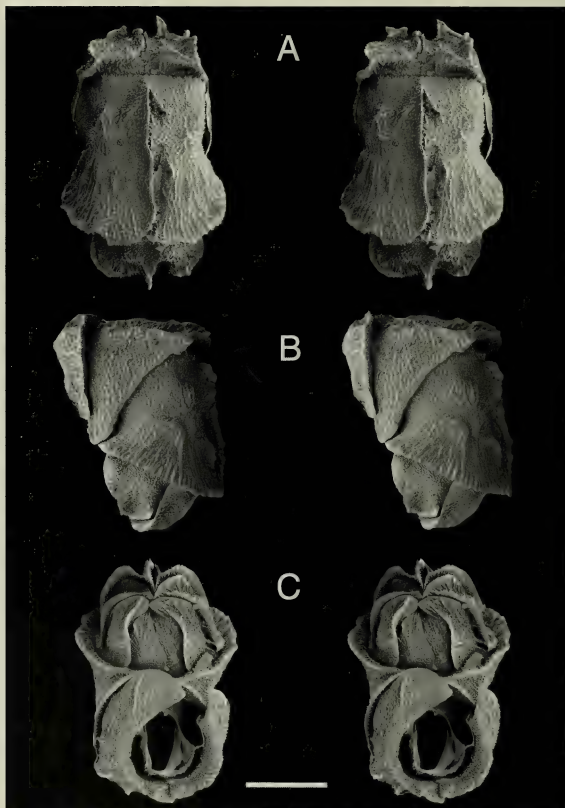


Fig. 6. *Paracalyptophora josephinae*, holotype, Swedish Museum of Natural History 1113: A, abaxial stereo view of a polyp; B, lateral stereo view of a polyp; C, adaxial stereo view of a polyp. Scale bar 0.5 mm.

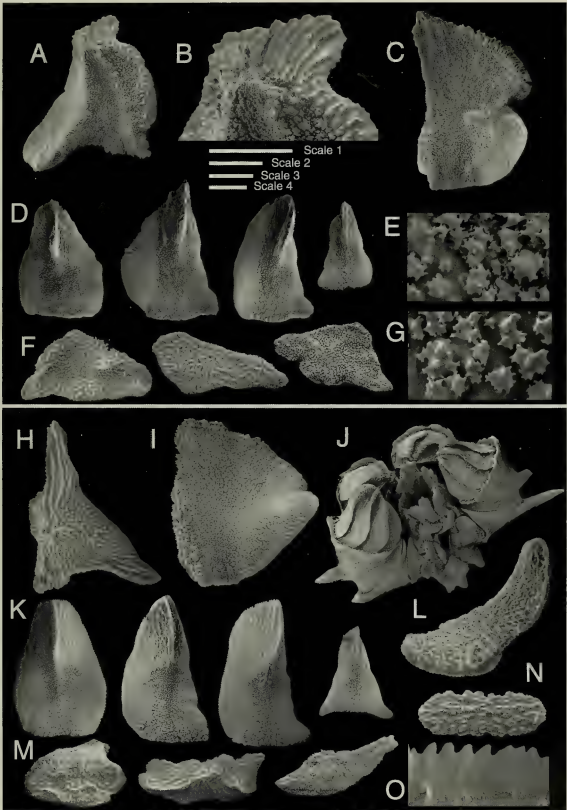


Fig. 7. A-G, *Paracalyptrophora josephinae*, holotype: A, B, inner side of basal scale, B showing the finely ridged projecting spine; C, buccal scale; D, ad-, OL, IL, and adaxial operculars; E, G, opercular and coenenchymal tubercles on lower side of opercular and coenenchymal scales, respectively; F, upper and lower faces of 3 coenenchymal scales. H-O, *Paracalyptrophora carinata*, holotype: H, basal scale; I, buccal scale; J, whorl of 4 polyps; K, ab-, OL, IL, and adaxial opercular scales; L, infrabasal scale; M, 3 coenenchymal scales showing ridging; N, tentacular scale; O, margin of opercular scale. Scale bar 1: E, G, N, O = 25 μ m; 2: D, F = 0.25 mm; J = 0.75 mm; L = 0.125 mm; 3: A, C, I, K, M = 0.25 mm; B = 0.083 mm; 4: H = 0.25 mm.

eastern Atlantic holotype and subsequently reported colonies has not been described. Evidently the "splendid specimen" 5.5 decimeters long was not available to Ver-sluis (1906) or Aurivillius (1931:301) for their re-description of Lindström's type, as Aurivillius reported only "a number of fragments, about 5–8 mm long", and we received on loan only a small branch for comparison. The size stated by Aurivillius must be centimeters rather than millimeters, as some of the pieces had one or two bifurcations. Nonetheless, Lindström's allusion to the diameter of the "basis" (=main stem) indicates that he probably had a complete colony, and, had it been a biplanar colony, Lindström surely would have mentioned this fact. Observation of the type specimen by Stockholm curator Björn Sohlenius (pers. comm., 2002) confirms that the holotype is uniplanar. Furthermore, according to M. Grasshoff (pers. comm., 2002), most of the specimens he collected and observed in situ (see synonymy) were uniplanar.

Distribution.—Eastern and mid-Atlantic: Bay of Biscay; Josephine, Great Meteor, and Atlantis Seamounts; Azores (south of Flores and Alice Bank); 214–1480 m. The undocumented references of *P. josephinae* from the western Atlantic (Grasshoff 1985b, 1986) probably pertain to the types of *P. carinata*.

Paracalyptrophora carinata, new species
Figs. 1G, 7H–O, 8A–C, 9

Calyptrophora josephinae.—Grasshoff, 1985b:73 (in part: western Atlantic reference); 1986:27 (in part: western Atlantic reference).

Material examined/Types.—Lesser Antilles, southwest of St. Lucia: 13°34'N, 61°04'W, 514 m, black sand, bottom temperature 8.4°C, Alb-2752, 4 Dec 1886, one colony (holotype) with part of holdfast, and 5 detached branches, USNM 49948 (SEM 264, C1055–56, 63), paratypes.

Lesser Antilles, between St. Lucia and

St. Vincent: 13°34'N, 61°03'W, 514 m, black sand, bottom temperature 8.4°C, Alb-2753, 4 Dec 1886, one incomplete colony with part of holdfast and tangled with hemp fibers from the tangle-bar, USNM 49968, paratype.

Type locality.—13°34'N, 61°04'W (southwest of St. Lucia, Lesser Antilles), 514 m.

Description.—Colonies consist of a robust, vertical main stem, which gives rise to a pair of parallel, dichotomously branching fans. The main stem is anchored in a dense, white, irregularly-shaped calcareous mass—the holdfast—the largest of the two observed being 18 mm in width. The main stem of the larger specimen (the holotype) is inflexible, 5 cm in height, and 4.4 mm in maximum diameter, supporting fans up to 18 cm in height and 8 cm broad, the entire colony being 23 cm in height. The stem axis is golden-yellow to bronze in color and faintly longitudinally striate. Branching is uniformly dichotomous (but not lyrate), the first two internodes being quite short, the remaining internodes, which may number up to 10 for certain terminal branches, are spaced fairly uniformly at intervals of 18–21 mm throughout the colony. Occasionally terminal branches are up to 8 cm in length. A slight irregularity in the branching pattern of the paratype has led to three of the first four branches contributing to one fan, the opposite, parallel fan being smaller, originating from only one of the original four branches.

Polyps are arranged in whorls and directed downward, each whorl consisting of 4–8 polyps (usually 6); 12–14–16 whorls occupy 3 cm of axial length. In general, polyp whorls are well spaced, such that each whorl is separated by 0.60–0.65 mm. Polyps are common on the main stem, often arranged in spirals around the axis. Individual polyps are 1.50–1.75 mm in length and 0.80–0.92 mm in width.

Each polyp is protected by two pairs of large abaxial body wall scales and a pair of smaller crescent-shaped infrabasals, which

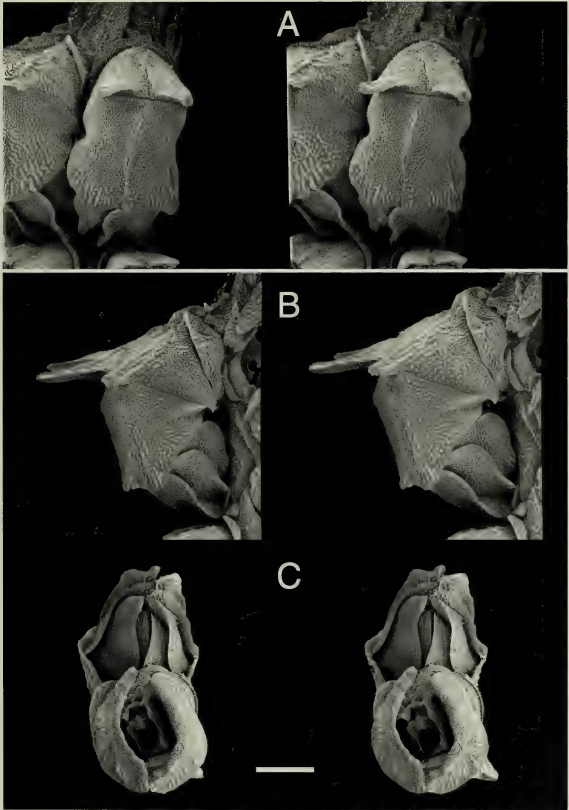


Fig. 8. *Paracalyptrophora carinata*, holotype, USNM 49948: A, abaxial stereo view of polyps; B, lateral stereo view of a polyp; C, adaxial stereo view of a polyp. Scale bar 0.5 mm.

are about 0.30 mm in height and typical in shape for the genus. The basal scales are the largest sclerites, up to 1.2 mm in height, the distalmost 0.45–0.50 mm consisting of a prominent, pointed, finely serrated spine. Each spine is covered with several rows of closely spaced teeth. The dorso-lateral margins of the basal scales are not ridged, but acutely curved to cover the lateral sides of the polyp. The buccal scales are 0.9–1.0 mm long and have fairly straight, finely serrate (apices of triangles about 6 μm tall) distal margins that are not flared and overlap the basal margins of the operculars by only 0.10–0.15 mm, which exposes most of the opercular scales in lateral or adaxial views (Figs. 8A–B). There is a slight swelling on the center of the proximal third of each buccal from which a low ridge originates and continues along the dorso-lateral margin of the sclerite (Fig. 8A). The opercular scales are triangular in shape, and, in general, decrease in size and H:W ratio from ab- to adaxial direction. Of the two abaxial operculars, usually only one is symmetrical, the other being more developed on the adaxial side. These operculars are up to 0.85 mm in height, the symmetrical one having a H:W of 1.58, the asymmetrical of 1.9. The outer-lateral operculars are of equal height but similar to the asymmetrical abaxials in shape. The inner-lateral operculars are also asymmetrical in shape but slightly smaller and squatter in shape, only up to 0.7 mm in height, having a H:W of 1.7–1.8. The adaxial operculars are symmetrical, rarely over 0.55 mm in height, and have a broad base with a H:W of 1.2–1.4. Tentacular sclerites are very rare, shaped as flattened rods up to 82 μm in length and 26 μm in width.

Coenenchymal sclerites are elongate to irregular in shape, up to 0.87 mm in maximum length. The exterior surface is covered by small granules (14–15 μm in diameter) and prominent longitudinal or reticulately arranged ridges (Fig. 7M). The inner surface of the coenenchymal scales, as well as those of the polyps, are covered with

complexly ornamented tubercles 10–12 μm in diameter.

Etymology.—Latin *carinata* = keeled, an allusion to the ridged coenenchymal scales.

Comparisons.—*Paracalyptophora carinata* is easily distinguished from the two other western Atlantic species by its polyp morphology: having non-flared, straight-edged buccal sclerites that cover only the bases of the opercular scales. In addition, *P. carinata* has larger polyps and thus less whorls per axis length, non-ridged basals, ridged coenenchymal scales, and small tentacular scales (see Table 1). Tentacular scales are also present in Japanese material of *P. kerberti* (Versluys) but the taxonomic significance of this character in *Paracalyptophora* has yet to be determined.

Paracalyptophora carinata is most similar to the eastern Atlantic *P. josephinae*, especially in polyp morphology, both species having very similarly-shaped buccal scales with non- or only slightly flared, straight distal margins. However, *P. carinata* differs in having a biplanar colony and having larger polyps with consequently larger opercular scales. It also has much taller basal spines and a lesser developed dorso-lateral ridge of the basal scales. Furthermore, *P. carinata* has non-flared buccal scales, whereas those of *P. josephinae* are slightly flared, and the operculars of *P. carinata* are pointed outward, whereas those of *P. josephinae* are usually pointed downward toward the branch axis. Each of these differences taken separately might indicate range of variation or perhaps a subspecies of *P. josephinae*, but taken together these consistent differences are considered to warrant differentiation as a different species.

Distribution.—Known only from southwest of St. Lucia, Lesser Antilles (Fig. 9); 514 m.

Paracalyptophora mariae

(Versluys, 1906)

Figs. 1H, 10A–C

Calyptophora mariae Versluys, 1906:107–109, pl. 9, fig. 25, text-figs. 140–145 (Ti-

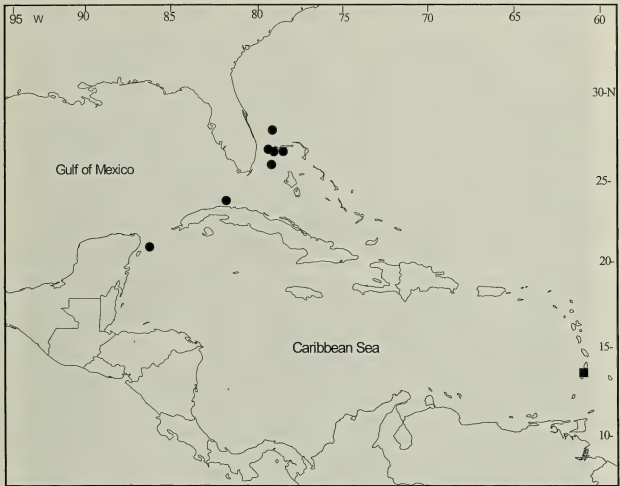


Fig. 9. Distribution of *Paracalyptophora simplex* (circles) and *P. carinata* (square).

mor Sea).—Kükenthal, 1919:474 (diagnosis); 1924:317, 318–319 (key, diagnosis).—Aurivillius, 1931:301 (key).—van Soest, 1979:103 (type deposition).

Calyptophora (*Paracalyptophora*) *mariae*.—Kinoshita, 1908:58 (listed).

Paracalyptophora mariae.—Bargibant in Forges, Grandperrin & Laboute, 1987:34 (listed).—Bayer, 2001:367 (listed).

Material examined.—Chalcal II, CP25 (HGP-44), 23°38.6'S, 167°43.12'E (Stylaster Bank, on Norfolk Ridge just southeast of New Caledonia), 418 m, 1 large colony (NMNH) and SEM stubs 1202–1204 (USNM).

Types.—A fragment of the holotype is deposited at the ZMA (Coel. 7414), but the larger colony is missing (van Soest 1979). Type Locality: 10°39'S, 123°E (Roti Strait between Timor and Roti), 520 m.

Diagnosis.—Colonies biplanar, the largest of the two known specimens (the holotype) 27.5 cm in height, consisting of a main stem 5.5 cm in height and two parallel fans, each about 22 cm in height and 16 cm in width. Branching dichotomous (equal, not lyrate), occurring every 2–3.5 cm in the lower half of fan, the distal branches often over 10 cm in length and rarely the result of more than 5 bifurcations. Stem axis black; branches often a metallic gold. Polyp whorls consist of 4–7 polyps, the larger number on thicker branches; 11–15 whorls occur over 3 cm branch axial length; adjacent whorls separated by 0.5–1.0 mm, depending on branch diameter. Polyps 1.4–1.8 mm in length and about 0.9 mm in width. Infrabasal scales crescent shaped and about 0.15 mm in height, each bearing one prominent longitudinal ridge. Basals about 0.85

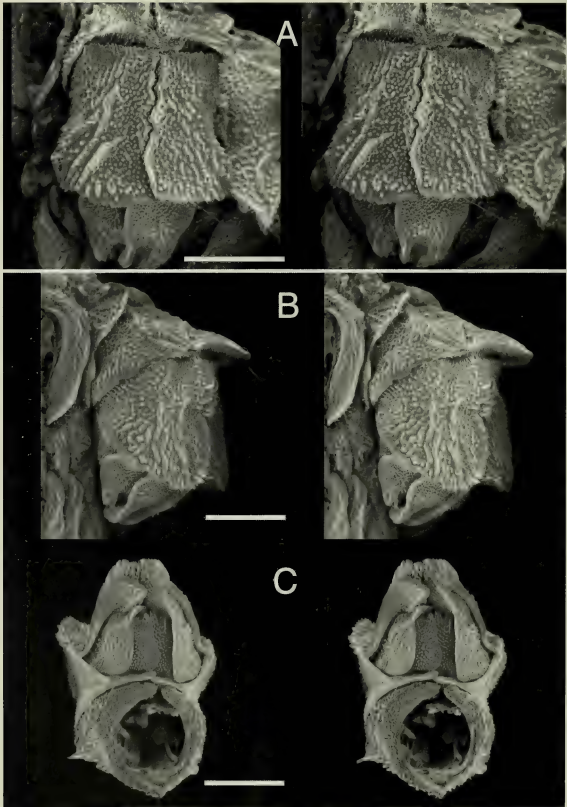


Fig. 10. *Paracalyptophora mariae*, Chalcal II, CP 25, USNM Stub 1202, 1204: A, abaxial stereo view of a polyp; B, lateral stereo view of a polyp; C, adaxial stereo view of a polyp. Scale bars 0.5 mm.

mm in height, the distal 0.20 mm being a robust, projecting spine. Dorso-lateral margins of basals bear 3 or 4 prominent, serrate ridges (Fig. 10B). Buccal scales about 0.85 mm in length and have a slightly flared and slightly projecting dorso-lateral distal margin, which nonetheless covers only the basal part (about 0.2 mm) of the opercular scales. Dorso-lateral margin of each buccal scale bears 4 or 5 prominent ridges (Fig. 10A). Operculars typical for the genus, the abaxial operculars up to 0.83 mm in height and adaxials only 0.36 mm, but most operculars maintaining a H:W of 1.5–1.7. Tentacular scales not noted. Coenenchymal branch sclerites irregular in shape, rarely more than 0.5 mm in maximum length, and covered externally with granules and prominent ridges (Fig. 10B).

Comparisons.—*Paracalyptophora mariae* is distinguished from all other species by having prominently and multiply-ridged body wall scales (Table 1), including the infrabasals, as well as ridged coenenchymal scales.

Remarks.—Despite a moderate synonymy, this species is known from only two specimens, the holotype and the specimen listed without comment by Bargibant (1987), illustrated herein, who must also be credited with the new combination. The New Caledonian specimen is similar to the description of the holotype, differing primarily in having slightly smaller polyps (1.4 mm vs. 1.6–1.8 mm) and thus more whorls per 3 cm (14–15 vs. 11–12).

Distribution.—Timor Sea and southeast of New Caledonia; 418–520 m.

Paracalyptophora kerberti
(Versluys, 1906)

Figs. 11, 11A–C, 12A–J

Calyptophora japonica.—Studer, 1878: 642 (Japan).

Calyptophora kerberti Versluys, 1906: 105–107, text-figs. 134–139 (Japan).—Nutting, 1912:59 (Japan).—Kükenthal, 1919:472–473, text-figs. 223–226 (Ja-

pan); 1924:318, text-fig. 173 (key, diagnosis).—Aurivillius, 1931:301 (key).—van Soest, 1979:103 (type deposition).—Utinomi, 1979:1011–1013, fig. 2a–i (Sagami Bay).

Calyptophora (Paracalyptophora) kerberti.—Kinoshita, 1908:58, 63–65, pl. 4, fig. 29 (Japan).

Calyptophora (Paracalyptophora) Kerberti (sic).—Kinoshita, 1909:8–9, pl. 1, fig. 2, 2 text-figs. (Japan).

Paracalyptophora kerberti.—Bayer, 2001: 367 (listed, new comb.).

Material examined.—Japan: Alb-5093, 1 colony, USNM 30105 (reported by Nutting, 1912), SEM C1058–62, 1064.

Types.—The holotype is deposited at the ZMA (Coel. 2294) (van Soest 1979). The second specimen described by Versluys, also from Japan (Hilgendorf collection), is interpreted as a paratype, and is deposited at the ZMB (2065). Type Locality: “Japan”, depth unknown (Bloemhoff collection), although Utinomi (1979) suggests that the specific type locality is Sagami Bay.

Diagnosis.—Colonies biplanar, the largest known colony (Kükenthal 1919) 24 cm in height and 11 cm in fan width; greatest stem length (Versluys 1906) 9 cm. Branching dichotomous (equal, not lyrate), most branching occurring in lower half of fan, the distal branches rarely over 6.5 cm in length are rarely the result of more than 6 or 7 bifurcations. Stem axis brown, black, or golden. Polyp whorls consist of 4–8 (usually 5) polyps; 8–13 (usually 10) whorls occur over 3 cm branch length; adjacent whorls widely spaced, 0.5–2.0 mm. Polyps 2.0–3.0 mm in length and about 1.2 mm in width. Infrabasals crescent shaped, about 0.35 mm in height. Basals 1.4–1.5 mm in height, the distalmost 0.6–0.8 mm a prominent sharp spine, which bears one finely serrate ridge on its outer surface; otherwise the basal scales are unridged and fairly smooth. Buccal scales 1.3–1.9 mm in length, the longer scales those having a dis-

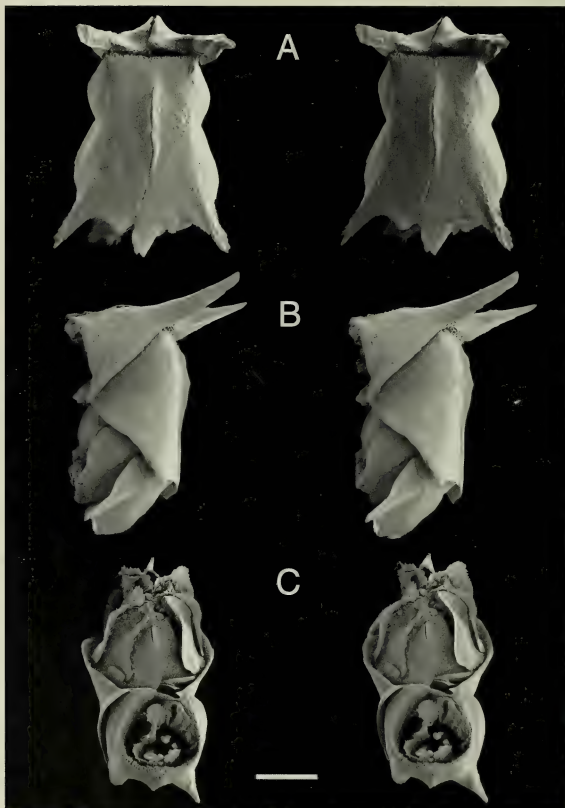


Fig. 11. *Paracalyptrophora kerberti*, Alb-5093, USNM 30105: A, abaxial stereo view of a polyp with spinose buccal scales; B, lateral stereo view of a polyp with straight-margins buccal scales; C, adaxial stereo view of a polyp. Scale bar 0.5 mm.

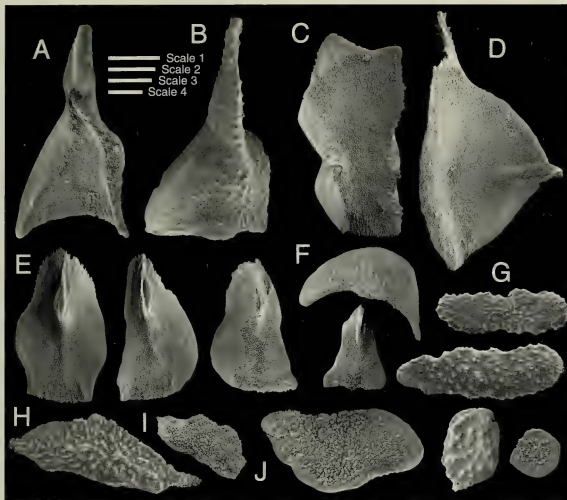


Fig. 12. *Paracalyptrophora kerberti*, Alb-5093, USNM 30105: A, B, inner and outer view of a basal scale; C, buccal scale with a small distal, triangular distal margin; D, buccal scale with a prominent distal spine; E, ab-, OL, IL, and adaxial operculars; F, infrabasal scale; G, 2 tentacular scales; H-I, upper and lower views of coenenchymal scales; J, 3 adaxial buccal scales. Scale bar 1: H, I = 0.25 mm; 2: G = 25 μ m; 3: J = 0.125 mm; 4: A-F = 0.25 mm.

tal spine; only slightly flared at distal margin, which covers only the basal part of the opercular scales; and relatively smooth, without any ridges and with only sparse granulation. Distal margin of buccals may be straight (Fig. 11C), jagged (Figs. 11B, 12C), or bear a prominent, serrate spine up to 0.35 mm in length projecting from the dorso-lateral margin (Figs. 11A, 12D), all variations present on the same colony. One to five small (up to 0.47 mm in length and 0.22 mm in width), flat, elliptical to oval-shaped adaxial buccal scales often present between the interior, adaxial ridge of the buccal scales and the adjacent adaxial and inner-lateral operculars. These scales usu-

ally are not paired. Abaxial operculars symmetrical, up to 1.10 mm in height, having a H:W of 1.4-1.7. Outer-lateral operculars equal in height but usually slightly narrower than abaxials and asymmetrical, having a H:W of 1.7-2.3. Inner-laterals up to 0.92 mm in height, asymmetrical; H:W = 1.8. Adaxial operculars almost equilateral in shape (H:W = 1.1-1.2), and much smaller (only up to 0.7 mm in length). Distal margins of the abaxials and outer-laterals are coarsely serrate. All operculars bear prominent keels on their distal, inner surfaces, those on the larger operculars (e.g., abaxials and outer-laterals) sometimes divided into 3 or 4 parallel crests (Fig. 12E). Outer faces

of all operculars fairly smooth, like the other body wall sclerites; inner surface tuberculate, but tubercles restricted to the central region, the margins fairly smooth. Tentacular sclerites flattened rods up to 92 μm in length and 26 μm in width. Coenenchymal sclerites elongate but irregular in shape, up to 1.0 mm in length but usually only about 0.5 mm. Their upper surfaces are covered with low granules 12–14 μm in diameter; there are no ridges.

Comparisons.—*Paracalyptrophora kerberti* is the most distinctive species in the genus, having several unique characters. It is the only species known to have adaxial buccal scales. It is also distinctive in having the largest polyp size and thus the smallest number of polyp whorls per cm (Table 1). Furthermore, as mentioned by Nutting (1912), it is distinctive in often, but not always, having one prominent spine on the distal dorso-lateral margin of each buccal scale. Finally, the exterior sculpture of all scales is extremely reduced, the body wall scales almost appearing as smooth.

Remarks.—Although Versluys (1906) described the holotype as being uniplanar, he qualified his description as being based on a small damaged specimen, and also reported a paratype that was biplanar. It was Kinoshita's (1908:63) opinion, based on "several" specimens, that the species bears two parallel fans, and all subsequent records of this species were based on biplanar colonies.

Distribution.—Off Honshu, Japan; 150–731 m.

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We wish to thank Björn Sohlenius (Swedish Museum of Natural History) for the loan of a fragment of the holotype of *Calyptrophora josephinae*, and Lisa Levi (Museo Regionale di Scienze Naturali, Turin) for the loan of the type of *Primnoa regularis*. We are also grateful to Manfred Grasshoff for sharing his knowledge of eastern Atlantic *Paracalyptrophora*. Final-

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Notes on the genus *Dicliptera* (Acanthaceae) in Bolivia

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Abstract.—Taxonomic notes on *Dicliptera* are presented in preparation for the authors' forthcoming annotated and illustrated checklist of Bolivian Acanthaceae. Two new species (*D. palmariensis* and *D. purpurascens*) are described and illustrated. Intraspecific variation of *D. squarrosa* is discussed. A key to all of the recognized species of *Dicliptera* from Bolivia is also provided.

Dicliptera is one of the most difficult genera taxonomically in the Acanthaceae. Like *Dyschoriste* the genus often lacks clear-cut characters to distinguish among species. Most authors have depended on bract characters to differentiate among species but in fact the bracts are quite variable within most species so this character needs to be used with caution and in conjunction with other characters such as corolla size, which is often useful. We have taken a broad view of each species both in this paper and in our planned treatment of Bolivian Acanthaceae. By doing this it seems that the species we recognize make some geographical and ecological sense, although the variation found in almost every case is quite extreme. This applies both to local endemic species such as *Dicliptera cochabambensis* Lindau and to the more widespread species such as *D. squarrosa* Nees and *D. jujuyensis* Lindau.

Seven species of *Dicliptera* are presently recognized in Bolivia. Two are new, one of which (*D. palmariensis*) is endemic to Bolivia. Of the other five, one (*D. cochabambensis*) is endemic to Bolivia, two extend to northern Argentina (*D. jujuyensis* and *D. scutellata* Griseb.) and two (*D. sexangularis* (L.) Juss. and *D. squarrosa* Nees) are widespread in South America. The seven

species can be separated by the following key.

Key to Species of *Dicliptera* in Bolivia

1. Inflorescence of naked spikes forming a panicle of spikes; bracts minute, oblanceolate, < 5 mm long *D. sexangularis*
1. Inflorescence varied but if paniculate, leafy; bracts usually > 8 mm long, not oblanceolate 2
2. Cymule bracts ovate, elliptic or obovate, scarcely broader than long, not leaf-like; corolla deep pink 3
2. Cymule bracts linear to linear-(ob-)lanceolate, sometimes with a leaf-like apex, always much broader than long; corolla red, orange or yellow 4
3. Cymule bracts ovate, 6–15 mm wide; leaves pubescent below *D. scutellata*
3. Cymule bracts elliptic to obovate, 3–6 mm wide; leaves almost glabrous below *D. cochabambensis*
4. Cymule bracts usually leafy at the apex; flowers usually in dense, sessile clusters or heads in the leaf axils *D. squarrosa*
4. Cymule bracts not leafy at the apex; flowers in pedunculate, axillary cymes, often forming a leafy panicle 5
5. Cymule bracts narrowly linear-elliptic, broadest in the middle; leaves softly pubescent above *D. palmariensis*
5. Cymule bracts linear-lanceolate, broad-

- est at the base; leaves soon glabrescent above 6
6. Inflorescence branches leafless, usually short; bracts linear-oblong, acute; corolla lobes almost half as long as the tube *D. jujuyensis*
6. Inflorescence branches often with subtending leaves, often well-developed; bracts lanceolate, finely acuminate; corolla lobes less than one fourth as long as the tube *D. purpurascens*

Dicliptera palmariensis Wassh. & J. R. I.

Wood, sp. nov.

Fig. 1 A–H

Quoad formam bractearum cymulorum *Diclipteram garciae* Leonard tangit, ob folia pilis lanatis induta, bracteas acutas, non apiculatas ab ea removendum.

Ascending or weakly erect, much-branched, probably perennial herb to 0.75 m; stems dark purplish-green, obscurely ridged with paler vertical lines along the depressions, densely pilose with long, patent, straggly, multicellular trichomes; leaves petiolate, the petioles 0.3–1.6 cm long, pilose, the blades ovate or elliptic, acute at apex, narrowed to the base and \pm attenuate on the petiole, 3–9 cm long, 1–4 cm wide, both surfaces pilose with large-celled trichomes, especially on the veins, cystoliths abundant above, the margin entire or obscurely repand, ciliate; inflorescence of pedunculate cymes in the axils of the upper leaves, the cymes typically few-flowered and the flowers often aborting, the inflorescence thus rather lax and open; peduncles 1–10 cm long, subtending bracts leaf-like, shortly petiolate, the petioles 3–5 mm long, the blades lanceolate or lanceolate-elliptic, acute, 0.7–2 cm long; cymules pedicellate, the pedicels ca. 0.5 mm long; cymule bracts slightly unequal, 8–15 mm long, 3 mm wide, narrowly oblong-elliptic, acute at both ends, pilose, the base often pale; inner bracts 6–10 mm long, lanceolate, ciliate on the upper margins; bracteoles lanceolate, ca. 4 mm long; calyx 2.5–3 mm long, 5-lobed to just above the base, the lobes

equal, ca. 2 mm long, lanceolate, acute, ciliate; corolla red, 25–28 mm long, cylindrical from a slightly bulbous base, gradually widened to ca. 3 mm, pilose without, 2-lipped, the lips ca. 3 mm long; anthers equaling the corolla; filaments 14 mm long, sparsely pilose, inserted ca. 14 mm above the base of the corolla, anther thecae at different heights, glabrous, ca. 1.25 mm long; ovary pubescent; style ca. 25 mm long, with a few scattered trichomes; capsule 6 mm long, obovoid, pubescent, 2-seeded; seeds with a few, short trichomes, lenticular, ca. 2.25 mm wide.

Type.—BOLIVIA: Tiraque, 1–2 km above El Palmar along the old road from the Chaparé to Cochabamba, 900 m, 6 Jul 1997, *J. R. I. Wood 12403* (holotype K!; isotypes LPB, US!).

Additional specimens.—BOLIVIA: Tiraque, 1–2 km above El Palmar along the old road from the Chaparé to Cochabamba, 1200 m, 6 Jun 1998, *J. R. I. Wood 13674* (K, LPB, US); El Palmar, 155 km along old road from Cochabamba to Villa Tunari [17°5'S, 62°31'W], 750 m, 4 Sep 1996, *Kessler et al. 8115* (GOET, LPB, US).

The only possible Bolivian species *D. palmariensis* could be confused with is *D. purpurascens* but it can readily be distinguished by its diffuse ascending habit, very pubescent indumentum, pedunculate cymes, smaller corollas and above all by the shorter, narrowly oblong-elliptic bracts, broadest in the middle and narrowed to both an acute apex and base. However, there are two collections from San Martin Department in Central Peru (*Schunke 3349* and *4370*, both at K and F), which are in many ways intermediate between *D. palmariensis* and *D. purpurascens*. The bracts are similar in shape to those of *D. palmariensis* but the apex is acuminate and apiculate and the specimens lack the distinct pilose indumentum of *D. palmariensis*. Given the wide variation found in many species of *Dicliptera* these specimens might suggest *D. palmariensis* should be included in a very variable *D. purpurascens* but they are far re-

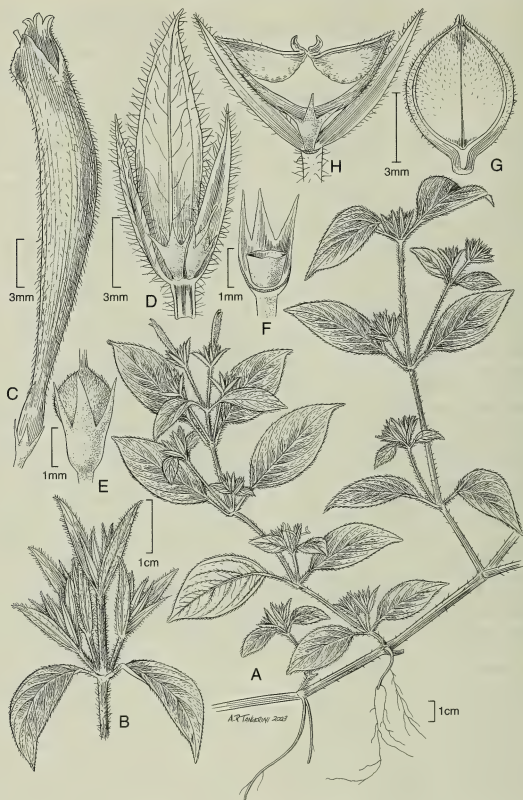


Fig. 1. A–H, *Dicliptera palmariensis* (J. R. I. Wood 12403). A, Habit; B, Pedunculate cymes; C, Calyx and corolla; D, Inner bract, bracteoles, calyx and aborted flower; E, Calyx and pistil; F, Calyx lobes and nectar disk; G, capsule; H, Capsule dehiscent.

moved geographically from *D. palmariensis* and are not exactly intermediate between the two recognized species. It seems best, therefore, to recognize the two species particularly as there are no intermediates in Bolivia.

Dicliptera purpurascens Wassh. & J. R. I.
Wood, sp. nov.
Fig. 2 A–F

Species nova plerumque purpurascens bracteae longis (usque 2.5 mm) lanceolatis, long-acuminatis bene distincta.

Annual or short-lived perennial herb, 0.5–2.5 m high, usually erect in open situations but commonly ascending or even decumbent in moister, shady conditions; stems stout, somewhat woody below, strongly angled, usually purplish, scurfy-pubescent, much branched; leaves petiolate, the petioles 0.5–4 cm long, scurfy-pubescent, the blades equal or nearly so, ovate or ovate-elliptic, 4–15 cm long, 2–7 cm wide, acute or shortly acuminate at apex, tapering at the base, entire, often purplish, darker green above than below, glabrous except for the usually ciliolate margins and a few scattered, usually multicellular trichomes, especially on the veins, cystoliths scattered on both surfaces; inflorescence of shortly pedunculate or sessile, axillary and terminal cymes, these becoming very dense on older plants with 1–3 cymes arising from each axil, commonly purplish and glandular-pilose but sometimes greenish and very thinly pilose; peduncles 0–3 cm long, scurfy-pubescent; subtending bracts leaf-like, petiolate, the petioles 0–3 mm long, the blades typically narrowly oblong-elliptic, to 3 cm long; cymules pedicellate, the pedicels 0–4 mm long; cymule bracts slightly unequal, 20–25 mm long, 2–5 mm wide, lanceolate, long-acuminate; inner bracts linear-acuminate, 12–15 mm long; bracteoles similar but only to 10 mm long; calyx 3–4 mm long, 5-lobed to just above the base, the lobes subulate, minutely ciliolate; corolla orange-red, 34–40 mm long,

cylindrical from a slightly bulbous base, gradually widened to 3–4 mm, sparsely pilose and minutely gland-dotted without, 2-lipped, the lips ca. 4 mm long; anthers equalling the corolla; filaments 17 mm long, sparsely pilose, inserted ca. 13 mm above base of corolla, anther thecae at different heights, glabrous, ca. 1.5 mm long; ovary pubescent; style ca. 29 mm long, glabrous; stigma globose; capsule 7 mm long, 4 mm wide, obovoid, pubescent, 2-seeded; seeds papillose, lenticular, ca. 1.25 mm wide.

Type.—BOLIVIA: Carrasco, ca. 5 km E of Valle de Sajta on main road from Chimore to Santa Cruz, 240 m, 29 May 1996, *Wasshausen, Brummitt, Wood & Ritter 2067* (holotype US!; isotypes K!, LPB).

Habitat and distribution.—*Dicliptera purpurascens* is locally frequent in moist lowland rain forest between 200 and 600 m in Bolivia and Peru. It is essentially a plant of the SW basin of the Amazon River with an outlying population in a very moist area of the Andean foothills in Bolivia. It has not yet been found in Brazil but is likely to occur in Acre as well. This disjunct distribution is shared with a number of other Acanthaceae species, notably *Pachystachys spicata* (Ruiz & Pavon) Wassh., *Ruellia inflata* Rich., *R. yurimaguensis* Lindau, *Justicia megalantha* Wassh. & J. R. I. Wood (in press), *J. pilosa* (Ruiz & Pavon) Lindau and *J. riedeliana* (Nees) V. A. W. Graham and appears to be a common pattern.

Additional specimens.—BOLIVIA: Santa Cruz, Ichilo, by track from Escuela Ichilo to Campamento Ichilo on E side of Río Ichilo, Amoró Park, 400 m, 27 Jul 1999, *J. R. I. Wood 14943* (K, LPB); Cochabamba, Carrasco, Valle de Sajta, 1 Jul 1988, *Hensen 6* (BOL, US); km 228, Santa Cruz road, Río Murillo, Valle de Sajta, 212 m, 18 Jul 1990, *Sigle 510* (US); Experimental Station, Valle de Sajta, 280 m, 11 Aug 1990, *I. Vargas 673* (LPB, USZ); Valle de Sajta, ca. 235 km NW of Santa Cruz, 400 m, *J. R. I. Wood 10072* (K, LPB, US); 0.5 km E of Valle de Sajta, 250 m, 29 May 1996, *J. R. I. Wood 11178* (K, LPB); 12 de Julio,



Fig. 2. A–F, *Dicliptera purpurascens* (Wasshausen 2007). A, Habit; B, Pedunculate cymes; C, Inner bracts, bracteoles, calyx and pistil; D, Calyx and pistil; E, Corolla; F, Nectar disk, pistil and calyx lobes.

ca. 9 km S of Israel, on E side of Río Sajta, 400 m, 24 Jul 1999, *J. R. I. Wood 14893* (K, LPB); Zona del Arroyo de 6 de Agosto, Cerro de la Concordia, E bank of Río Ichoa, 600 m, 27 Jul 1999, *J. R. I. Wood 14935* (K, LPB); Pando, Abuná, Nacebe, Río Ortón, 11 Oct 1989, *Beck et al. 19283* (LPB, US); *Gentry et al. 77583* (MO, US). PERU; Cuzco, Convención, along Río Pichari, 2 km E of Colonización Pichari, 620 m, 13 Jun 1975, *Wasshausen & Encarnación 544* (K, US); Paucartambo, Kosñipata District, along trail behind and W of Pilcopata, 580 m, 26 Jun 1975, *Wasshausen & Encarnación 583* (K, US); Quispicanthis, 3 km E of Quincimil, 960 m, 7 Oct 1976, *Wasshausen & Encarnación 735* (US); Madre de Dios, Manu, Adan Rajo, km 225, Shintuya-Pilcopata, 520 m, 26 Jun 1975, *Wasshausen & Encarnación 575* (K, US); Talmamanu, Chiliñas, km 18 on Iberia-Iñapari road, 1 Jun 1978, *Encarnación 1169* (K, US); near Shintuya, along Alto Río Madre de Dios, 450 m, 13 Oct 1979, *Gentry et al. 26736* (MO, US); Manu, Parque Nacional de Manu, Est. Cocha Cashu [11°50'S, 71°25'W], 350 m, 4 Aug 1984, *Foster 9746* (MO, US); Explorer's Inn, near confluence of Río Tambopata and Río La Torre, 29 km SW of Puerto Maldonado [12°50'S, 69°20'W], 9 Jul 1987, *Smith, Smith & Condon 938* (K, US); Río Tambopata [12°48'S, 69°17'W], 200 m, 9 Jul, 1998, *Michelangeli 477* (US); Ayacucho, La Mar, on trail between Santa Rosa and Sanabamba along Río Santa Rosa, 700 m, 9 Jun 1975, *Wasshausen & Encarnación 531* (K, US).

There is considerable variation in the indumentum and color of *Dicliptera purpurascens*. The purple colored form is the only form found in central Bolivia in the Departments of Cochabamba and Santa Cruz while only green forms are known from Pando. Both forms occur in Peru but the purple one is a good deal more common. All plants from Bolivia are densely glandular-pilose. In Peru plants are more commonly glandular-pilose but thinly pilose forms also occur.

Dicliptera purpurascens is obviously related to *D. palmariensis* but the two species are immediately distinguished by the different bracts.

Dicliptera squarrosa Nees

Dicliptera squarrosa Nees, in Mart., Fl. Bras. 9:161. 1847. Type: Brazil, Minas Gerais, *Reidel 34* (lectotype, here chosen, GZU!; isolectotype NY!); sin loc., *Schüch s.n.* (syntype W, not seen).

Dicliptera sericea Nees, in Mart., Fl. Bras. 9:162. 1847. Type: Brazil, São Paulo, Sorocoba, *Riedel & Lund 1984* (lectotype, here chosen, LE!; isolectotype NY!).

Dicliptera pohliana Nees, in Mart., Fl. Bras. 9:162. 1847. Type: Brazil, Minas Gerais, Tazenda de Roma, *Pohl 2973* (lectotype, here chosen, W!).

Dicliptera tweediana Nees, in DC., Prodr. 11:482. 1847. Type: Uruguay, Porto Alegre, *Sellow 13 (d585)* (syntype B, destroyed); *ibid*, *Sellow 16 (d531)* (syntype B, destroyed); Argentina, Buenos Aires, *Tweedie s.n.* (syntype K!).

Dicliptera niederleiniana Lindau, Bot. Jahrb. 19, Beibl. 48:18. 1894. Type: Argentina, Entre Ríos, Primer Misionero de Hernandez, *Puck & Fernandez 42* (holotype B, destroyed ?).

Dicliptera imminuta Rizzini, Arquiv. Jard. Bot. Rio de Janeiro, 8:348. 1948. Type: Brazil, Santa Catarina, *Reitz, C861* (holotype RB).

Dicliptera rauhii Washh., Beitr. Biol. Pflanzen 63:425. 1988. Type: Peru, Cuzco, prov. Urubamba, Machu Picchu, *Rauh & Hirsch P804* (holotype HEID!).

Dicliptera squarrosa is an exceptionally widespread species extending from Brazil south of the Amazon region westward to the eastern slopes of the Andes in Bolivia and then southward to Uruguay and central Argentina. Its occurrence further north is uncertain although we feel that *Dicliptera rauhii* Washh. from Peru belongs to this species and probably also several species described by Leonard from Colombia. *D.*

squarrosa is very variable with a welter of different forms throughout its range all intergrading with each other and forming no discrete units except perhaps at a very local level. We can make out the following rather imprecise geographical forms:

Form 1.—Plants from Argentina, Uruguay and Paraguay corresponding to the types of *D. tweediana* and *D. pohliana* have glabrous, narrowly lanceolate, obtuse leaves and relatively few-flowered axillary cymes, which become congested above into a terminal thyrse. This form does not occur in Bolivia but some Argentinian plants, especially from the Tucuman region have broader leaves which approach form 4 (below) found in Bolivia although the leaves always appear to be glabrous.

Form 2.—Fig. 3 A–G. Some populations in the Río Unduavi Valley along the road from La Paz to Sud Yungas appear very distinct. These plants have subglabrous leaves and a relatively long inflorescence of axillary cymes forming many distinct pseudoverticels, which are not confluent above. The corollas are yellow and the cymule bracts are oblong, gray-pubescent and ciliate-margined with distinct squarrose tips. Collections corresponding to this form include: BOLIVIA: La Paz, Nor Yungas, on N side of Río Unduavi valley, on road to Sud Yungas, 2200–2400 m, 9 Jul 1974, *Wood 8596* (K, LPB, US); *ibid*, 2400 m, 1 Jul 1995, *Wood 9952* (K, LPB); ca. 2 km above El Velo de la Novia on the Sud Yungas road, 2400 m, 14 Jun 1998, *Wood 13716* (K, LPB); Sud Yungas, km 66 on Sud Yungas road to Puente Villa ca. 50 m from El Castillo, 1830 m, 12 Jun 1996, *Wasshausen & Brummitt 2123* (CAS, GOET, K, LPB, US).

However, forms similar to form 2 but with reddish-orange corollas and bracts with few or no cilia occur elsewhere in the La Paz region and also in Peru. All these forms are difficult to distinguish from *Dicliptera scandens* Leonard from Colombia except that they bear no field notes to suggest they are scandent. Even *D. scandens*

itself is not always scandent. Collections which conform to this more broadly-defined form 2 include: BOLIVIA: La Paz, Tamayo, on descent into Río Yuyo, ca. 60 km S of Apolo on road to Charazani, 1150 m, 12 Jun 2000, *Wood & Wendleberger 16438* (K, LPB); Murillo, 29.3 km NE of the summit along Zongo Valley, 2200–2300 m, *Solomon, Luteyn & Dorr 19068* (LPB, MO, US); Zongo Valley, 1900 m, 28 Jun 1997, *Wood 12349* (K, LPB); Sud Yungas, ca. 15 km from Huancané on road to San Isidro, 2300 m, 1 Jul 1995, *Wood 9964* (K, LPB, US); 2 km E of Puente Villa, 1200 m, 12 Jun 1996, *Wasshausen & Brummitt 2124* (K, LPB, US); Inquisivi, *Lewis 39127* (LPB, MO, US); Cochabamba, Ayopaya, 1 km above Independencia, 2500 m, 13 May 2000, *Wood & Zaraté 16339* (K, LPB); Cochabamba, Ayopaya, 4 km S of Saila Pata, *Kessler 12364* (LPB, US). PERU: La Merced-Oxapampa, 2300 m, 17 Aug 1976, *Palmer 44* (K); San Martín, Zepalacio near Moyobamba, 1200–1600 m, Mar 1934, *Klug 3601* (F, K).

Form 3.—In the northern Bolivian Andes, mostly at lower altitudes and particularly in areas of high rainfall, there is another form. This also has glabrous leaves but the bracts are relatively broad, leaf-like and mucronate, usually elliptic or obovate, never ciliate or squarrose but commonly pubescent to subglabrous. The axillary cymes are relatively few-flowered. Specimens that conform to this form include: BOLIVIA: Pando, W bank of Río Madeira, 3 km above Riberão, 27 Jul 1968, *Prance et al. 6539* (K, NY, US); Beni, Ballivian, 10 km S of Rurrenabaque, 250 m, 29 Jul 1998, *Wasshausen & Wood 2162* (US, LPB); La Paz, Caranavi, 2 km up road behind Caranavi, 640 m, 10 Jun 1996, *Wasshausen et al. 2118* (K, LPB, US); Sud Yungas, Santa Ana de Alto Beni, 580 m, 20 Aug 1963, *Holliday 26* (K); 7.5 km N of end of Road to San José, 26.5 km along road to La Asunta, 1040 m, 5 Aug 1991, *Acevedo et al. 4451* (K, US); stream at bottom of ascent to Huancané, ca. 5 km from

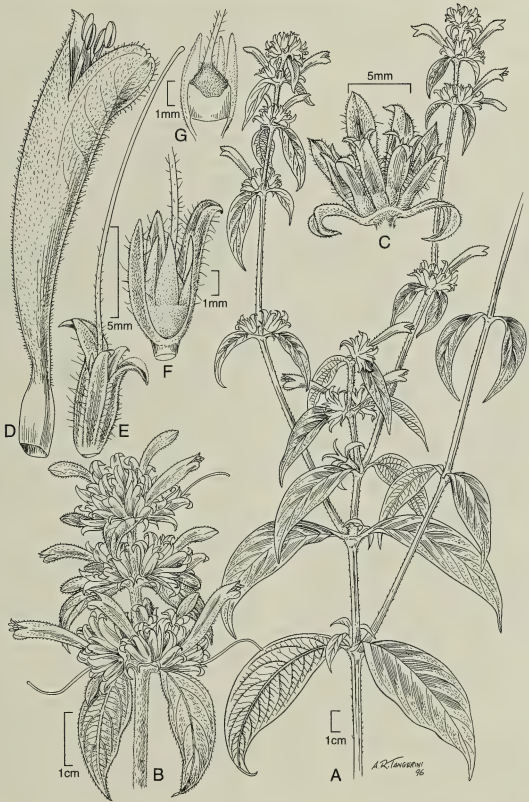


Fig. 3. A-G, *Dicliptera squarrosa* Form 2 (Wasshausen 2133). A, Habit; B, Inflorescence; C, Cymes; D, Corolla; E, Inner bract, bracteoles and pistil; F, Inner bract, bracteoles, calyx lobes and pistil; G, Nectar disk, pistil and calyx lobes.

Puente Villa, 1200–1300 m, 10 Jul 1994, *Wood 8616* (K, LPB); 0.5 km from Puente Villa along Río Unduavi, 1200 m, 14 Jun 1996, *Wasshausen & Brummitt 2130* (K, LPB, US); 1 km above Puente Villa market in side valley, 1100 m, 14 Jun 1998, *Wood 13709* (K, LPB); Cochabamba, Chaparé, 15 km W of Villa Tunari along road to Cochabamba, 800 m, 19 Jun 1994, *Wood 8528* (K, LPB); Carrasco, 6 km W from main road at Bulo Bulo, 500 m, 2 Nov 1997, *Wood 12784* (K, LPB); Santa Cruz, Ichilo, 4 km S of Huaytu towards San Rafael de Amboró, 500 m, 21 May 1995, *Wood 9838* (K, LPB).

This form occurs over quite a wide area and is not uniform in the size or shape or indumentum of the bracts. The obovate bracts of *Holliday 26*, for example, are very different from the long, elliptic to subrhomboid bracts of *Wasshausen et al. 2118*. Similarly the pilose bracts of *Prance et al. 6539* are rather different from the subglabrous to thinly pubescent bracts more commonly seen. The common elements are the nearly glabrous, distinct and few-flowered pseudoverticels and large bracts.

Form 4.—This form is characterized by its pubescent leaves and distinct inflorescence. The flowers are mainly in the uppermost leaf axils and the uppermost verticels support many-flowered cymes, which are confluent into a dense, terminal thyse. This is essentially a plant of bushy stream gullies in the Tucuman-Bolivian forest area extending from around Pojo in the Siberia area south to Tarija, where it perhaps intergrades with *Form 1*, which differs in little more than the glabrous leaves. It also extends east into the Chuiquitania plains where it intergrades with *Form 5*. It is also similar to some plants from Peru including *Dicliptera rauhi* and two collections from the Macchu Pichu area [*Ugent 5339* (K) and *Stafford 790* (K)], which seem to differ only in having glabrous leaves. Specimens that conform to this form include: BOLIVIA: Cochabamba, Carrasco, on ascent from Pojo to Siberia, 2300 m, 2 Feb 1996, *Wood*

& *Ritter 10515* (K, LPB); Santa Cruz, Vallegrande, 35 km SE of Vallegrande on road to Masicuri, 1750 m, 24 May 1996, *Wasshausen, Brummitt & Wood 2039* (K, LPB, US); Florida, 2 km W of Samaipata, 1600 m, 15 May 1994, *Wood 8639* (K, LPB, US); La Yunga de Mairana, 2300 m, 18 Sep 1994, *Wood 8674* (K, LPB, US); ca. 5 km above Bermejo towards Samaipata, 1100 m, 17 Jul 1995, *Wood 9995* (K, LPB, US); Ichilo, Río Surutú, 400 m, 2 Aug 1924, *J. Steinbach 6312* (US); Guarayos, ca. 5 km from Ascension on road to Perseverancia, 300 m, 19 Jul 1995, *Wood 9999* (K, LPB, US); Chavez, between Perseverancia and El Arroyan, 300 m, 22 Jul 1995, *Wood 10048* (K, LPB, US); Chuquisaca, Azurduy, 4 km N of Mollini, Sopachuy-Azurduy road, 2000 m, 15 Feb 1999, *Wood & Serrano 14510* (K, LPB, US); Boeto, 10 km N of Villa Serrano, 2300 m, 16 Apr 1995, *Wood 9753* (K, LPB); 1 km below Nuevo Mundo towards Río Grande, 2100 m, 17 Mar 1996, *Wood 10867* (K, LPB, US); Tomina, gorge of Río Sillani, 3 km W of Padilla, 2200 m, 13 Feb 1994, *Wood 7946* (K, LPB); 10 km W of Padilla, 2300 m, 9 Apr 1994, *Wood 8218* (K, LPB, US); on ridge between Padilla and Monteagudo, 2500 m, 10 Apr 1994, *Wood 8229* (K, LPB); Río Limon Valley, ca. 5 km above Thiu Mayo, 1300 m, 15 Jun 1997, *Wood 12305* (K, LPB, US); Siles, 12 km E of Monteagudo towards Camiri, 1300 m, 14 Apr 1995, *Wood 9685* (K, LPB); Calvo, Río Taperillas valley between Monteagudo and Muyu Pampa, 1300 m, 14 Apr 1995, *Wood 9722* (K, LPB, US); Serrania Inca Huasi, 8 km from Muyu Pampa towards Lagunillas, 1500 m, 8 Mar 1998, *Wood, Goyder & Serrano 13255* (K, LPB, US); Tarija, Los Pinos near Tarija, 2200 m, 11 Mar 1904, *Fiebrig 3133* (K).

Form 5.—This form is essentially the same as the previous form except that the flowers are clearly in axillary pseudoverticels rather than in a terminal thyse and so somewhat intermediate with *Form 3*. It is apparently local in relatively open grassy habitats in the Santa Cruz region. It is not

clear whether it is simply an adaptation to open situations or differs genetically in some way. Specimens that conform to this form include: BOLIVIA: Santa Cruz, Ichilo, km 27 on old road to Cochabamba up side road to Los Espejillos, 500 m, 20 Jul 1994, *Wood 8621* (K, LPB); Chavez, San Javier, 500 m, 23 Jul 1995, *Wood 10062* (K, LPB); 15–20 km W of Concepción on road to San Javier, 500 m, 4 Aug 1997, *Wood 12540* (K, LPB).

Form 6.—This form appears to be restricted to the Tarija area. It is characterized by having some inflorescences borne on long, axillary peduncles. The specimen that

conforms to this form: BOLIVIA: Tarija, O'Connor, 5–6 km W of Entre Rios, 3 Jun 2000, *Wood 16384* (K, LPB).

Acknowledgments

Our special thanks to Alice Tangerini who skillfully prepared the line drawings.

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BIOLOGICAL SOCIETY OF WASHINGTON

130th Annual Meeting, 20 May 2003

President Roy McDiarmid called the meeting to order at 11:00 a.m. in the Waldo Schmitt Room, National Museum of Natural History (NMNH). Council members present: Marilyn Schotte and Don Wilson (Elected Council), Rafael Lemaitre (President Elect), Richard Sternberg (Editor), Chad Walter (Treasurer), Carole Baldwin (Secretary), and Richard Banks, Stephen Cairns, Bruce Collette, Brian Kensley, David Pawson, and Storrs Olson (Past Presidents).

Minutes of the 129th Annual Meeting were summarized by Secretary Baldwin. Those minutes did not appear in the *Proceedings* last year as usual but will appear in Volume 116(2). Following approval of the minutes, McDiarmid called on Chad Walter for the Treasurer's Report (Table 1). Income for the period 1 January 2002 to 31 December 2002 was \$119,712.34, and expenses for the same period were \$103,855.39. Total Society assets as of 15 April 2003 were \$89,614.17. The value of the endowment fund decreased by \$9,513.60 for the calendar year, a loss that includes fees paid to buy into the American Funds Investment Company of America as well as a net loss from stock-market fluctuations. The Audit Committee, Brian Kensley and Richard Banks, indicated that they had reviewed the books and ledgers of the Treasurer and found all financial records to be accurate and in good order. The Treasurer's report was approved.

Editor Richard Sternberg reported that four issues of Volume 115 were published comprising 69 papers and 909 pages. As of 20 May 2003, there were 27 submissions, down from 42 in 2002 but close to the 33 submissions at the same date in 2001. There continues to be no backlog for papers accepted in the *Proceedings*.

Sternberg announced that beginning with Volume 116(1), the table of contents and abstracts for the *Proceedings* can be viewed at www.allenpress.com in their "apt.online" section. Sternberg also noted that during the past year, a few authors had pulled manuscripts from the *Proceedings* at late stages in the publication process when they discovered they would have to pay page charges. Those authors indicated that they were transferring their papers to *Zootaxa*, a taxonomic journal available both online and in printed form that does not require contributors to pay page charges. President McDiarmid announced that he will appoint a special committee to investigate the effects *Zootaxa* and other largely online journals with rapid publication rates might have on the *Proceedings*. The Editor's report was accepted.

The Finance Committee (Stephen Cairns, Oliver Flint, Frank Ferrari, and Chad Walter) reported that three of the four recommendations approved last year by the Council had been put into effect (increasing the cost of reprints, increasing the cost of library subscriptions, and re-investing \$55,000 of the Society's endowment funds into the American Funds Investment Company of America). Gift-fund categories for potential benefactors have not yet been defined.

Custodian of Publications Storrs Olson announced that the organized separates have been distributed to appropriate NMNH Divisions, and a plan to decrease the stock of bound issues of the *Proceedings* will be formulated once the Society's Web site is online. Steve Gardiner, Associate Editor for Invertebrates for the *Proceedings*, has been working on the Web site on behalf of the Society. He projected sample pages from the site for comments and discussion.

In response to suggestions made at the 2002 annual meeting that a single annual meeting be held in the future that combines the Council meeting and the annual meeting, a single meeting was held this year with Council members meeting fifteen minutes prior to the commencement of the annual meeting. The annual meeting was adjourned at 12:20 p.m.

Respectfully submitted,
Carole C. Baldwin
Secretary

Summary Financial Statement for 2002

	General Fund	Endowment Fund	Total Assets
Assets: January 1, 2002	(6,991.95)	75,790.67	68,798.72
Total Receipts for 2002	111,624.46	8,087.88 ^a	119,712.34
Total Disbursements for 2002	86,253.91	17,601.48 ^b	103,855.39
Assets: December 31, 2002	18,378.60	66,277.07	84,655.67
Net Changes in Funds	25,370.55	(9,513.60)	15,856.95

^a Annual gain in value of Endowment.

^b Annual loss in value of Endowment.

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings of the Biological Society of Washington* contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers are published in English (except for Latin diagnoses/descriptions of plant taxa), with an Abstract in an alternate language when appropriate.

Submission of manuscripts.—**Submit three copies of each manuscript in the style of the Proceedings to the Editor, complete with tables, figure captions, and figures** (plus originals of the illustrations). Mail directly to: Richard Banks, Dept. of Zoology, MRC-116, National Museum of Natural History, Smithsonian Institution, Washington, D.C., 20013-7012.

Presentation.—Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is recommended for descriptions and diagnoses. The style for the Proceedings is described in "GUIDELINES FOR MANUSCRIPTS for Publications of the BIOLOGICAL SOCIETY OF WASHINGTON," a supplement to Volume 114, number 4, December 2001. Authors are encouraged to consult this article before manuscript preparation. Copies of the article are available from the editor or any associate editor.

The establishment of new taxa must conform with the requirements of appropriate international codes of nomenclature. Decisions of the editor about style also are guided by the General Recommendations (Appendix E) of the International Code of Zoological Nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Review.—One of the Society's aims is to give its members an opportunity for prompt publication of their shorter contributions. Manuscripts are reviewed by a board of Associate Editors and appropriate referees.

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Pseudopaguristes shidarai, a new species of hermit crab
(Crustacea: Decapoda: Diogenidae) from Japan,
the fourth species of the genus

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AUG 26 2004

Abstract.—*Pseudopaguristes shidarai*, a new species of the recently established diogenid genus *Pseudopaguristes* McLaughlin, is described and illustrated from Okinawa, Japan. This is the fourth species assigned to this genus.

The diogenid genus *Pseudopaguristes* McLaughlin, 2002, was established for *P. janetkae* McLaughlin, 2002, on the basis of specimens from Guam, the Mariana Islands. The genus is characterized by eight functional gills, male chelipeds with the right larger than the left and dissimilar armature, female chelipeds similar from left to right, fourth pereopods with a clump of long capitate setae on the carpi, and the paired first and second pleopods modified as gonopods. The second species, *P. bollandi* Asakura & McLaughlin, 2003, and the third species *P. bicolor* Asakura and Kosuge, 200x, were recorded from Okinawa, tropical Japan. Through the courtesy of Mr. Hiroyuki Shidara, the author recently obtained the fourth species of this genus, which was again collected from Okinawa. This new species is separated from all of the described species by coloration and morphology of antenna and telson.

The holotype is deposited in the Natural History Museum and Institute, Chiba (CBM-ZC). The terminology used follows McLaughlin (1974, 2002) with the exception of the fourth pereopods as defined by McLaughlin (1997), gill structure by McLaughlin & de Saint Laurent (1998), and the posterior carapace by McLaughlin (2000). Abbreviation used is; SL, shield length as measured from the tip of the rostrum to the posterior margin of the shield.

Pseudopaguristes shidarai, new species
Figs. 1–12

Material.—Holotype: male, SL = 2.55 mm, 20–25 m, SCUBA diving, Miyakojima Island, Okinawa, Feb. 2003, CBM-ZC 6814. Paratypes: 2 males, SL = 1.85, 2.05 mm, 1 female, SL = 2.65 mm, data same as holotype, CBM-ZC 6815.

Description of holotype and paratype males.—Eight functional pairs of quadriserial, phyllobranchiate gills (Fig. 1A): no pleurobranchs on fifth and eighth thoracic somites, arthrobranchs of third maxillipeds and chelipeds vestigial (Fig. 1B). Shield (Fig. 1C) 1.25–1.35 times longer than broad; anterior margin between rostrum and lateral projections concave; lateral projections triangular, with small submarginal spine; anterolateral angles each with blunt-tipped corneous spine, not visible dorsally; lateral margins nearly straight, somewhat irregular; posterior margin truncate; dorsal surface slightly convex, with some elevated areas bearing anterior row of spines and setae laterally. Rostrum (Fig. 1C) prominent, triangular, produced, with terminal spine. Posterior carapace lateral elements (Fig. 1C, arrow) small, well calcified, unarmed. Branchiostegites (Fig. 1D) each with row of spines on dorsal margin anteriorly.

Ocular peduncles (including corneas) (Fig. 1C) moderately long, 0.75–0.85 length of shield. Corneas (Fig. 1C) very

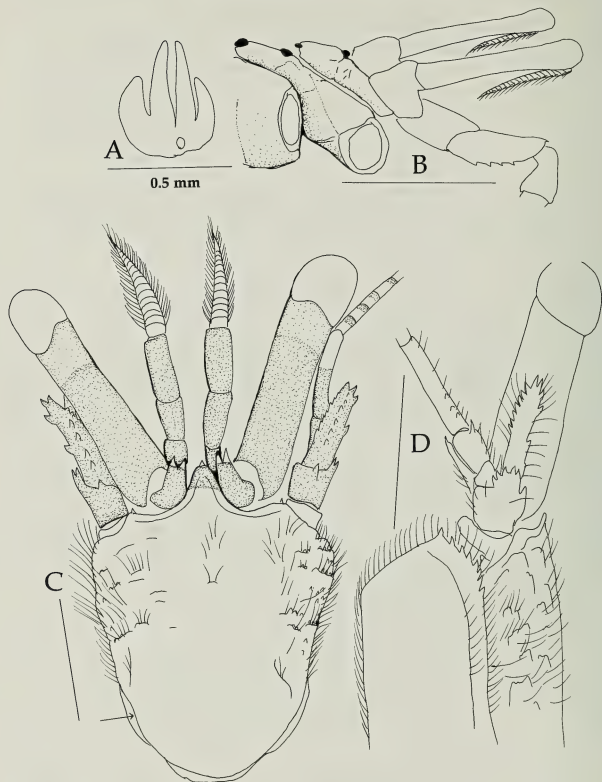


Fig. 1. *Pseudopaguristes shidarai*, new species: holotype male (CBM-ZC 6814), SL = 2.55 mm, off Miyako Is., Okinawa. A, arthrobranch gill lamella on fourth pereopod; B, vestigial gills on third maxilliped and cheliped; C, shield and cephalic appendages; D, left lateral view of distal half of cephalothorax and antenna. Color pattern indicated in C. Scales equal 0.5 mm (A) and 1 mm (B-D).

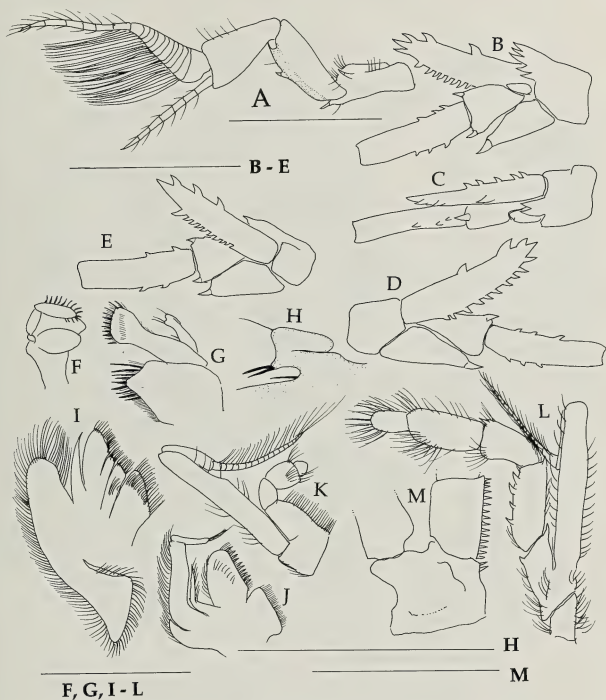


Fig. 2. *Pseudopaguristes shidarai*, new species: A-D, F-M: holotype male (CBM-ZC 6814), SL = 2.55 mm, off Miyako Is., Okinawa. E: paratype male (CBM-ZC 6815), SL = 2.05 mm, same locality. Left antennule: A, lateral. Left antennal peduncle: B, lateral; C, dorsal; D, mesial. Right antennal peduncle: E, mesial. Left mouthparts: F, mandible, internal; G, maxillule, external; H, same, endopod; I, maxilla, internal; J, first maxilliped, internal; K, second maxilliped, internal; L, third maxilliped, external; M, same, proximal portion, internal. Scales equal 1 mm.

slightly dilated. Ocular acicles (Fig. 1C) each with 2 or 3 strong spines on distal margin; separated basally by breadth of rostrum.

Antennular peduncles (Fig. 2A) stout,

scarcely setose; when fully extended, distal margins of ultimate segments reaching distal margins of corneas, spines onto segments all with semitransparent tips; ultimate segments unarmed; penultimate seg-

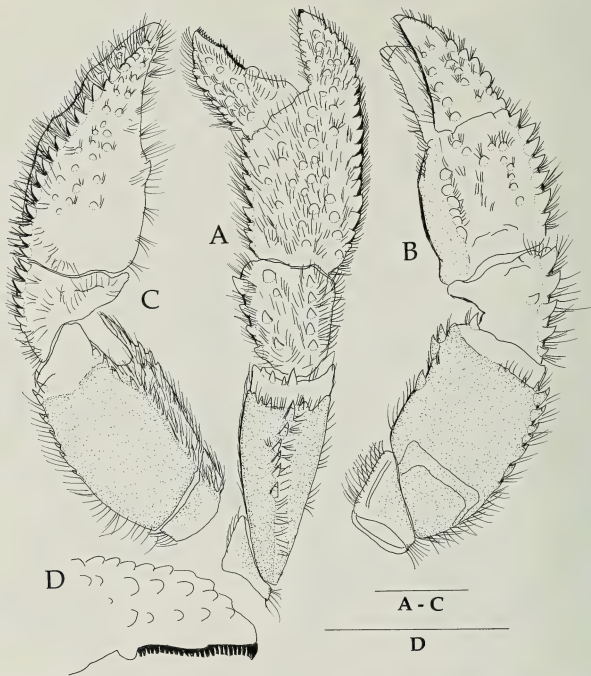


Fig. 3. *Pseudopaguristes shidarai*, new species: holotype male (CBM-ZC 6814), SL = 2.55 mm, Miyako Is., Okinawa. Right cheliped: A, dorsal; B, mesial; C, lateral; D, dactyl, dorsal. Color pattern indicated in A-C. Scales equal 1 mm.

ments with ventromesial margins each bearing acute spine; basal segments with ventromesial and ventrolateral distal angles each bearing acute spine and dorsolateral margins each bearing acute subdistal spine.

Antennal peduncles (Figs. 1C, D, 2B-E) moderately long, when fully extended, reaching basal portions of corneas; fifth

segments with dorsal and ventral margins each bearing 2 or 3 small spines; fourth segments with dorsodistal margins each bearing acute spine and ventrodistal margins each also bearing acute spine; third segments each with prominent spine at ventrodistal margin; spines on fourth and third segments often with semitransparent tips;

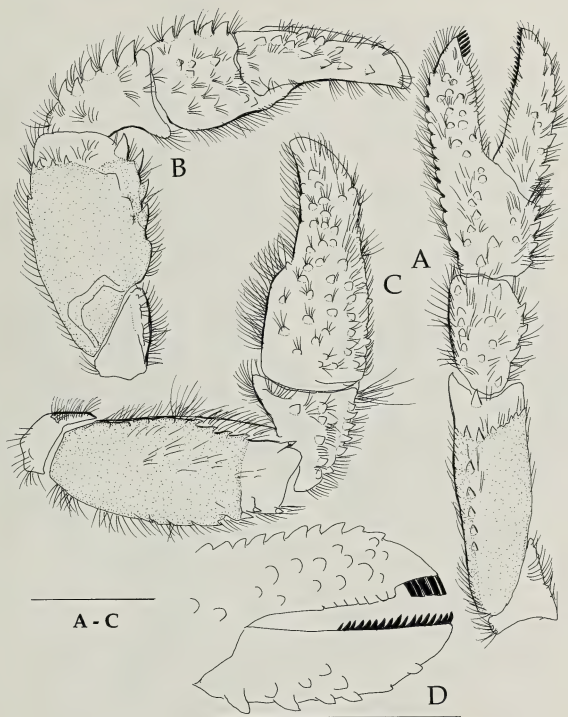


Fig. 4. *Pseudopaguristes shidarai*, new species: holotype male (CBM-ZC 6814), SL = 2.55 mm, Miyako Is., Okinawa. Left cheliped: A, dorsal; B, mesial; C, lateral; D, dactyl and fixed finger, dorsal. Color pattern indicated in A-C. Scales equal 1 mm.

second segments with dorsolateral distal angles produced, bearing strong bifid spine dorsally and 3 or 4 strong spines laterally, dorsomesial distal angles each with blunt-tipped, small spine; first segment unarmed. Antennal acicles moderately long, straight,

terminating in strong spine; dorsomesial margins each with 4-6 strong spines; dorsolateral margins each with 2 or 3 strong spines; ventral margins each with row of 9-11 acute spines. Antennal flagella scarcely setose.

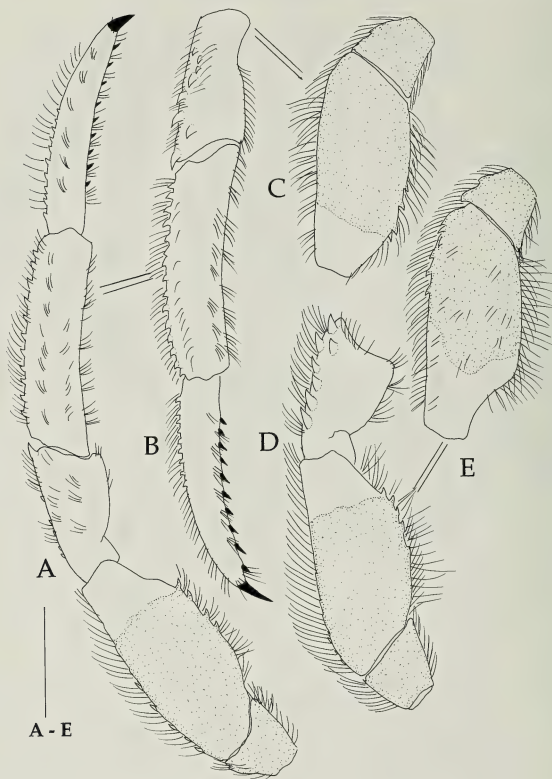


Fig. 5. *Pseudopaguristes shidarai*, new species: holotype male (CBM-ZC 6814), SL = 2.55 mm, Miyako Is., Okinawa. Right second pereopod: A, lateral; B, dactyl, propodus, and carpus, mesial; C, merus and ischium, mesial. Left second pereopod: D, carpus, merus and ischium, mesial; E, merus and ischium, lateral. Color pattern indicated in A-E. Scale equals 1 mm.

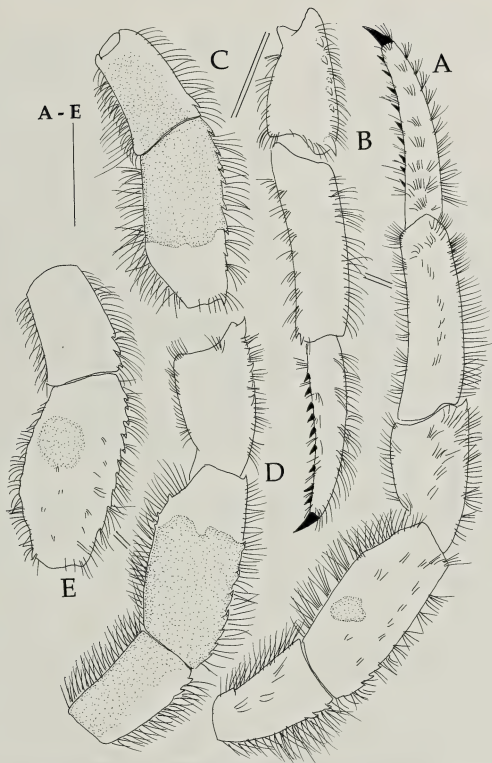


Fig. 6. *Pseudopaguristes shidarai*, new species: holotype male (CBM-ZC 6814), SL = 2.55 mm, Miyako Is., Okinawa. Left third pereopod: A, lateral; B, dactyl, propodus, and carpus, mesial; C, merus and ischium, mesial. Right third pereopod: D, carpus, merus and ischium, mesial; E, merus and ischium, lateral. Color pattern indicated in A-E. Scale equals 1 mm.

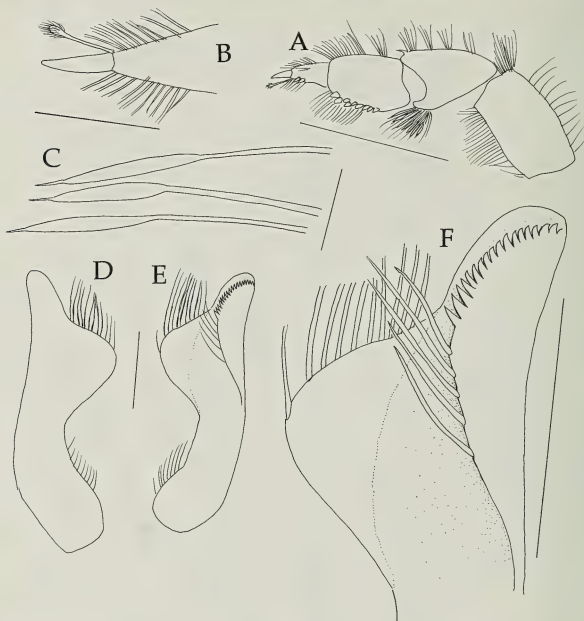


Fig. 7. *Pseudopaguristes shidarae*, new species: holotype male (CBM-ZC 6814), SL = 2.55 mm, Miyako Is., Okinawa. Left fourth pereopod: A, lateral; B, distal portion of dactyl, dorsal; C, ventral setae of carpus. Left first pleopod: D, external; E, internal; F distal portion, internal, enlarged. Scales equal 1 mm (A) and 0.2 mm (B-E).

Mandible (Fig. 2F) without distinguishing characters. Maxillule (Fig. 2G, H) with external lobe of endopod well developed and recurved, internal lobe with 2 bristles. Maxilla (Fig. 2I) with moderately narrow scaphognathite. First maxilliped (Fig. 2J) with well developed, setose epipod. Second maxilliped (Fig. 2K) without distinguishing characters. Third maxilliped (Fig. 2L, M) with carpus bearing dorsodistal spine; merus with dorsodistal spine, ventral margin

bearing 4 or 5 spines; ischium with strong ventrodistal and dorsodistal spines, crista dentata well-developed, no accessory tooth; basis with 2 sharp spines.

Male with both chelipeds bearing dense setae covering dorsal faces of dactyls, fixed fingers, palms and carpi and sometimes detritus densely accumulating on them resulting into yellow or yellowish brown colored appearance. Right cheliped (Fig. 3) stouter than, and dissimilar from, left; dactyl as

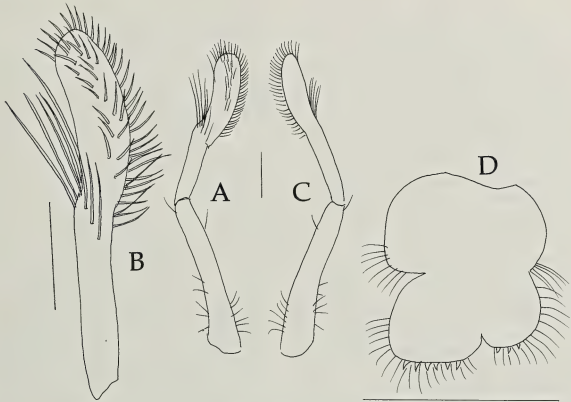


Fig. 8. *Pseudopaguristes shidarae*, new species: holotype male (CBM-ZC 6814), SL = 2.55 mm, Miyako Is., Okinawa. Left second pleopod: A, external; B, same, distal portion, enlarged; C, internal. D, telson. Scales equal 0.2 mm (A-C) and 1 mm (D).

long as palm, terminating in strong corneous claw; dorsal face flat, with 2 rows of large tubercles, dorsomesial margin with row of large tubercles; mesial face with 2 rows of tubercles; cutting edge with numerous corneous teeth on distal half and broad calcareous tooth medially. Fixed finger terminating in corneous claw; dorsal face flat, with scattered large tubercles; cutting edge with few corneous teeth distally. Palm 1.40–1.50 length of carpus; dorsal surface flat, with scattered large tubercles; dorsomesial margin with row of strong spines; dorsolateral margin of palm and fixed finger with row of strong spines. Carpus 0.40–0.50 length of merus; dorsal face flat, with few large tubercles or spines, dorsolateral and dorsomesial margins each with row of spines. Merus with dorsal face bearing large distal spine accompanied mesially with 1–3 small spines, subdistal transverse row of 3 or 4 spines, and, posterior to it, with dorsal longitudinal row of slender

semitransparent-tipped spines; ventromesial margin with 3 or 4 strong spines, ventrolateral margin with row of 4 slender, semitransparent-tipped spines. Ischium unarmed. Coxa with spine ventromesially.

Left cheliped (Fig. 4) slender. Dactyl 1.25–1.35 length of palm, terminating in strong corneous claw; dorsal face with only few tubercles, dorsomesial margin with few tubercles; mesial face with few spiniform tubercles; cutting edge with numerous corneous teeth on distal half. Fixed finger terminating in corneous claw; dorsal face flat, with scattered large tubercles; cutting edge with several corneous teeth distally. Palm as long as carpus; dorsal surface flat, with scattered large tubercles; dorsomesial margin with row of strong spines; dorsolateral margin of palm and fixed finger with row of large tubercles. Carpus 0.45–0.55 length of merus; dorsal face flat, with few large tubercles or spines, dorsolateral and dorsomesial margins each with row of spines

or tubercles; lateral face with several tubercles. Merus with dorsal face bearing large distal spine, subdistal transverse row of 3 or 4 spines, and, posteriorly, dorsal longitudinal row of spines; ventromesial margin with 3 or 4 strong spines, ventrolateral margin with row of 3–5 slender spines. Ischium unarmed. Coxa with spine ventromesially.

Second and third pereopods with dense setae present on dorsal margins of each segment and sometimes detritus densely accumulating on them resulting in yellow stripe-like appearance.

Second pereopods (Fig. 5) with armature similar from left to right; right 1.10 length of left. Dactyls 0.90 (left) or 1.00 (right) length of propodi, each terminating in strong corneous claw; dorsal margins each with row of strong spines, larger proximally; ventral margins each with row of 9 or 10 strong corneous spines. Propodi 1.85–1.90 (left) or 1.80–1.85 (right) length of carpi, each with row of strong spines on dorsal margin; ventromesial distal margins with or without spine. Carpi 0.40–0.50 length of meri, dorsal margins each with row of strong spines. Meri each with row of spines on ventral margin; dorsal margins each with row of spines on proximal half. Ischia each with or without small spine dorsally. Coxae unarmed.

Third pereopods (Fig. 6) with armature similar from left to right, right 1.10 length of left. Dactyls 0.95–1.00 length of propodi, each terminating in strong corneous claw; dorsal margins unarmed; ventral margins each with row of 8 or 9 strong corneous spines. Propodi 1.75–1.80 (left) or 1.90–2.00 (right) length of carpi; dorsal faces unarmed; ventromesial distal angles each with 1 or 2 acute spines. Carpi 0.60–0.65 (left) or 0.55–0.65 (right) length of meri, each with strong spine at dorsodistal angle; dorsal margin with 3 or 4 small spines. Meri with ventral margins each bearing few small spines or unarmed; dorsal margins each with row of slender, semitransparent-tipped spines. Ischia each with 1 or 2 small dorsodistal spines. Coxae unarmed.

Sternite of third pereopods with anterior lobe rectangular, unarmed.

Fourth pereopod (Fig. 7A) subchelate. Dactyl terminating in strong corneous claw; prominent preungual process present at base of claw (Fig. 7B); ventral face with 1 or 2 corneous spines laterally. Propodal rasp with 1 or 2 rows of corneous scales. Carpus with acute dorsodistal spine; ventral face with clump of long capsulate setae (Fig. 7C).

Fifth pereopod chelate; dactyl and propodus with well-developed rasps.

Male first pleopods (Fig. 7D–F) paired, modified as gonopods; basal lobe with several setae at superior mesial angle; inferior lamella with distal margin bearing row of short spines, and lateral margin with several setae; internal lobe with row of setae on mesial margin; external lobe exceeding inferior lamella in distal extension. Male second pleopods (Fig. 8A–C) paired, modified as gonopods; basal segment with scattered setae proximally and few setae distally; endopod with several long setae; appendix masculina twisted; lateral and distal margins and inferior face with moderately long setae. Third to fifth left pleopods each with exopod well developed, endopod reduced.

Uropods asymmetrical, left larger than right; rasps of exopods and endopods well developed; protopods each with row of spines posteriorly.

Telson (Fig. 8D) with lateral constrictions; anterior portion unarmed; posterior lobes separated by deep median cleft, left lobe larger than right, terminal margins with 5 or 6 spines (left) or 2 or 3 spines (right).

Description of female paratype.—Female paratype differs from holotype and paratype males as follows: Chelipeds (Figs. 9, 10) subequal, right very slightly larger; armament generally similar. Dactyl as long as (right) or 1.10 length (left) of palm, terminating in strong corneous claw; dorsal faces of both chelipeds each with 6 large, spiniform tubercles (right) or 1 small spine (left), dorsomesial margins each with row of large



Fig. 9. *Pseudopaguristes shidarai*, new species: paratype female (CBM-ZC 6815), SL = 2.65 mm, Miyako Is., Okinawa. Right cheliped: A, dorsal; B, mesial; C, lateral. Color pattern indicated in A-C. Scales equal 1 mm.

(right) or small (left) spines; mesial faces with several spiniform tubercles or spines; cutting edges with numerous corneous teeth on distal halves. Fixed fingers each terminating in corneous claw; cutting edges with several corneous teeth distally. Palms 1.10 length of carpi; dorsal surfaces of palms and fixed fingers flat, each with row of strong spines, right, accompanied mesially

by small tubercle on palm and row of 3 tubercles on fixed finger, dorsolateral margins of palms and fixed fingers each with row of strong spines, dorsomesial margins of palms each with row of strong spines; mesial faces each with few spines (right) or unarmed (left); lateral faces each with row of tubercles (right) or few spines (left). Carpus 0.50 (right) or 0.40 (left) length of mer-

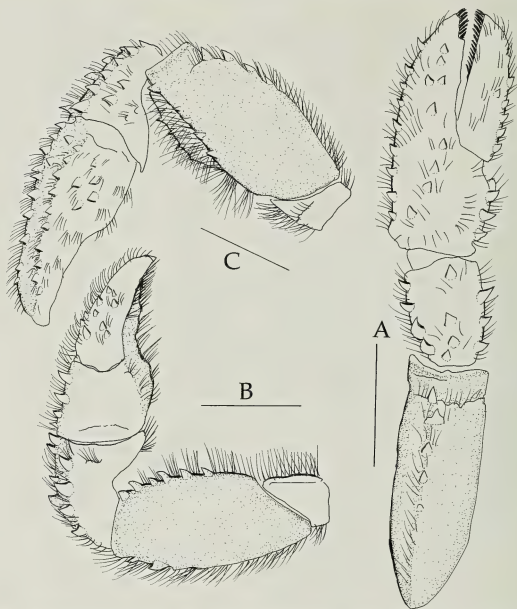


Fig. 10. *Pseudopaguristes shidarai*, new species: paratype female (CBM-ZC 6815), SL = 2.65 mm, Miyako Is., Okinawa. Left cheliped: A, dorsal; B, mesial; C, lateral. Color pattern indicated in A-C. Scales equal 1 mm.

us; dorsal faces flat, each with row of spines on midline, dorsolateral and dorsomesial margins each with row of strong spines; lateral faces with several spines or tubercles; mesial faces unarmed. Meri with dorsodistal spine developed (right) or vestigial (left); dorsal margins each with row of spines; ventromesial and ventrolateral margins each with row spines. Ischia each with row of small spines or tubercles on ventromesial margin. Coxae each with spine ventromesially.

Coxa of only left third pereopod with gonopore (Fig. 11B).

First abdominal somite with paired uniramous pleopods modified as gonopods (Fig. 11B); second through fourth abdominal somites each with unequally biramous left pleopod (Fig. 11C); fifth with exopod well developed, endopod rudimentary; brood pouch represented by row of setae.

Color in life (Fig. 12).—Shield cream, rostrum red; antennules with flagella semi-transparent red, other surfaces uniformly

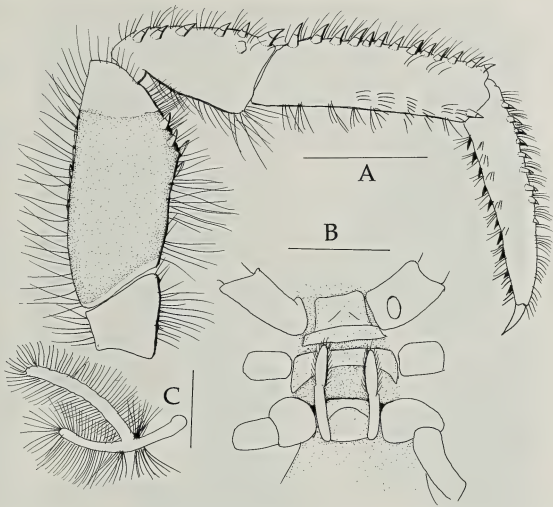


Fig. 11. *Pseudopaguristes shidarae*, new species: paratype female (CBM-ZC 6815), SL = 2.65 mm, Miyako Is., Okinawa. A, left second pereopod, mesial. B, coxae and sternites of third to fifth pereopods, first abdominal somite, and first pleopods. C, second pleopod.

red; antennas with flagella bearing alternative red and white bands, fifth segment with proximal 0.30–0.40 lighter red, other surfaces uniformly red; ocular peduncles uniformly red or with lighter red band on proximal 0.20; ocular acicles red except for lighter red distal spines; second and third maxillipeds uniformly red. Both chelipeds generally cream in males, but orange in female; meri red except for distal 0.10–0.25. Second pereopods generally cream; meri red except for distal 0.20–0.40; ischium lighter red. Third pereopods generally cream; meri with lateral face uniform cream or small light red patch, mesial face uniform red except for distal 0.30–0.40; ischium with lateral face uniform cream or very faint red, mesial face uniform lighter red.

Etymology.—This species is named for Mr. Hiroyuki Shidara, an amateur hermit crab collector and marine aquarist, who kindly made the specimens available for this study.

Distribution.—Known only from the type locality.

Remarks.—Despite their general similarities in morphology, the new species, *P. shidarae*, differs from the other three species of the genus in shape of telson. In *P. shidarae*, the terminal margins of the telson are horizontal, and each posterior lobe is armed with at most only 6 (left) or 3 (right) spines (Fig. 8D). In contrast, the terminal margins of the telson of the holotype of *P. bollandi*, and only known specimen, are oblique and the posterior lobes each is armed with 16

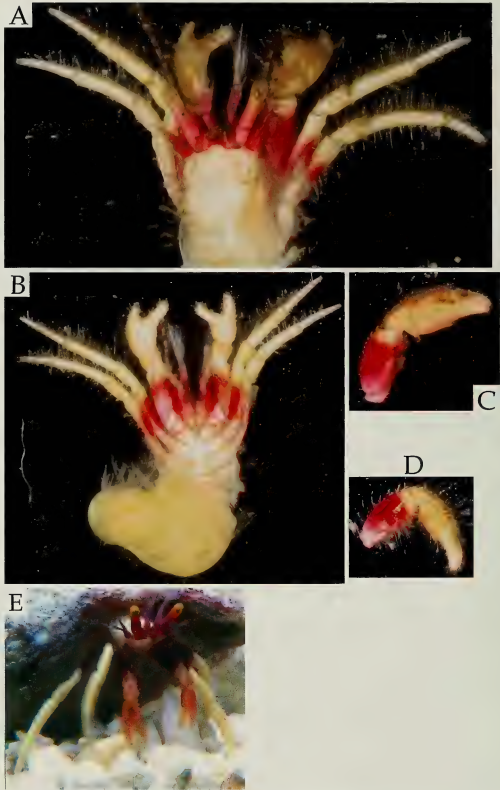


Fig. 12. *Pseudopaguristes shidarai*, new species: A–B, paratype male (CBM-ZC 6815); C–D, holotype male (CBM-ZC 6814); E, female. A, anterior half, dorsal. B, whole animal, ventral. C, right cheliped, lateral. D, left cheliped, mesial. E, living individual of female. Photos by Akira Asakura (A–D) and Kiyohiko Sakuma (E).

Table 1.—Color difference between *Pseudopaguristes shidarai*, new species and *P. janetkae* McLaughlin.

Character	<i>P. shidarai</i>	<i>P. janetkae</i>
Shield anterior margin	Cream	Cranberry red
Ocular peduncles	Uniform red or with lighter red band on proximal 0.20	Cranberry red on proximal 0.25–0.35, remainder yellow-orange
Antennule peduncles		
Ultimate segment	Red	Red-orange
Penultimate segment	Red	Cranberry red on proximal 0.5, remainder red-orange
Basal segment	Red	Cranberry red
Antennal peduncles		
Fifth segment	Red, with proximal 0.30–0.40 lighter red	Yellow
Fourth segment	Red	Yellow
Third segment	Red	Yellow
Second segment	Red	Cranberry red, with yellow produced dorsolateral distal angle
First segment	White	Cranberry red
Chelipeds		
Dactyl and fixed finger	Cream (male) Orange (female)	Tan tinged with cranberry red
Palm	Cream (male) Orange (female)	Cranberry red, becoming lighter distally
Carpus	Cream (male) Orange (female)	Cranberry red
Merus	Red, with distal 0.15–0.25 cream	Cranberry red
Third pereopods		
Merus lateral face	Uniformly cream or with only small, faint red patch	Cranberry red except cream distal portion

(left) or 13 (right) spines. Although McLaughlin (2002) made no mention of number of the telsonal terminal spinules in *P. janetkae*, it is 25 (left) or 13 (right) in the illustration of the holotype (McLaughlin 2002: Fig. 20). The terminal margins of the telson of *P. bicolor* are strongly oblique, and armed with 9 (left) or 6 (right) spines.

The armament of the antennae can separate *P. shidarai* from both *P. bicolor* and *P. janetkae*. Produced dorsolateral distal angles of the second segments of the antennae each has strong, dorsal, bifid spine and 3 or 4 strong lateral spines in *P. shidarai* (Figs. 1D, 2B). The same portions of both *P. bicolor* and *P. janetkae* are only armed with a dorsal bifid spine and have no lateral spines. The ventral margins of antennal acicles are each armed with a row of numerous

spines in *P. shidarai* (Figs. 1D, 2D, E), but they are unarmed in *P. bicolor* and *P. janetkae*.

By differences in coloration in life, *P. shidarai* is readily distinguished from both *P. bicolor* and *P. bollandi*. The chelipeds and the second and third pereopods are uniformly red in *P. bollandi* and have alternating red and white bands in *P. bicolor*. In *P. shidarai*, these appendages are generally cream, with red areas on the meri.

Although the coloration of *P. shidarai* is somewhat similar to that of *P. janetkae* in having cream colored ambulatory pereopods with red proximal portions, many minor but apparent differences are seen as in Table 1. The chelipeds of males of this species are generally cream, with proximal red portions (Fig. 12A–D). However, those of

females are generally orange except for the proximal red portions (Fig. 12E). This may exhibit sexually dimorphic color of chelipeds in this species. However, since only a few specimens are examined, future collection effort will be needed to evaluate this point. McLaughlin (2002) made no mention on sexual difference in coloration of *P. janetkae*.

In addition to the differences in the telson and antennas as mentioned above, *P. shidarai* differs morphologically from *P. janetkae* in several important characters. The propodus of the second left pereopod of the female *P. janetkae* differs from the right and also from the propodi of the males in having scattered spinules on the mesial face. However, in *P. shidarai*, the armature of the propodi of the second pereopods is similar from left to right (Fig. 11A) and also similar to those of the males. In the female *P. shidarai*, the dorsal face of the palms of the chelipeds each bears a longitudinal row of spines. The same surfaces of *P. janetkae* are armed with widely-spaced and somewhat scattered, small spines.

Since so few specimens of each species have been collected in each species, future collection efforts will be needed to evaluate intraspecific variation and interspecific difference more precisely.

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A new species of *Procambarus* (Crustacea: Decapoda: Cambaridae) from Veracruz, Mexico

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Abstract.—*Procambarus (Villalobosus) chacalli* is a new species of crayfish from ponds at Manantial de Dejigui, Huayacocotla County, Veracruz, Mexico. It can be placed in the Erichsoni Group of the subgenus because the gonopod (first pleopod) of the first form male has a flared, broadly curved caudal process. Within the Group it is most similar to *P. (V.) erichsoni* Villalobos and *P. (V.) contrerasi* (Creaser). It can be distinguished from these and other members of the subgenus by a combination of gonopod characters that includes a short mesial process with a slightly flattened, caudodistally directed tip; a cephalic process that originates on the caudal process and is longer than the other terminal elements, and a platelike caudal process with a strong fold on the caudolateral surface. Another distinctive character is the subovate annulus ventralis, with two stronger ventral crests that form a deep submedian depression, and a sinus that extends to the caudomedian margin.

The subgenus *Villalobosus* Hobbs, 1972, of the genus *Procambarus* Ortmann, 1905, as defined by Hobbs (1972), includes 10 species with the following characters: presence of hooks on the fourth pereopods, and rarely vestigial hooks on the third pereopods, of males; and asymmetrical gonopods that reach the coxae of the second pereopods, with a tuberculiform or acute central projection. No new species has been described in this subgenus since Hobbs (1982) described *Procambarus (Villalobosus) cuetzalanae* Hobbs, 1982, from a series of springs, caves and deep holes in the environs of Cuetzalan, Puebla.

The species of *P. (Villalobosus)* inhabit the southern portion of the Huasteca region, within the states of Hidalgo, Puebla and Veracruz. This is a very mountainous region, with a number of narrow valleys and can-

yons that play an important role in isolating crayfish populations (López-Mejía 2001). The members of this subgenus have been found in rivers, small streams, impoundments, and springs, and in subterranean environments as stygophiles (Villalobos 1955; Hobbs 1975, 1982, 1984). The new species described herein has been found only in three ponds at the type locality, Manantial de Dejigui.

The specimens studied are deposited in the Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México (CNCR), and in the Colección de Crustáceos de Referencia, Universidad Autónoma Metropolitana—Unidad Xochimilco (CCR-UAMX). Other abbreviation used is: TCL, total carapace length.

Procambarus (Villalobosus) chacalli,
new species
Figs. 1, 2

Diagnosis.—Body pigmented, eyes normally developed, facets well defined. Rostrum reaching distal border of third antennular article, length 15.8 to 20.8% ($x = 17.9\%$, $n = 26$) of TCL, without marginal spines (Fig. 1A). Areola 4.9 to 7.2 ($x = 5.9$, $n = 26$) times as long as wide, length 32.3 to 38.6% ($x = 35.1\%$, $n = 26$) of TCL, 39.7 to 46.1% ($x = 42.8\%$, $n = 26$) of postorbital carapace length, with 2 or 3 punctations across the narrowest part. Cervical and infraorbital spines absent, branchiostegal spine present. Antennal scale 1.8 to 2.3 ($x = 2.1$, $n = 26$) times longer than wide, with longitudinal groove throughout whole length, groove shallow anteriorly, becoming deeper posteriorly. Chelipeds shorter than total body length; mesial surface of palm of chela with 7 tubercles in irregular row, based on holotypic male form I; all tubercles with small tufts of short setae anteriorly; fingers as long as palm, both fingers with 3 longitudinal ridges along ventral and dorsal surfaces (Fig. 1C). Ischium of fourth pereopod with hook extending beyond basioischial articulation (Figs. 1D–E), ischium of third pereopod with vestigial hook. Cephalic lobe of epistome approximately hexagonal, with margins undulating slightly, irregular and asymmetrical anteriorly; lateral angles well defined, devoid of setae (Fig. 1F).

First pleopods of form I male asymmetrical, reaching coxae of second pereopods, with 2 rows of scattered setae running throughout whole length, setae more abundant and longer proximally. Mesial process short, slightly truncated distally, directed distolaterally; central projection triangular, divided into 2 sections, caudocephalically oriented; cephalic process spiniform, directed distocephalically, longer than rest of terminal elements, originating on caudal process; caudal process in cephalic position platelike, corneous, wrapping around cen-

tral projection, with strong fold on caudolateral margin (Figs. 2A–D, F–G). Preannular plate of female with 2 strong lateral crests extending laterally and surrounding annulus ventralis, with scattered short setae on posterior portion of plate (Fig. 1G). Preannular plate and annulus in loose contact. Annulus approximately circular, with 2 strong crests anteriorly, forming deep, V-shaped depression; posterior half of dextral crest curved laterally, becoming less defined; sinistral crest curving laterally to form tongue-like expansion; rectangular projection on medial posterior section, forming margin of sinus. In ventral view, postannular plate ovoid, in caudal view approximately conical; apical surface bearing small punctations with short setae; plate not in contact with annulus. First pleopods present in females.

Measurements of types.—Provided in Table 1.

Holotypic male, form I.—Body and eyes pigmented. Cephalothorax becoming thicker posterior to cervical groove, maximum width at posterior margin, 0.97 times length of abdomen. Areola 6.2 times as long as wide, 32.3% of TCL, with 3 punctations across narrowest part, with slight median crest; branchiocardiac grooves well defined. Surface of carapace densely punctate, punctations increasing in density laterally. Rostrum excavated dorsally, margins convergent, without spines; anterior width 2.9 mm, posterior width 3.8 mm. Acumen reaching distal border of third article of antennular peduncle, slightly shorter than antennal scale, tip oriented dorsally, length of acumen 28.2% of rostrum length, ventral keel without spines. Postorbital ridge straight, moderately strong, with very small cephalic tubercle. Suborbital angle acute, branchiostegal spine present on both sides of carapace, directed anteriorly. Cervical groove describing acute angle over hepatic groove, cervical spine absent (Fig. 1B).

Abdomen slightly longer than carapace. Surface of somites covered with regularly distributed punctations. Uropods with pro-

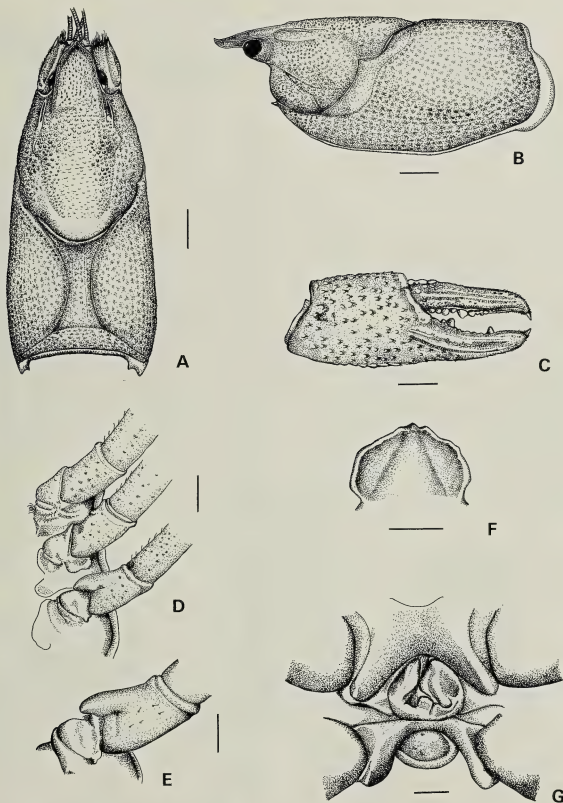


Fig. 1. *Procambarus (Villalobosus) chacalli*, new species, all from holotypic male, form I, except G from allotypic female. A, carapace, dorsal view; B, carapace, lateral view; C, distal podomeres of right cheliped; D, basal podomeres of left second, third and fourth pereiopods; E, detail of basis and ischium of left fourth pereiopod; F, epistome, cephalic lobe; G, annulus ventralis. Scale bars represent 3 mm (A, B, C), 2 mm (D, E), and 1 mm (F, G).

Table 1.—Measurements (mm) of type specimens of *Procambarus chacalli*, new species.

	Holotypic male, form I	Allotypic female	Morphotypic male, form II
Total length	51.2	55.5	48.7
Carapace			
Total length	24.1	26.9	23.6
Postorbital length	19.6	22.6	19.3
Width	11	12	10.2
Height	10	12.1	9.3
Areola			
Length	7.8	10.4	8.6
Width	1.2	1.7	1.7
Rostrum			
Length	4.5	4.25	4.2
Width	3.8	4.2	4.8
Antennal scale			
Length	3.9	4.1	3.5
Width	2.1	2.4	2.2
Cheliped			
Length of mesial margin of palm	10.5	9.5	10.5
Width of palm	7.5	7.1	7.1
Length of lateral margin of propodus	18.9	18.2	19
Length of dactyle	10.2	9.5	10.1
Length of carpus	6.8	6.6	7.3
Length of merus	10.7	10.7	10.3
Abdomen			
Length	27.1	28.6	25.1
Width	10.4	11.3	9.8

topodite bearing short spines; endopodite with dorsal median ridge ending posteriorly in small spine, and well developed distolateral spine. Telson covered with tufts of short setae, loosely forming 4 longitudinal rows; cephalic portion with 4 spines on posterolateral angle, two lateral ones larger, second one articulated.

Cephalic lobe of epistome irregular, without cephalomedian extension; distal half asymmetrical, with central depression. Antennule with prominent ventral spine on basal podomere, with setae on its base; antenna shorter than total body length. Antennal scale 1.8 times longer than wide, lateral margin ending in acute spine, maximum width at distal half (Fig. 2E). Third maxilliped reaching distal border of third article of antennal peduncle; internal margin of ischium with array of 26 irregular spines; all

segments of third maxilliped with small tufts of short setae.

Chelae 1.2 times shorter than TCL, robust, ovate, 2.5 times longer than wide. Palm 1.4 times longer than wide, surface covered with small, blunt tubercles each with small tuft of setae; irregular row of tubercles along mesial surface. Movable finger with subsquamate tubercles anteriorly. Opposable margins of fingers with small tufts of setae; opposable surface of movable finger with 10 tubercles, that of fixed finger with 7 tubercles, third from base largest; both fingers ending in corneous tip.

Carpus of cheliped short, approximately conical, dorsal surface with scattered tubercles; lateral and ventral surfaces with small subsquamate tubercles, with tufts of short setae, distal margin with blunt spine on in-

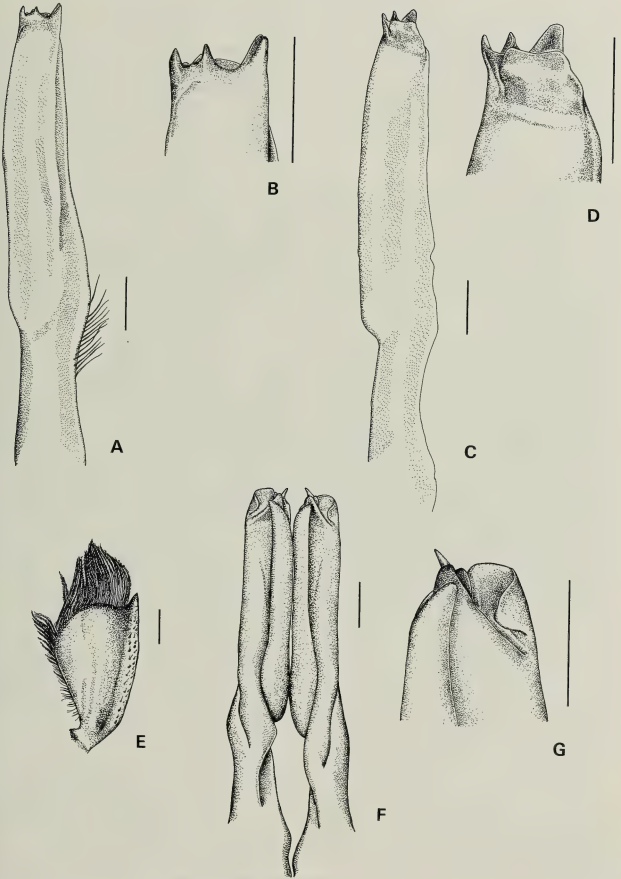


Fig. 2. *Procambarus (Villalobosus) chacalli*, new species, all from holotypic male, form I, except H from morphotypic male, form II. A, left gonopod, mesial view; B, detail of apex of left gonopod, mesial view; C, left gonopod, lateral view; D, detail of apex of left gonopod, lateral view; E, antennal scale; F, caudal view of gonopods; G, detail of apex of left gonopod, caudal view; H, caudal view of gonopods. Scale bars represent 1 mm.

ternal surface. Merus slightly tuberculate; dorsal surface with large, strong, subdistal tubercle, and other smaller tubercles; ventral surface with 2 longitudinal rows of blunt tubercles, distal margin with strong tubercle. Ischium with dorsal and ventral surfaces punctate, and row of 6 blunt tubercles along ventromesial margin, increasing in size distally.

Ischium of third pereopod with vestigial hook, left and right sides different in size. Ischium of fourth pereopod with strong, thick, cylindrical hook, extending beyond basioischial articulation, reaching mid-length of basis. Coxa of fourth pereopod with prominent acute boss on caudomesial ventral angle.

Gonopods as described in Diagnosis.

Allotypic female.—Similar to holotype, differing in following characters: telson bearing 2 movable spines on left caudolateral angle of cephalic portion and 1 on right side. Areola 6.2 times as long as wide. Antennal scale 1.8 times longer than wide. Eight tubercles on opposable margin of movable finger. Rostrum reaching first third of third article of antennular peduncle. Cephalic lobe of epistome asymmetrical as in holotype, distal border with small variations with respect to holotype. Annulus ventralis as described in Diagnosis.

Morphotypic male, form II.—Differing from holotype in following characters: first pleopod with apical elements poorly developed, cephalic process conical and reduced, central projection small, caudal process surrounding central projection, mesial process undefined. Areola 4.9 times as long as wide. Antennal scale 1.6 times longer than wide. Chelae with irregular row of four tubercles on surface of palm. Protuberance on ischium of third pereopod extremely reduced. Ischium of fourth pereopod with small hook, not surpassing basioischial articulation. Rostrum shorter, acumen reaching middle part of third podomere of antennular peduncle.

Type locality.—Nacimiento de Dejigui (altitude 1675 m), 4 km east of Huayaco-

cotla, Municipio de Huayacotla, Veracruz, Mexico (20°32'6"N, 98°26'15"W).

Disposition of types.—Holotypic ♂ form I, CNCR 20529; allotypic ♀, CNCR 20530; and morphotypic ♂ form II, CNCR 20531. Paratypes: 2 ♂ I, 2 ♂ II, 8 ♀, CNCR 20532; 5 ♂ II, 6 ♀ CCR-UAMX 1001.

Material examined.—All from type locality: 1 ♂ form I (CNCR 20529), 14 Nov 1999, coll. M. López-Mejía, L. M. Mejía-Ortiz; 1 ♀ (CNCR 20530), same date and coll. as holotype; 1 ♂ form II (CNCR 20531), 2 ♂ form I, 2 ♂ form II, 8 ♀ (CNCR 20532), 5 ♂ form II, 6 ♀ (CCR-UAMX 1001), 2 Nov 2001, coll. M. López-Mejía, L. M. Mejía-Ortiz, M. Signoret, J. A. Viccon-Pale, J. Cruz-Hernández, H. Solís.

Etymology.—The specific epithet "*chacalli*" is taken from the nahuatl word "*chacalli*", common name used for the crayfishes in northern Hidalgo, Mexico.

Remarks.—*Procambarus (Villalobosus) chacalli*, new species, can be placed in the Erichsoni Group due to the presence of a platelike caudal process on the male gonopod (Villalobos 1955). The new species is morphologically similar to *Procambarus (Villalobosus) contrerasi* (Creaser, 1931), and *Procambarus (Villalobosus) erichsoni* Villalobos, 1950, from which it may be distinguished by the following characters: a longer rostrum, with tip reaching the distal border of the third antennular article; a wider areola with a slight median crest; and an epistome bearing a cephalic lobe with an undulated surface. Regarding the gonopod morphology of the form I male, *P. chacalli* exhibits the following unique characters: a short and slightly truncated mesial process, directed distolaterally; a cephalic process which is the largest of the terminal elements, originating on the caudal process; and a platelike caudal process with a strong fold on the margin. In *P. erichsoni* and *P. contrerasi* the rostrum reaches the distal part of the second antennular article, the areola is narrower, and the surface of the epistome is smooth; their gonopods bear

shorter cephalic processes, that originate between the central projection and the mesial process, and the caudal process is slightly folded. The annulus ventralis of *P. chacalli* differs from those of *P. erichsoni* and *P. contrerasi* in the extension of the lateral projections of the preannular plate, the shape of the crests and sinus in the annulus, and the size and shape of the postannular plate.

Procambarus (Villalobosus) chacalli has been collected only at the type locality, where specimens were captured in three small, shallow ponds next to the spring. The largest pond was 8 m², and the deepest one was 0.4 m. The recorded water temperatures ranged from 18.9 to 20.4°C.

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***Brackenridgia ashleyi*, a new species of terrestrial isopod from
Tumbling Creek Cave, Missouri (Isopoda: Oniscidea: Trichoniscidae)**

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Abstract.—*Brackenridgia ashleyi*, a new species of troglobitic trichoniscid isopod, is described and illustrated from Tumbling Creek Cave, Taney Co., Missouri. The genus *Brackenridgia* was previously known only from the western United States and Mexico. The discovery of *B. ashleyi* in the Ozark Plateaus physiographic province extends the range of the genus over 800 kilometers to the northeast. This species is closest geographically to *B. cavernarum* and *B. reddelli* in Texas, but is morphologically more similar to *B. heroldi* in California. Despite the presence of large amounts of bat guano in the cave, *B. ashleyi* is not guanophilic. By not using the guano microhabitat *B. ashleyi* avoids many of the predators present in the cave community.

In the eastern United States troglobitic trichoniscid isopods have long been known from the karst areas of the Appalachian Valley and Interior Low Plateaus. From the caves of this region have been described six species of *Amerigoniscus* (or *Caucasonethes*, from which *Amerigoniscus* was split by Vandel 1950) and four species of *Miktoniscus* (Vandel 1950, 1965, 1978; Jass & Klausmeier 2001). Other genera of trichoniscids occurring in the eastern U.S. are *Androniscus*, *Haplophthalmus*, *Hyloniscus*, *Trichoniscus*, and *Trichoniscoides* (Leistikow & Wägele 1999, Jass & Klausmeier 2001), but within these the only species of significance in caves is *Haplophthalmus danicus*. This Mediterranean species is a widely introduced exotic in the U.S., where it frequents caves (Vandel 1965).

In the Ozark Plateaus Craig (1975) and Gardner (1986) reported undescribed trichoniscids in Missouri caves including Tumbling Creek Cave. This cave is inhabited by a diverse assemblage of troglobites, although several of the species remain undescribed. Motivation to describe these taxa was presented by a decline within the cave's ecosystem leading to listing of the

endemic hydrobiid Tumbling Creek Cave-snail *Antrobia culveri* as a federal endangered species (U.S. Fish & Wildlife Service 2001). Given this situation, there was a need for characterization of the fauna and specimens of the trichoniscid were collected for the purpose of preparing a description of the species.

Because of reports (Aley 1975, Craig 1975, Gardner 1986, U.S. Fish & Wildlife Service 2001) listing this species as *Amerigoniscus* (or *Caucasonethes*) the material considered herein was received with the presumption that it represented a species in that genus. Examination of the isopod proved this assumption was wrong as evidenced by: (1) antenna 1 with short, stout aesthetascs on the distal article, (2) pereopod 7 propodus with distinct distal tuft of setae, and (3) male pleopod 1 with vestigial endopod. These characteristics eliminated the species from *Amerigoniscus* (Vandel 1953, 1965, 1978; Schultz 1982, 1994).

Other North American genera for consideration were listed variously in the First Division Trichoniscinae by Vandel (1965) or Tribe Typhlotricholigiodini (Tabacaru 1993, Schultz 1994): *Brackenridgia*, *Typhlotri-*

cholioides, *Cylindroniscus* and *Mexiconiscus*. The morphological characteristics listed above for the Tumbling Creek Cave isopod are exhibited by *Brackenridgia* and *Cylindroniscus*. Schultz (1994) listed the following characteristics of *Cylindroniscus* that separate the genus from *Brackenridgia*: (1) an elongate, semi-cylindrical body, (2) antenna 2 that projects from the front of the cephalon, and (3) uropod basis with elongate endopod and exopod. *Cylindroniscus* has been reported from Cuba and Mexico, but is not known to occur in the United States (Schultz 1970). Although the separation of *Brackenridgia* and *Cylindroniscus* is not entirely distinct, the Tumbling Creek Cave trichoniscid seems most appropriately placed in *Brackenridgia*. The ten species now recorded from this genus occur from Missouri to California and into Mexico (Rioja 1950, 1951, 1955; Vandel 1965; Schultz 1984; Dearolf 1953) as presented in Fig. 1.

Materials and methods.—The isopods were placed on a glass slide in a drop of glycerin and appendages were dissected directly into the glycerin to produce temporary mounts. All drawings were made on a Leica compound microscope with an optical drawing tube. After completion all appendages were then replaced in microvials and stored in 70% ethanol. The geographic coordinates for the type-locality were recorded with a Garman Map76 GPS. Temperature readings in Tumbling Creek Cave were taken with a Taylor digital thermometer.

Family Trichoniscidae

Brackenridgia Ulrich 1902

Brackenridgia ashleyi, new species

Figs. 2–5

Caucasonethes.—Aley, 1975:1.

Caucasonethes sp.—Craig, 1975:4 [in part].

Caucasonethes n. sp.—Gardner, 1986:15 [in part, Tumbling Creek Cave record only];

U.S. Fish & Wildlife Service, 2001: 66804.

Material examined.—Missouri: Taney Co., Tumbling Creek Cave, 22 Apr 2001, Catherine and Thomas Aley, 2.8 mm holotype ♂ (USNM 1008288); same locality and collectors, 2.3 mm paratype ♂ (USNM 1008289), 25 Nov 2001; same locality, Julian J. Lewis and David Ashley, 2.7 mm paratype ♂ (USNM 1014382), 23 Apr 2003, same locality 21 Feb 1998, William Elliott, 2.2 mm paratype ♂. The first three specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. under catalog numbers as noted. The Elliott collection is deposited in the Enns Entomological Museum, University of Missouri, Columbia.

Description of male.—Eyeless, unpigmented, longest 2.8 mm. Body about 2.8× as long as wide, dorsal surface covered with short, stout triangular spine-like setae. Head, anterior margin biconcave, rostral area broadly rounded. Pereonites with lateral margins with short, stout triangular spine-like setae and short setae; pereonite 1 directed cephalad, 5–7 directed caudad. Lateral margins of pleonites contiguous, telson with posterior margin produced, broadly rounded, with 4 small setae.

Antenna 1 with 5–6 short, stout aesthetascs on distal article. Antenna 2 flagellum with 5 indistinctly demarcated articles, distal article with longitudinally striated apical organ. Mandibles with well developed molar process. Right mandible with plumose setae between molar process and incisor, lacinia mobilis apically lobed. Left mandible with two plumose setae between pars incisiva/lacinia mobilis and molar process. Maxilla 1, endopod with 3 bladlike setae; exopod with 8 spine-like setae (4 dominant robust + 4 smaller). Maxilliped palp segmentation indistinct, basal article relatively narrow, not obscuring endite.

Pereopod 1, propodus with 6 subtriangular spine-like setae along outer margin. Pereopods 5–7 with row of stout spine-like



Fig. 1. Distribution of *Brackenridgia* species and source of records: (1) *B. ashleyi*, (2) *B. cavernarum* (Texas records—Vandel 1965, Mitchell and Reddell 1971; New Mexico record—Dearolf 1953, needs confirmation); (3) *B. reddelli* (Vandel 1965, Mitchell & Reddell 1971); (4) *B. sphinxensis* (Schultz 1984); (5) *B. heroldi* (Vandel 1965); (6) *B. bridgesi* (Vandel 1965, Reddell 1981); (7) *B. palmitensis* (Mulaik 1960); (8) *B. villalobosi* (Vandel 1965, Reddell 1981); (9) *B. acostai* (Vandel 1965, Reddell 1981).

setae along distal margin of carpus and merus (scales of Vandel 1965 or Schultz 1994). Pereopod 7 propodus with spine-like setae in row on outer margin leading to dense tuft of setae adjacent to junction of dactyl.

Pleopod 1, exopod with small spinules along lateral margin, tip simple, produced

into subtriangular structure with low, slightly produced knobs subapically; endopod vestigial, reduced to a subtriangular flange. Pleopod 2 endopod thin, elongate, tapering to a point; exopod about $0.3\times$ length of endopod, small, subovate with one apical setule. Pleopods 3–5 undifferentiated. Uropods about $1.5\times$ length of telson, about

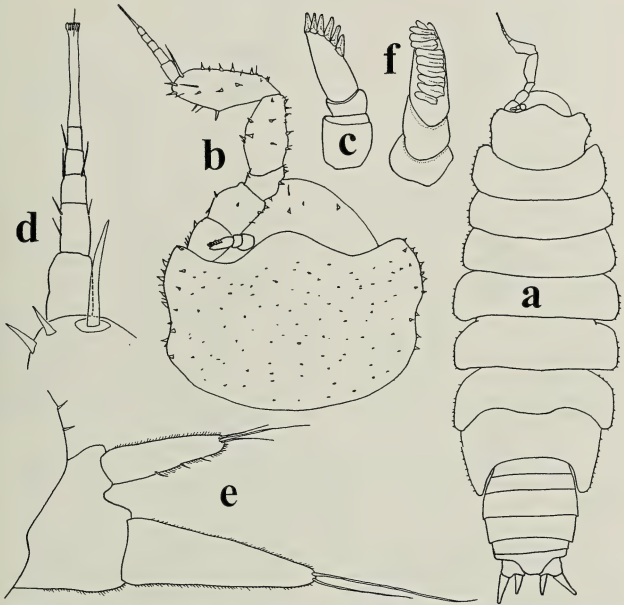


Fig. 2. *Brackenridgia ashleyi*, male from Tumbling Creek Cave, Taney Co., Missouri: (a) habitus, (b) head, labrum and antennae, (c) antenna 1 with aesthetascs, (d) antenna 2, (e) uropod; *B. reddelli*, male from Valdina Farms Sinkhole, Medina Co., Texas: (f) antenna 1 in situ.

0.3× length of pleon, endopod about 0.6× length of exopod, rami with 2–3 elongate apical setae.

Erymology.—The species is named in honor of Dr. David Ashley, of Missouri Western State College, in recognition of his years of outstanding effort monitoring the ecosystem of Tumbling Creek Cave.

Distribution and ecology.—*Brackenridgia ashleyi* is known only from the type-locality in the Springfield Plain of the Ozark Plateau physiographic province in south-

western Missouri. Tumbling Creek Cave has 2,815 meters of mapped passages formed in the predominantly dolomitic Jefferson City Formation of Ordovician age. The cave is on the property of the Ozark Underground Laboratory and has two entrances: (1) the natural entrance marked Bear Cave on the U.S. Geological Survey Protem Quadrangle map at N36.55471, W92.80275; and (2) an artificial entrance marked Tumbling Creek Cave at N36.54951, W92.80807. Tumbling Creek

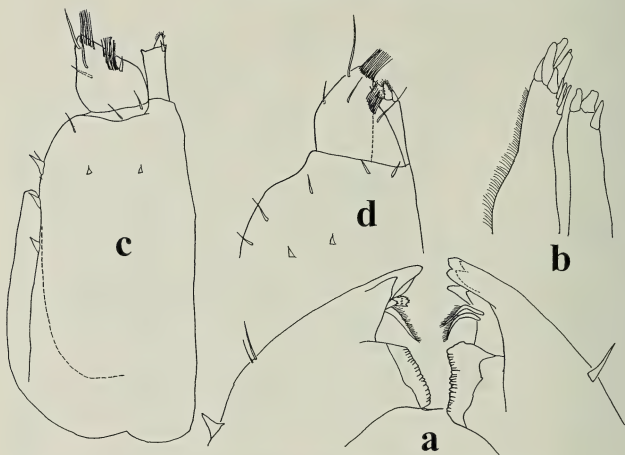


Fig. 3. *Brackenridgia ashleyi*, male from Tumbling Creek Cave, Taney Co., Missouri: (a) mandibles (b) maxilla 1, (c) maxilliped; *B. heroldi*, Crystal Cave, Sequoia National Park, California: (d) distal elements of maxilliped.

Cave was dedicated by the U.S. Department of the Interior as a Natural Landmark in 1980.

Tumbling Creek Cave has been the site of detailed ecological studies concerning the community associated with the bat guano of the Gray bat *Myotis grisescens* (Martin 1980, Fletcher 1982). Martin (1980) reported the air temperature of the cave was 14.4°C ($\pm 1^\circ$) and relative humidity at or near 100%. Temperature measurements by Lewis and Ashley on 23 April 2003 of the substrate of the isopods were 14.7°C in the East Passage and 14.3°C in the main stream passage.

Martin (1980) reported 54 invertebrate taxa occurring on guano, bat carcasses and wood in Tumbling Creek Cave. Typical of caves with Gray bat maternity colonies, most surfaces between the bat roosts and

entrance are peppered with bat guano and piles as much as a meter deep occur in some areas. Martin found 49 taxa inhabiting these guano piles, several of which were predators, including the pseudoscorpion *Hesperocheles occidentalis*, an unidentified harvestman, and beetles *Platynus tenuicollis*, *Bembidion* sp. and *Atheta* sp. In contrast, the terrestrial isopods were never found on guano nor bat carcasses, only wood. Of the 14 species recorded from wood by Martin, only *B. ashleyi* and the millipeds *Pseudopolydesmus pinetorum* and *Scoterpes* s. latu *dendropus* did not also occur on guano or carcasses. This habitat partitioning by these species excluded them from the richest food source in the cave, but eliminated significant predation pressure as well. A fact not appreciated by Martin, who did not identify the terrestrial isopods, was

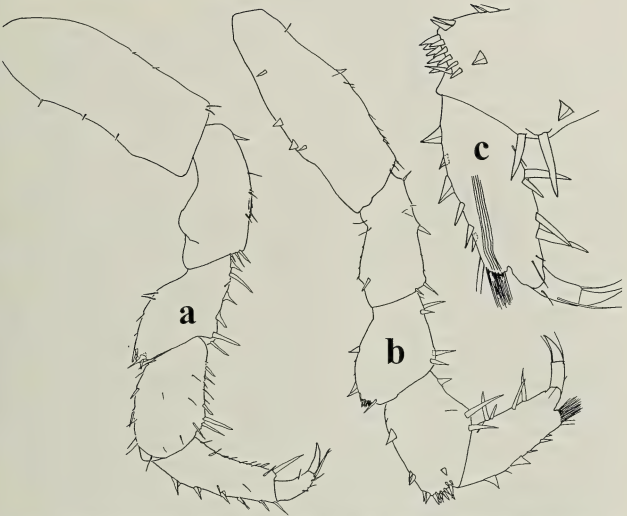


Fig. 4. *Brackenridgia ashleyi*, male from Tumbling Creek Cave, Taney Co., Missouri: (a) pereopod 1, (b) pereopod 7, (c) pereopod 7 propodus and dactylus.

that the exotic *Haplophthalmus danicus* was also living on the wood and therefore possibly competing with *B. ashleyi*.

The wood on which the isopods were most easily observed consists of pieces of pine boards placed in the cave to attract invertebrates for viewing purposes (the cave is operated among other things as an educational facility). The isopod presumably feeds on microbial decomposers occurring on the wood. As the presence of the wood is artificial, under natural circumstances *Brackenridgia* must live on the ubiquitous mud banks. All of the isopods collected for study herein were found associated with wood on relatively dry mud banks along the main stream passage or in the upper level East Passage. When observed, *Bracken-*

ridgia moved about within an area of a few square centimeters, with its antennae actively probing the environment when walking.

Life history.—Nothing is known of the reproduction of *B. ashleyi*. In examining material of other *Brackenridgia* two ovigerous females of *B. heroldi* were found in a collection from Hurricane Crawl Cave, Sequoia National Park, California (collection date unknown). One was a 3.2 mm specimen with four embryos in the brood pouch. The other was 3.5 mm in length and was carrying one 1.1 mm juvenile.

Discussion.—With the exception of the humicolous *B. heroldi*, the species of *Brackenridgia* are troglobites restricted to karst areas isolated from one another by

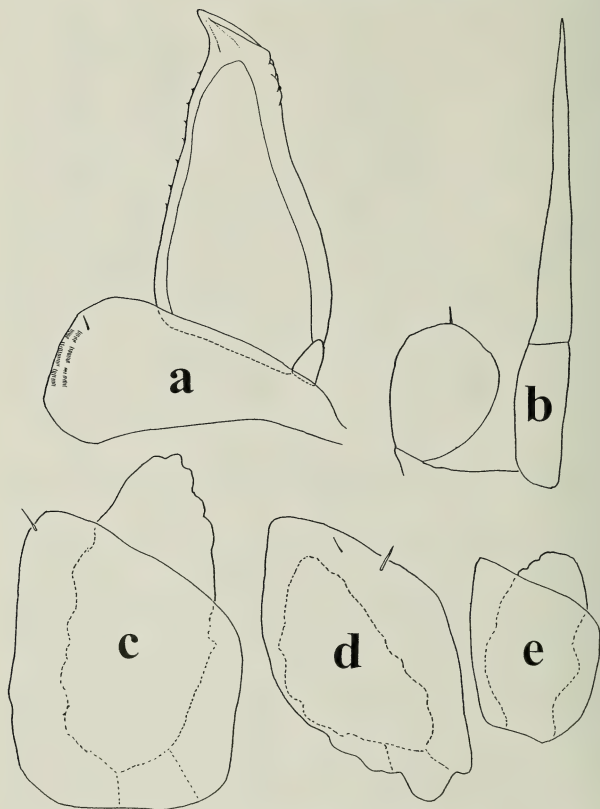


Fig. 5. *Brackenridgia ashleyi*, male from Tumbling Creek Cave, Taney Co., Missouri: (a) pleopod 1, (b) pleopod 2, (c) pleopod 3, (d) pleopod 4, (e) pleopod 5.

hundreds of kilometers of non-cavernous rocks. Dispersal and gene flow between populations is thus very unlikely, leaving little doubt as to the speciation of these animals in their respective karst islands. For example, *B. ashleyi* in the Ozarks is separated from its nearest relatives inhabiting the karst of the Balcones Fault Zone in Texas (*B. cavernarum* and *B. reddelli*) by over 800 kilometers (Fig. 1).

That notwithstanding, the morphological expression of this speciation is conservative among the members of the genus. The subtriangular shape of the male first pleopod exopod is similar in all species of the genus. The species of *Brackenridgia* can be separated from one another by relatively small differences in the structures present at the tip of this exopod. In the most primitive species, e.g., *B. cavernarum* or *B. sphinxensis*, the exopod tip is undifferentiated. A variety of specializations into spinose or digitiform structures occur in *B. reddelli*, *B. ashleyi* and *B. villalobosi*, with the bi-spinose pleopod 1 exopod tip (Vandel 1965) of *B. bridgesi* presumably apomorphic. Although *B. ashleyi* is closest geographically to *B. cavernarum* and *B. reddelli* in Texas, the slight modification of the pleopod 1 exopod tip is more similar to that of *B. heroldi* in California.

Much work remains in the systematics of *Brackenridgia*. In *B. reddelli* and *B. sphinxensis* none of the mouthparts have been illustrated. The latter species is known from a single tiny dissected specimen so there is little hope for a better understanding of the species without additional collecting. Similarly, *B. palmitensis* (Mulaik 1960) remains unidentifiable (Vandel 1965) and attempts to collect a male have been unsuccessful (Reddell 1981). The regional variation reported by Vandel (1965) for *B. reddelli* is suggestive of a cluster of closely related species inhabiting the caves associated with the Balcones Fault Zone in Texas. Confusion has also been created by Vandel's (1965) interpretation of the lateral margin of the male pleopod 1 protopod of

B. villalobosi (illustrated by Rioja 1950 fig. 44) as the exopod tip.

Vandel (1965) published a key to the species of the genus known at the time, while Rioja (1955) included only the Mexican fauna. I have updated these works to encompass nine members of the genus, including the addition of *B. sphinxensis* and *B. ashleyi*, but excluding *B. palmitensis*. The identity of *B. palmitensis* remains obscure, although Mulaik (1960 fig. 43) illustrated 8 short, stout aesthetascs on the distal article of antenna 1. This characteristic separates this species from the majority of *Brackenridgia* species, including *B. ashleyi*.

Key to Species of the Genus *Brackenridgia*

- 1a. Pereonites with prominent tubercles (fig. 6a), antenna 1 with elongate aesthetascs *B. acostai* (caves, Chiapas, Mexico)
- 1b. Pereonites without prominent tubercles (fig. 2a) (2)
- 2a. Male pleopod 1 exopod tip undifferentiated (fig. 6b) (3)
- 2b. Male pleopod 1 exopod modified, tapering to 1–2 processes (figs. 5a, 6c, d) (4)
- 3a. Length excluding antennae and uropods <2 mm; antenna 1 distal article with 5 aesthetascs *B. sphinxensis* (Sphinx Cave, Cochise County, Arizona)
- 3b. Length excluding antennae and uropods >4 mm; antenna 1 distal article with 10+ aesthetascs *B. cavernarum* (caves, southcentral Texas, unconfirmed in southeastern New Mexico)
- 4a. Male pleopod 1 exopod tapering to a single point (figs. 5a, 6c) (5)
- 4b. Male pleopod 1 exopod tip with two processes (fig. 6d) (7)
- 5a. Male pleopod 1 exopod tapering to a digitiform process, antenna 1 aesthetascs 8 *B. villalobosi* (caves, Veracruz)
- 5b. Male pleopod 1 exopod tapering to a point (figs. 5a, 6c), antenna 1 aesthetascs 5–6 (fig. 2c) (6)
- 6a. Maxilliped palp basal segment broad, obscuring endite (fig. 3d); male pleopod 1 exopod without subapical knobs (fig. 6c) *B. heroldi* (humus and caves, southern California)

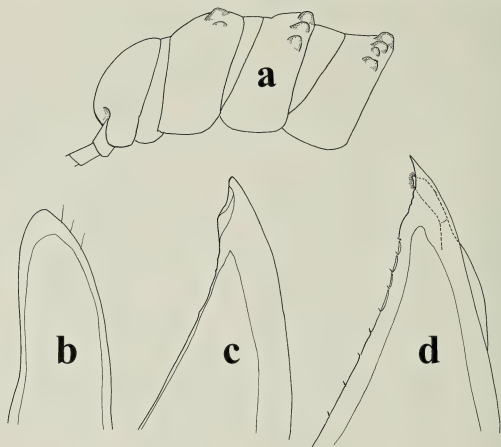


Fig. 6. *Brackenridgia acostai*, Cueva del Ticho, Chiapas: (a) head and pereonites 1-3; *B. cavernarum*, Kappelman Salamander Cave, Comal Co., Texas: (b) pleopod 1 exopod tip; *B. heroldi*, Crystal Cave, Sequoia National Park, California: (c) pleopod 1 exopod tip; *B. reddelli*, Valdina Farms Sinkhole, Medina Co., Texas: (d) pleopod 1 exopod tip.

- 6b. Maxilliped palp basal segment narrow, not obscuring endite (fig. 3c); male pleopod 1 exopod with low, subapical knobs (fig. 5a) *B. ashleyi* (Tumbling Creek Cave, Missouri)
- 7a. Male pleopod 1 exopod tapering to two acute spines, antenna 1 aesthetascs 14 ... *B. bridgesi* (caves, northeastern Mexico)
- 7b. Male pleopod 1 exopod tapering to an acute spine and a second brush-like process (6d); antenna 1 aesthetascs 9-10 (fig. 2f)
... *B. reddelli* (caves, southcentral Texas)

Acknowledgments

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Schultz and Dr. Stefano Taiti for reading the manuscript and making suggestions for its improvement. The loan of specimens from the collections of the Smithsonian Institution was kindly provided by Ms. Marilyn Schotte and Dr. Brian Kensley. The description of *B. ashleyi* was funded by the U.S. Fish & Wildlife Service, The Nature Conservancy and the Ozark Underground Laboratory.

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New species and records of Bopyridae (Crustacea: Isopoda) infesting species of the genus *Upogebia* (Crustacea: Decapoda: Upogebiidae): the genera *Orthione* Markham, 1988, and *Gyge* Cornalia & Panceri, 1861

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Abstract.—Two bopyrid genera whose species parasitize only *Upogebia* spp. are reviewed and revised. *Orthione* Markham, 1988, heretofore known only from its type-species, *O. furcata* (Richardson, 1904), is rediagnosed and enlarged. *Orthione griffenis*, new species, infests *Upogebia pugettensis* (Dana, 1852) in Oregon, U.S.A. *Orthione mesoamericana*, new species, infests *U. spinigera* (Smith, 1871) on the Pacific coasts of Costa Rica and Colombia. The genus *Metabopyrus* Shiino, 1939, is incorporated into *Gyge* Cornalia and Panceri, 1861, which is rediagnosed, and a key is given to the four known species. *Gyge ovalis* (Shiino, 1939), formerly *Metabopyrus ovalis* Shiino, 1939, is re-described on the basis of new material found infesting *U. edulis* Ngoc-Ho & Chan, 1992, in Taiwan, a new host and geographical record.

In a recent compilation of the known bopyrid parasites of thalassinidean decapod crustaceans throughout the world (Markham 2001), I listed 26 species of the genus *Upogebia* known to harbor a total of 27 species of bopyrid isopods. Since then, additional material of parasites of species of *Upogebia* has become available for examination or has been reliably reported to me. It includes two new species of *Orthione* Markham, 1988, described herein, as well as new host and geographic records for *Metabopyrus ovalis* Shiino, 1939, which is re-described and reassigned to the genus *Gyge* Cornalia & Panceri, 1861.

Materials and Methods

Host specimens bearing parasites, or parasites that had been removed from their hosts, have become available for study from various sources over a period of several years. Some were already in scientific collections, while others are being newly donated to institutions housing such collections. Those institutions are indicated thus:

Museo de Zoología, Universidad de Costa Rica, MZUCR; Naturhistorisches Museum, Wien, Austria, NHMW; Naturhistoriska Riksmuseet, Sweden, SMNH; and Natural History Museum, Smithsonian Institution, USNM.

Results

Family Bopyridae Rafinesque-Schmaltz,
1815

Subfamily Pseudioninae Codreanu, 1967
Genus *Orthione* Markham, 1988

Type-species, by original designation, *Pseudione furcata* Richardson, 1904. Number of previously known species: 1, *O. furcata* (Richardson, 1904), infesting *Upogebia affinis* (Say, 1818), Massachusetts to North Carolina, U.S.A.

Revised generic diagnosis, based on three known species.—Female. Body outline oblong, about twice as long as wide, sides nearly parallel, axis only slightly distorted, all body regions and segments distinct dorsally. Head deeply set into pereon, its an-

terior margin completely covered by frontal lamina and forming continuous curve with pereon; maxilliped lacking palp; barbula with single prominent lanceolate process on each side, rarely minute process lateral to it. Pereopods slightly to much larger posteriorly; oostegites generously enclosing brood pouch, first one with prominent but unadorned internal ridge, no posterolateral point. Pleon of six pleomeres, much broader than long, final pleomere deeply enclosed by fifth; five pairs of biramous pleopods and similar uniramous uropods completely covering lateral margins and all but center of dorsal surface of pleon, endopodites of first pair larger and medially extended.

Male. Body oblong, at least three times as long as wide; all body regions and segments distinct. Head nearly semicircular; second antennae prominently extended. Pereopods relatively small, though overall larger and with smaller dactyli posteriorly, all clustered medially. Pleon about $\frac{1}{2}$ of total body length, of six pleomeres; pleopods absent or as low incomplete oval uniramous flaps; final pleomere largely surrounded by fifth, ending in pair of uniramous flaplike uropods.

Hosts. All in genus *Upogebia*.

Key to Three Species of *Orthione*, Based on Mature Females

1. Pereopods with propodal cups receiving tips of dactyli, bases produced into large carinae; pleopodal rami somewhat ovate
O. griffenis new species [Oregon, U.S.A.].
- Pereopods lacking propodal cups to receive tips of dactyli, bases lacking carinae; pleopodal rami lanceolate 2.
2. Head much broader than long, with minute barbular projection lateral to main process; final pleomere visible dorsally
. . . *O. mesoamericana* new species [Pacific coast from Costa Rica to Colombia].
- Head about as broad as long, only single process on each side of barbula; final pleomere more or less hidden dorsally
. *O. furcata* (Richardson, 1904)
[Atlantic coast of U.S.A.].

Orthione griffenis, new species

Figs. 1–3

“New species . . . [of] . . . *Orthione*.”—David, 2001:6.

Material examined.—Infesting *Upogebia pugetensis* (Dana, 1852). Collected and hosts det. by B. D. Griffen. Mudflats, Idaho Inlet, Yaquina Bay, Oregon, USA, 44° 35.4'N, 124°01.5'W, unspecified date, 2000: 1 ♀, holotype, USNM 1008784, 1 ♂, allotype, USNM 1008785. Same locality, 23 June 2001, 9 ♀♀, 7 ♂♂, paratypes, USNM 1008786. Collected and hosts det. by T. H. DeWitt: Riverbend, Yaquina Bay, Oregon, 12 November 1999, Sample 59MDF-U31: 1 ♀, dextral, 1 ♂, paratypes, USNM 1008787. Idaho Flat, Yaquina Bay, Oregon, 24 September 1999, Sample 59UU104M: 1 ♀, sinistral, immature, paratype, USNM 1008788.

Description.—Holotype female (Fig. 1). Length 11.0 mm, maximal width 9.2 mm, head length 2.2 mm, head width 2.1 mm, pleon length 2.9 mm; distortion 15°, dextrally. Outline oval, nowhere abruptly broader or narrower; all body regions and segments distinct. No pigmentation (Fig. 1A, B).

Head almost square, deeply set into pereon, its anterior edge continuous with pereon margin. Distinct rather long frontal lamina extending completely across front of head but not beyond its sides. First antennae long and extended beyond margin of head, of 5 articles, distal two terminally setose; second antennae greatly reduced, of 1 to 3 articles (Fig. 1C). Barbula (Fig. 1D) with single long falcate process on each side, central region entire. Maxilliped (Fig. 1E) subtriangular, lacking palp, with plectron short and blunt; anterior article nearly rectangular, much longer than triangular posterior article.

Pereon widest across pereomeres 4–5. Pereomere 1 curved strongly around head, it and pereomere 2 markedly concave anteriorly; pereomeres 3–4 nearly straight across; pereomeres 5–7 concave posterior-



Fig. 1. *Orthione griffenis*, new species. Holotype female. A. Dorsal. B. Ventral. C. Right antennae. D. Right side of barbula. E. Right maxilliped. F. Right oostegite 1, external. G. Same, internal. H. Right pereopod 1. I. End carpus and dactylus of same. J. Right pereopod 7. K. End carpus and dactylus of same. Scale: 3.60 mm for A, B, E-G; 1.20 mm for C; 2.40 mm for D; 1.00 mm for H, J; 0.4 mm for I, K.

ly. Pereomere 1 shortest, all others about same length. Shallow elongate depression near each side of dorsal surface of pereomeres 2-5. Pereomeres 1-6 bordered by coxal plates on long side of body, those on pereomeres 5-6 with crenulate margins; smaller coxal plates on short sides of pereomeres 1 and 5. First oostegite (Fig. 1F, G) subcircular, its articles of about same size, separated by deep but narrow groove externally; internal ridge smoothly curved and lacking ornamentation. Oostegites 2-5 all long and relatively slender, each reaching about $\frac{2}{3}$ of distance across brood pouch and together completely enclosing it. Fifth oostegite with fringe of long setae along posterior margin. Pereopods (Fig. 1H, J) with all articles distinct, more than doubling in size posteriorly; all bases produced into broadly rounded carinae; short comma-

shaped dactyli (Fig. 1I, K) with sharp tips fitting into lip-like receptacles on distal corners of propodi; all carpi densely setose distally.

Pleon of 6 pleomeres, all sharply concave posteriorly, its posterior margin almost straight across sides of all pleomeres. Ventrally, sides of pleon completely covered by 5 pairs of overlapping lanceolate uniramous lateral plates and uropods, and its middle region equally covered by 5 pairs of biramous pleopods, all of their rami of size and structure similar to lateral plates, except that endopodites of first pleopods much larger than others and crossing each other in middle of pleon.

Allotype male (Fig. 2). Length 8.0 mm, maximal width 3.0 mm, head length 1.1 mm, head width 1.9 mm, pleon length 2.7 mm. Body straight on both sides, rounded

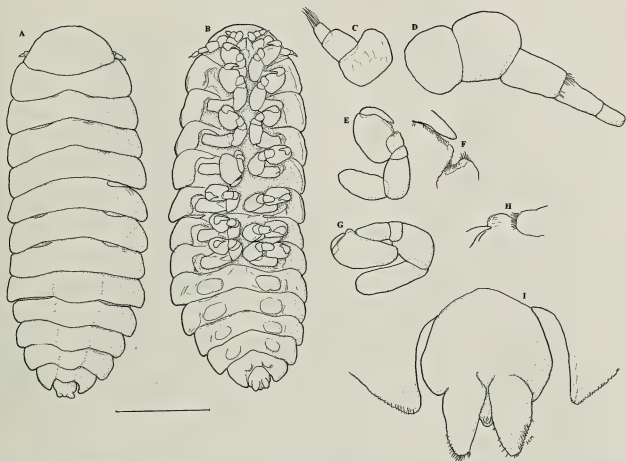


Fig. 2. *Orthione griffenis*, new species. Allotype male. A. Dorsal. B. Ventral. C. Right antenna 1. D. Left antenna 2. E. Right pereopod 1. F. End carpus and dactylus of same. G. Right pereopod 7. H. End carpus and dactylus of same. I. End of pleon, ventral. Scale: 2.00 mm for A, B; 0.84 mm for E, G; 0.24 mm for C, D, F, H, I.

at both ends. All body regions and segments distinctly separated (Fig. 2A, B). No pigmentation.

Head almost semicircular, markedly narrower than any pereomeres. Antennae (Fig. 2C, D) of 3 and 5 articles, respectively, both pairs directed laterally; first antennae distally setose; second antennae extending beyond margins of head.

Pereon broadest across pereomere 6, but only slightly so. Most pereomeres deeply separated by anterolateral notches. Low broad middorsal ridge along full length of pereon. Pereopods (Fig. 2E, G) relatively small, clustered medially under body; all of about same size, but their dactyli smaller posteriorly. All propodi bearing corneous ridges on surfaces met by folded dactyli (Fig. 2F, H); distal corner of propodus of

pereopod 7 extended into receptacle for end of dactylus (Fig. 2G, H); all carpi distally setose.

Pleon of 6 distinct pleomeres, each narrower than that before it. Five pairs of distinct but sessile oval pleopods, progressively smaller posteriorly. Final pleomere (Fig. 2I) deeply set into fifth, produced into pair of stubby pointed uniramous uropods, their margins bearing many short setae.

Remarks on paratypes (Fig. 3).—Of the nine paratype females, five are dextrally distorted, as is the holotype, three are sinistrally, and one is too immature for assessment. They range in length from 6.2 mm to 18.8 mm and in width from 2.7 to 13.3 mm (Fig. 3A–G). Most of the mature females have the endopodites of the first pair of pleopods prominently visible (Fig. 3A). One

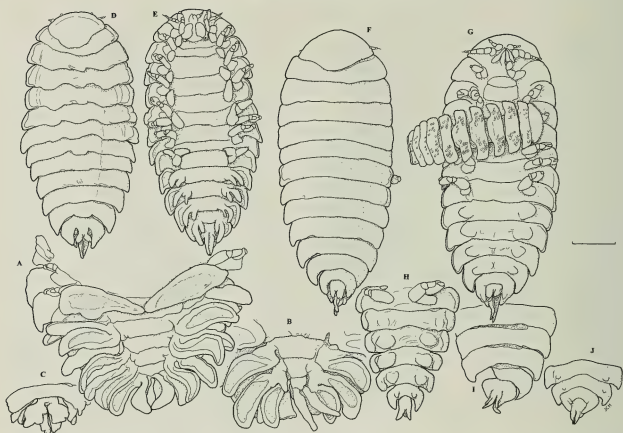


Fig. 3. *Orthione griffenis*, new species. Paratypes. A–G, females. H–J, males. A. Pleon, ventral. B. End of pleon, ventral. C. End of pleon, ventral. D. Immature, dorsal. E. Same, ventral. F. Late larva, dorsal. G. Same, with male attached, ventral. H. Pleon, ventral. I. Pleon, ventral. J. Immature, end of pleon, ventral. Scale: 4.20 mm for C; 2.10 mm for A, B, D, E; 1.00 mm for F–J.

has long slender extended uropods (Fig. 3B); one mature female has the fifth pleomere deeply separated from the preceding one (Fig. 3C), as does one immature female (Fig. 3D). In a very immature female (Fig. 3F, G), all oostegites are absent, and pleopods are only uniramous flaps. At a slightly later stage, an immature female (Fig. 3D, E) has rudimentary oostegites and small but distinctly pleopods, the endopodites of the first pair already pointing medially.

The seven paratype males (Fig. 3G–J) are 6.1 to 10.7 mm in length, and 2.0 to 3.2 mm in width. All are very similar to the allotype, but one has a more elongate pleon, its pleomeres deeply separated (Fig. 3H); one has a deformed fifth pleomere (Fig. 3I); and one has only very tiny traces of pleopods (Fig. 3J).

Etymology.—The name *griffenis*, genitive singular of a name regarded as a Latin

third-declension noun, is selected to honor Blaine D. Griffen, who, in the course of an ecological study of the host, *Upogebia pugettensis*, collected most of the material, called it to my attention and furnished it and collection data for this description.

Remarks.—*Upogebia pugettensis* has been reported many times as the host of *Phylloporus abdominalis* Stimpson, 1857, which attaches to its abdomen throughout the host's geographic range from British Columbia to central California (Williams 1986, Markham 1992), though the coast of Oregon remains a gap in the known distribution of *P. abdominalis*. This is the first record of infestation of *U. pugettensis* by a branchial bopyrid. So far this new species, *Orthione griffenis*, is known only from Yaquina Bay, Oregon, in the middle of the range of *U. pugettensis*, but there it appears to be fairly common. *Upogebia pugettensis*



Fig. 4. *Orthione mesoamericana*, new species. Holotype female. A. Dorsal. B. Ventral. C. Right antennae. D. Right maxilliped. E. Plectron of same. F. Right side of barbula. G. Right oostegite 1, external. H. Same, internal. I. Right pereopod 1. J. Right pereopod 7. Scale: 2.00 mm for A, B, D, F–H; 1.00 mm for E; 0.36 mm for C, I, J.

attains densities of up to 300 burrows per square meter in Yaquina Bay and occurs throughout the lower region of that estuary (Griffen 2002). For comparison of *Orthione griffenis* with other species in the genus, see the remarks on the following species.

***Orthione mesoamericana*, new species**
Figs. 4, 5

“Bopyrid Isopod.”—Holthuis, 1952:9 [Buenaventura, Colombia; infesting *Upogebia spinigera* (Smith)].

Material examined.—Infesting *Upogebia spinigera* (Smith, 1871). Puerto Jiménez, Golfo Dulce, Puntarenas, Costa Rica, 08°32'30"N, 83°18'20"W, 13 January 1977. 1 ♀, holotype, 1 ♂, allotype, MZUCR 2194-04. Lund University Chile Expedition. Buenaventura, Colombia, 03°77'N, 77°02'W, on beach, under lump of clay, 30

August 1948. H. Brattström and E. Dahl, colls., L. B. Holthuis det. of host: 1 ♂, paratype, SMNH 5325.

Description.—Holotype female (Fig. 4). Length 6.5 mm, maximal width 5.4 mm, head length 1.3 mm, head width 1.8 mm, pleon length 2.2 mm. Body axis distortion 4°, dextrally. Body nearly oval, all regions and segments distinct. No pigmentation except for dark eyespots (Fig. 4A, B).

Head slightly convex anteriorly, nearly semicircular posteriorly, deeply embedded into pereon. Frontal lamina very short but extending completely across anterior of head but not beyond. Eyes as prominent slender slashes near anterolateral corners of head. Antennae (Fig. 4C) well-developed, of 3 and 6 articles, respectively, first ones extending plainly beyond front margin of head. Barbula (Fig. 4F) with two projections on each side, outer one minute, inner

one extended and curved, both with entire margins; no decoration in middle of barbula. Maxilliped (Fig. 4D) suboval, lacking palp but with notch in anterior margin; plectron (Fig. 4E) small and slender, pointing anteriorly.

Pereon broadest across pereomere 4, all pereomeres distinctly separated laterally. Tergal plates on both sides of pereomeres 1-4, though only faint on first one. Oostegite 1 (Fig. 4G, H) with nearly parallel sides, slightly convex ends, both segments about equally wide and long, separated by deep external groove, no posterolateral projection; internal ridge unornamented, produced into long right-angled flap. Oostegites 2-5 overlapping and reaching nearly across and completely enclosing brood pouch. Pereopods (Fig. 4I) more than doubling in size posteriorly, but none extending beyond body margin; all dactyli short and fairly blunt and retracting into anterior notches of distally extended propodi; carpi all sparsely setose distally, meri and carpi of anterior pereopods fused.

Pleon of 6 distinct pleomeres, final one deeply embedded in preceding one. Five pairs of biramous pleopods, uniramous lateral plates and uniramous uropods. Endopodites of first pair of pleopods large, inflated and extending medially, touching each other and overlapping fifth oostegites anteriorly. Other pleopodal rami, lateral plates and uropods all similar to each other, all as lanceolate flaps with entire edges, completely covering margins of pleomeres.

Allotype male (Fig. 5).—Length 3.3 mm, maximal width 1.2 mm, head length 0.3 mm, head width 0.9 mm, pleon length 1.0 mm. Sides of body nearly parallel, rounded at each end. All body regions and segments distinctly separated. No pigmentation (Fig. 5A, B).

Head semicircular, lacking eyes. Antennae (Fig. 5C) prominent, first ones of 3 articles, second ones of 6 or 7 articles; second antennae extending far beyond margins of head.

Pereomeres separated by anterior notches

reaching inward nearly $\frac{1}{3}$ of body width. Pereopods (Fig. 5D, E) all of nearly same size, all their articles distinct; dactyli of pereopods 1 and 2 long and sharply pointed, others short and blunt; carpi of pereopods 5-7 much longer than others.

Pleon of 6 pleomeres, first one as wide as pereon, others tapering rapidly posteriorly. Pleopods (Fig. 5F) as sessile plates fairly conspicuous on pleomere 1, much fainter on pleomeres 2-5, absent behind. Sixth pleomere embedded in fifth, produced posteriorly into blunt clublike uropods extending rearward unequal distances, both sparsely fringed by minute setae.

Comparison of paratype male.—The other male is considerably larger, with these dimensions: length 4.2 mm, maximal width 1.4 mm, head length 0.6 mm, head width 0.9 mm, pleon length 1.7 mm. It is the same as the allotype in all respects except that both second antennae are 7-articled, and its uropods are equal in length.

Etymology.—Adjective *mesoamericana* selected to indicate the known range of the new species, along the Pacific coast of Central America.

Remarks.—The paratype male from Colombia is the unidentified bopyrid reported by Holthuis (1952). Because there was no female accompanying it, it could not be identified until the allotype was described here. The hosts are the same species in both collections.

Comparison of three known species of Orthione.—Females. One important addition to the original generic diagnosis (Markham 1988) is that the endopodites of the first pair of pleopods are markedly enlarged and medially directed in a manner highly distinctive for *Orthione*. This is the case in the type-species, *O. furcata*, as well as in the two new species, but I did not recognize its importance as a diagnostic character earlier. Of the two new species, *O. mesoamericana* is much more similar to *O. furcata* than is *O. griffenis*. Females of the first two species have heads wider than long, bearing slit-shaped eyes, and the in-

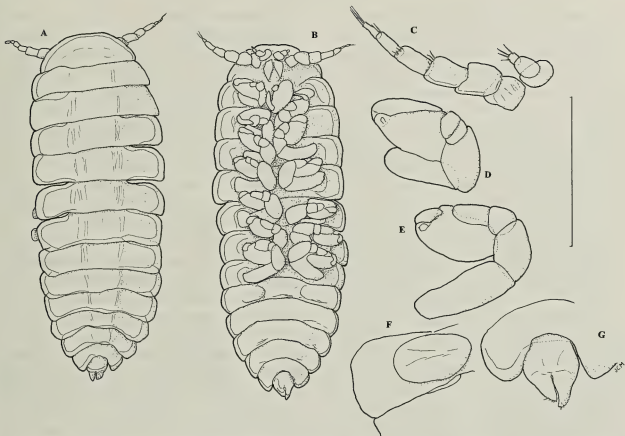


Fig. 5. *Orthione mesoamericana*, new species. Allotype male. A. Dorsal. B. Ventral. C. Right antennae. D. Right pereopod 1. E. Right pereopod 7. F. Right pleopods 1. G. Pleomeres 5, 6, ventral. Scale: 1.4 mm for A, B; 0.5 mm for C-G.

ternal ridge of the first oostegite is produced into a broad angled flap reaching far posteriorly, though that of *O. mesoamericana* is less extended. Also, females of both of those species have very slender pleopodal appendages, those of *O. mesoamericana* being relatively somewhat broader. All pereopods of *O. furcata* are about the same size, while those in the two new species more than double in size posteriorly. The minute flap lateral to the large projection on the barbula is unique to *O. mesoamericana*. Females of *O. griffenis* are distinctive in having heads longer than broad, margins of coxal plates crenulate rather than entire, pereopodal bases carinate, and pleopodal appendages ovate rather than lanceolate.

Males. All three species are very similar. Pereopods of *O. furcata* are much longer posteriorly, while those of the two new species are of nearly the same size throughout.

Similarly, uropods of *O. furcata* are much smaller than in either of the other two species. In *O. mesoamericana*, second antennae are greatly extended, and pleopods are mostly absent, in contrast with the other two species. The head of *O. furcata* has a medial region extending posteriorly, that of *O. griffenis* is smoothly rounded posteriorly, and that of *O. mesoamericana* is straight posteriorly.

Genus *Gyge* Cornalia & Panceri, 1861

Type-species, by monotypy, *Gyge brachialis* Cornalia & Panceri, 1861.

Revised diagnosis.—Female. Body oval to squarish, at least $\frac{3}{4}$ as broad as long, body axis only slightly distorted either dextrally or sinistrally, angle of distortion far forward. Head deeply set into pereon, its sides diverging slightly to greatly anterior-

ly, frontal lamina completely covering anterior, its posterior end rounded to pointed. Eyes usually absent. Antennae reduced. Barbula with two lateral processes on each side, they and middle region with deeply digitate margins. Maxilliped usually nearly straight across anterior margin, lacking palp, with slender forward-pointing plectron and at most only small posterior point. Pereon broadest across pereomere 4, smoothly rounded both ways, sides of first 4 or 5 pereomeres covered by conspicuous coxal plates. Pereopods all equally small, anterior ones with meri and carpi fused, bases large and often carinate. First oostegite produced onto long slender and usually curved posterior point. Other oostegites narrowly pointed and incompletely enclosing brood pouch. Pleon of 5 pleomeres, final one usually notched posteriorly. Three or four pairs of reduced biramous (or, intraspecifically, uniramous) pleopods not extending beyond pleonal edges, their leaflike rami all of same size and generally with digitately divided margins. Uniramous uropods tiny to quite large, flaplike, extended posteriorly and with entire margins.

Male. Body long and slender, its head well-extended and separated from pereon, with or without eyes. Antennae well-developed. Pereopods uniformly small, first two with proportionately longer dactyli, all with fused meri and carpi. No midventral tubercles. Pleon of 6 pleomeres, final one embedded in fifth. Pleopods absent or as sessile oval scars. No uropods.

Hosts: In genus *Upogebia*. Four species known, from Britain through Mediterranean to Black Sea; New Zealand; Japan and Taiwan; and Thailand.

Discussion.—I am hereby incorporating *Metabopyrus* Shiino, 1939, and its two species, the type-species *M. ovalis* Shiino, 1939, and *M. irregularis* Markham, 1985, into *Gyge* Cornalia & Panceri, 1861, which contained two species, *G. branchialis* Cornalia & Panceri, 1861, and *G. angularis* Page, 1985. The new diagnosis above is based on all four species. Bourdon (1968:

151) observed that “Ce genre [*Gyge*] ressemble beaucoup, en vue dorsale, à *Metabopyrus* Shiino (1939), également parasite d’*Upogebia* . . .” Similarly, Page (1985: 196) asserted that “. . . *Gyge* and *Metabopyrus* should be united,” but he did not formally make such a combination. In addition to the four species herein included in *Gyge*, two originally in *Gyge* and two in *Metabopyrus*, four other species have been cited as members of the genus, but all of them are either synonyms of *G. branchialis* or now considered to belong to other genera.

The date of publication of the paper by Cornalia & Panceri (1861), in which they established the genus *Gyge* and described its type-species *G. branchialis*, has been subject to some confusion. Bate & Westwood (1868) and Richardson (1905) listed the date as 1861, while Bonnier (1900) and Bourdon (1968) cited it as 1858. Reference to the original publication indicates that, while the volume in which the report appeared was for the year 1858, it actually appeared in 1861. Thus I am citing the date of publication for both the genus *Gyge* and its type-species *Gyge branchialis* as 1861.

Key to Four Species of *Gyge* Cornalia & Panceri, 1861, Based on Mature Females

- 1. Body smoothly rounded, oval; body axis distorted more than 30°; final pleomere extending farther rearward than any other pleomeres 2.
- Body with indistinct corners, subrectangular; body axis distorted less than 15°; final pleomere at least partly embedded in fifth pleomere and exceeded by one or more of other pleomeres 3.
- 2. Long sides of pereomeres distinctly set apart by extended posterolateral angles; posterior margin of pleon entire, large uropods not visible in dorsal view *G. irregularis* (Markham, 1985), n. comb. [Thailand]
- Long sides of pereomeres continuously curved; posterior margin of pleon deeply cleft, revealing minute uropods in dorsal view *G. branchialis* Cornalia & Panceri, 1861 [Europe]

3. Body segments all distinctly separated; margins of barbula projections digitately subdivided; internal ridge of oostegite 1 digitate *G. ovalis* (Shiino, 1939), n. comb. [Japan, Korea, Taiwan]
- Body segments only obscurely separated; margins of barbula projections smooth; internal ridge of oostegite 1 smooth *G. angularis* Page, 1985 [New Zealand]

Gyge branchialis Cornalia & Panceri, 1861

Abbreviated synonymy. (See Bourdon, 1968, for complete synonymy to 1968.)

Gyge branchialis Cornalia & Panceri, 1861: 87–111; plates I, II [Estuary of Venice, Italy; infesting *Upogebia pusilla* (Petagna, 1792)].—Bourdon, 1968:147, 151–159, 169, 322, 410; figs. 28–32; tables 23, 24 [synonymy, summaries of previous accounts, including records from Britain and Channel Islands through France to Adriatic and Black Seas, infesting *U. deltaura* Leach, 1815, *U. pusilla* and *U. stellata* (Montagu, 1808); re-description. Arcachon, France, and Napoli, Italy; infesting *U. pusilla*. Roscoff, France, and Plymouth, England; infesting *U. deltaura*. Roscoff, France; infesting *U. stellata*. Jersey, Channel Islands; no host].—Restivo, 1968:506 [Napoli; infesting *U. pusilla*].—Restivo, 1975:152, 153, 161–163; table 1 [Golfo di Napoli; infesting *U. pusilla*; study of hyperparasitism by *Paracabirops marsupialis* (Caroli, 1953)].—Dworschak, 1988:68 [Grado, north Adriatic Sea, Italy; near Trieste, Italy; Rovinj, Slovenia; infesting *U. pusilla*].—Astell et al., 1996:821–823; table 1 [Clyde Sea, Scotland, and Irish Sea; infesting *U. deltaura* and *U. stellata*. Arcachon Basin, France; infesting *U. pusilla*].

Gyges [sic] *branchialis*.—Grube, 1864:77 [Lussin Island, Croatia, Adriatic Sea; infesting *U. pusilla*].

Gyge galathea Bate & Westwood, 1868: 225–229 [Guernsey, Channel Islands, in-

festing *Galathea squamifera* Leach, 1814 {subsequently reidentified as *Upogebia stellata* by Norman, 1905:86}].

Not *Gyge branchialis* var. *arcassonensis* Carayon, 1943:46–47 [= *Progebiophilus euxinicus* (Popov, 1929)].

Material.—All identified and reported by Peter Dworschak.—Infesting *Upogebia pusilla*. Punta Spin, Grado, Adriatic Sea, Italy, 45°40'N, 13°23'E, D. Abed-Navandi coll., August 2000. 1 ♀ (ovigerous), 1 ♂, NHMW 19521. Infesting *U. tipica* (Nardo, 1868), off Isola Rossa, Rovinj, Croatia, Adriatic Sea, 45°05'N, 13°40'E, 18 m, D. Abed-Navandi coll. 4 July 2000, P. Dworschak det., 1 ♀, NHMW 19523.

Remarks.—This is the first record of bopyrid infestation of *Upogebia tipica*, and thus a new record for *Gyge branchialis*. *Gyge branchialis* is already known from the Croatian coast of the Adriatic Sea, and it does not need further re-description beyond the detailed accounts presented by Bonnier (1900) and Bourdon (1968). As indicated in the synonymy above, *G. branchialis* has been reported many times from Britain through the Mediterranean to the Black Sea as a parasite of three other species of *Upogebia*.

Gyge ovalis (Shiino, 1939), new combination
Fig. 6

Metabopyrus ovalis Shiino, 1939:88–91; figs. 7, 8 [Hakata Bay, Kyūsyū, Japan; infesting *Upogebia major* (de Haan, 1839) {subsequently corrected to *U. issaeffi* Balss, 1913}].—Shiino, 1958:48–49, fig. 10 [unknown specific locality, Japan; infesting unknown host; further descriptive notes].—Codreanu, 1941: 140.—Codreanu, 1961:140; fig. 1.—Codreanu & Codreanu, 1963:283.—Shiino, 1972:7.—Markham, 1982:340.—Markham, 1985:14.—Page, 1985:196.—Kim & Kwon, 1988:199, 201–203, 220; fig. 2 [Komso, southwest Korea; infesting *U. major*].—Markham, 2001:198, 201;

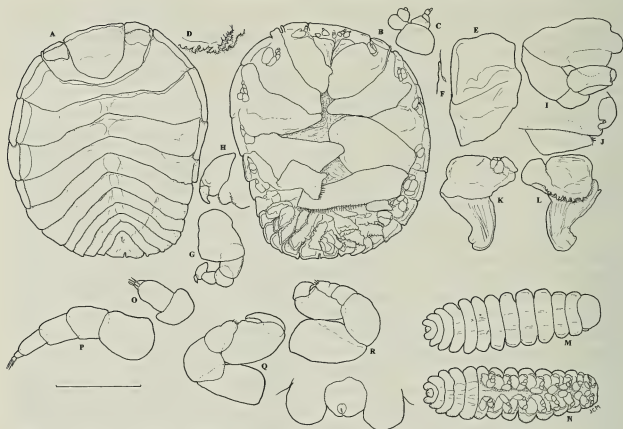


Fig. 6. *Gyge ovalis* (Shiino, 1939), new combination. A–L, female. M–S, male. A. Dorsal. B. Ventral. C. Left antennae. D. Left side of barbula. E. Left maxilliped, external. F. Plectron of same. G. Right pereopod 1. H. Distal end of same. I. Left pereopod 7. J. Distal end of same. K. Left oostegite 1, external. L. Same, internal. M. Dorsal. N. Ventral. O. Left antenna 1. P. Left antenna 2. Q. Left pereopod 1. R. Right pereopod 7. S. End of pleon, ventral. Scale: 4.00 mm for A, B, K, L; 1.93 mm for D, E, M, N; 1.00 mm for C, F; 0.88 mm for G, I; 0.35 mm for H, J, Q–S; 0.18 mm for O, P.

tables 1, 2.—Itani et al., 2002:72; fig. 1a9 [Yamaguchi Bay, Seto, Inland Sea, Japan; infesting *U. major*, study of response to host's molting].

Material examined.—Infesting *Upogebia edulis* Ngoc-Ho & Chan, 1992. Shan-kong mudflat, Chang-Hua County, southwest Taiwan, 24°06'25"N, 120°25'30"E, Tin-Yam Chan collector and det. of host: 1 ♀, 1 ♂, USNM 1008790.

Descriptive notes.—*Gyge ovalis* has now been collected five times, but no lot has been large. The original description (Shiino 1939) consisted of two pairs, the next two collections (Shiino 1958, Kim & Kwon 1988) were single females, and the present material is one pair. The size of the most recent Japanese collection (Itani et al. 2002) was not indicated; the photograph in that

report, derived from a frame of a videotape which was published only to show the female's orientation on its host, lacks recognizable details. Variations among the specimens are slight, but all are noticeably different. The present female (Fig. 6A–L) most resembles the figured syntype in proportions and shapes of body parts, though it lacks the prominent tergal plates seen on the long side of pereomeres 1–3 of all previously recorded females (Fig. 6A, B). The body of one female (Shiino 1958) is proportionately shorter, and another (Kim & Kwon 1988) lacks the posterior notch on the final pleomere. The barbula (Fig. 6D) is the same as in other females. The maxilliped (Fig. 6E) is less distinctly segmented than previously seen. The propodus of the first pereopod (Fig. 6G, H) is produced into

a helmet-like shape not previously seen. The first oostegite (Fig. 6K, L) is very much like that reported by Shiino (1958), while the one from Korea (Kim & Kwon 1988) was straight posteriorly. The male (Fig. 6M-S) has a much more extended head and an embedded final pleomere (Fig. 6S), in contrast to the figured syntype (Shiino 1939), whose head was little longer than any pereomere, and whose final pleomere was extended behind the preceding one.

Remarks.—The present material represents both a new host, *Upogebia edulis*, and new locality, Taiwan, for *Gyge ovalis*, although Tin-Yam Chan (pers. comm.) reports that it is commonly collected there. Gyo Itani (pers. comm.) informs me that he has found *Gyge ovalis* infesting five different species of *Upogebia* in Japan, although so far there are published records of only two host species there.

Acknowledgments

Tin-Yam Chan, National Taiwan Ocean University, provided material of *Gyge ovalis* that he had collected and information about it. Peter C. Dworschak, NHMW, provided information about his collections of *G. branchialis* and granted me permission to report on them. Christer Erséus and Karin Sindemark, SMNH, lent the paratype male of *Orthonoe mesoamericana*, to which Lipke B. Holthuis, Nationaal Natuurhistorisch Museum, The Netherlands, had referred me. Blaine D. Griffen and Theodore H. DeWitt, Oregon State University, collected and furnished the type material of *O. griffenis* and provided information on its collection. Gyo Itani, Seto Marine Laboratory, Japan, sent me reprints of his papers and provided information about collections he had made. Becky S. Jordan, Iowa State University Library, confirmed the date of publication of the paper by Cornalia & Panceri (1861). Nguyen Ngoc-Ho, Muséum National d'Histoire Naturelle, Paris, confirmed the current usage of names of *Upo-*

gebia spp. Marilyn Schotte, USNM, provided essential curatorial services and information on collections, lent much material for examination and description, furnished elusive references and information about them. Rita Vargas, MZUCR, lent type-specimens of *O. mesoamericana* and furnished details of their collection. Three anonymous reviewers provided helpful remarks.

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Three new species and a new genus of Farreidae (Porifera: Hexactinellida: Hexactinosida)

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Abstract.—Two new species of *Farrea* and a single new species of a closely related new genus, *Asceptrulum*, all members of the hexactinosan family Farreidae, are described from three widely distant locations. *Farrea herdendorfi*, new species, with a type series of eight specimens obtained from 2200 m off Charleston, South Carolina, U.S.A., NW Atlantic Ocean, is distinguished by two anchorate clavule forms (umbellate and thimble or thimble-shaped), both without spiral arrangement of claws. *Farrea seiri*, new species, represented by 3 fragments of a single specimen from 1450 m near the South East Indian Ridge, mid Indian Ocean, is characterized by only anchorate clavules of thimble form, a moderate proportion of which have claws spiralled. *Asceptrulum axialis*, new genus, new species, is represented by several fragments from a single specimen collected from 2387 m on the Juan de Fuca Ridge, northern Oregon, U.S.A., NE Pacific Ocean. It is distinguished by the combination of complete absence of sceptrules and a one-layered farreoid framework. The diagnosis of Farreidae is emended to encompass the new genus.

Although recognized 132 years ago, hexactinellid sponges, more familiarly referred to as “glass sponges”, are still obscure members of the deep sea invertebrate fauna. Members of the dictyonine family Farreidae Gray are among the most commonly encountered hexactinellids, distributed mainly on continental shelves and slopes, but extending into deep water to over 5200 m depth. This hexactinosan family presently includes 21 species distributed unevenly in 5 genera, 17 of those in the genus *Farrea*. The most recent family diagnosis (Reiswig 2002) focused on one class of free spicules, sceptrules, which here consist of at least one form of clavule or sarule, with or without lonchiole or aspidoscopule. Forms with narrow-head scopule were excluded from the family. A second common feature of most, but not all, members of the family, not included in that recent diagnosis, is the

minimal, one-layered dictyonial framework at the growing margin.

Specimens of three forms, obtained from moderately deep water and submitted to our laboratory for identification, have proven to be undescribed species of this family. Two of them are easily incorporated in the speciose genus *Farrea* Bowerbank, 1862, but the third entirely lacks sceptrules and thus cannot be assigned to a family on the basis of present diagnoses. Its assignment to a new genus erected within Farreidae requires emendation of that family diagnosis, proposed here.

Materials and Methods

Most submitted specimens (all *F. herdendorfi*, new species, and *Asceptrulum axialis*, new genus, new species) were collected by robot submersible and were ac-

compared by videotape of the collection process. Only *F. seiri* new species, was collected by dredge.

Small fragments of the sponge body wall were either whole-mounted in Canada balsam for light microscopy (LM), or were dissolved in hot nitric acid. The acid-cleaned skeletal frameworks were removed, rinsed and dried; the remaining spicule suspensions were filtered through 25 mm diameter, 0.2 mm-pore-size, nitrocellulose filters; filters with spicules were thoroughly rinsed with distilled water, dried, cleared with xylene, and mounted in Canada balsam on microscope slides. Characters of frameworks and spicules were measured by computer using a microscope-coupled digitizer. Data are reported as mean \pm standard deviation (range, number of measurements). Spicules for scanning electron microscopy (SEM) were similarly nitric acid cleaned, rinsed in distilled water and then directly deposited onto cover glasses mounted on SEM stubs. Acid-cleaned and rinsed fragments of body wall skeletal frameworks were mounted directly on stubs with epoxy. Following gold-palladium coating, specimens were viewed and photographed with a JEOL JSM-840 SEM. Spicule drawings were made by importing LM or SEM images into a computer image-processing program, and then tracing on screen. Type specimens of the new species have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM).

Family Farreidae Gray, 1872

Diagnosis (emended).—Hexactinosida typically with sceptrules in the form of clavules, or their derivatives, sarules, lonchiales or aspidoscopules, and typically with a farreoid dictyonal framework. Where sceptrules are lacking the framework is farreoid. Where the framework is eurentoid, sarules are present.

Remarks.—Emendation of the diagnosis

of Farreidae is required for inclusion of the new genus *Asceptrulum* as proposed below.

Genus *Farrea* Bowerbank, 1862

Type species.—*Farrea occa* Bowerbank, 1862, by monotypy.

Farrea herdendorfi, new species (Figs. 1–3; Table 1)

Holotype.—USNM 1001596; S.S. 'Central America' wreck, 300 km S. of Charleston, S.C., 31.5°N, 77°W, 12 Sep 1989, 2200 m depth, coll. C.E. Herdendorf, R/S 'Nemo' from R/V 'Arctic Explorer', dive UA.

Paratypes.—All from above sampling location and vessels; USNM 1001597, USNM 1001600, USNM 1001601, USNM 1001602, USNM 1001603, all 12 Sep 1989, col. C.E. Herdendorf, Dive UA; USNM 1001598, USNM 1001599, 21 Sep 1990, col. B. Evans, dive AC.

Diagnosis.—*Farrea* with only anchorate clavules, the heads of which vary between two extreme forms—an umbellate (hemispherical) form and a thimble (nearly cylindrical) form with straight claws nearly parallel to shaft. Shafts of all clavules are rough but lack conspicuous spines.

Description.—Size and shape: The holotype is 30 cm in height, with a branching element arising 16 cm above the lower end (base is missing), extending 11 cm at 60° from the primary axis (Fig. 1E). At widest points, the main body and lateral branch are, respectively, 5.0 and 4.2 cm thick. The central body of the sponge is cryptically bilaterally symmetrical (see below), composed of an original flat blade or stipe incorporated as one side of an axial tube by medial fusion of lateral undulations or ruffles. Through further lateral extension and tight curvature, the lateral ruffles fuse to form tubes appended onto the axial tube. The diameter of outer exposed tubular apertures of the holotype are 6.7 ± 2.0 mm (range 5–10 mm, $n = 12$).

A sequence of age/maturation stages is

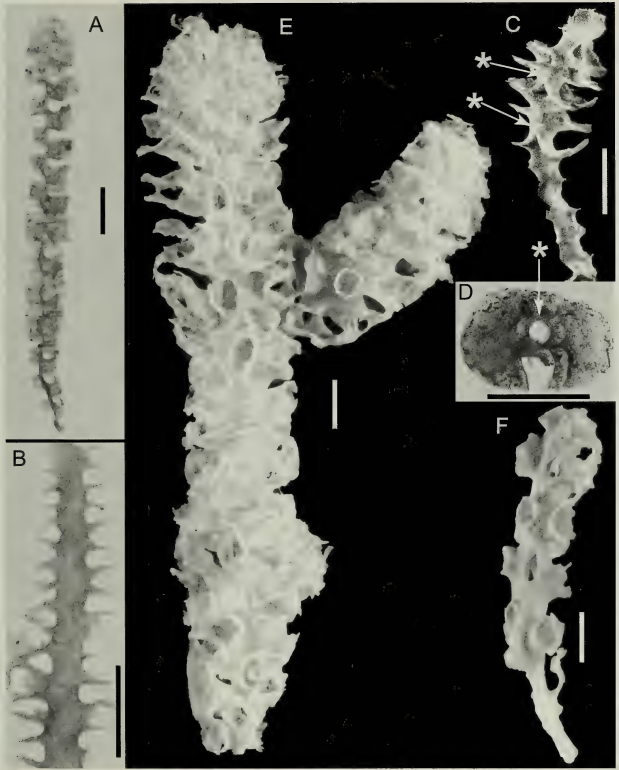


Fig. 1. *Farrea herdendorfi*, new species; body form. A. Paratype USNM 1001601 in lateral view. B. Same in frontal view. C. Paratype USNM 1001602 in frontal view, asterisks indicate fusion points of lateral pleats to form axial tube. D. Same viewed from distal end with axial tube closed by fusion series at asterisk. E. Holotype USNM 1001596, lateral view. F. Paratype USNM 1001597, with thickened walls, in frontal view. Scale bars = 2 cm.

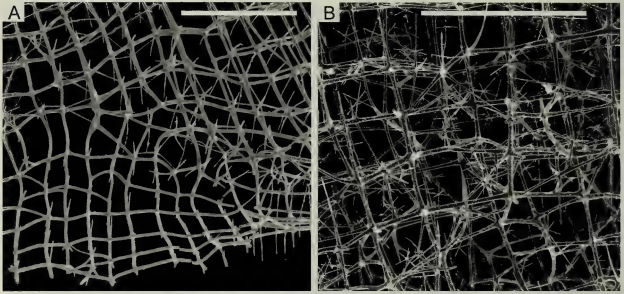


Fig. 2. *Farrea herdendorfi*, new species, framework (SEM). A. Single-layer primary framework in marginal area of paratype USNM 1001601, bearing long, usually straight spurs. B. Thickened main body area of holotype USNM 1001596 with irregular dictyonal layers added on dermal side. Scale bars = 1 mm.

apparent in the type series as inferred from wall thickness and degree of expansion and fusion of lateral edges—from a simple blade to the complex fused structure of the lateral tubes. The simplest paratype available (Figs. 1A, B) is an axial blade, 18.6 cm long, with undulatory expansion of lateral margins as ruffles but without fusion between them. A more complex and older but shorter specimen, 8.2 cm long (Fig. 1C), exhibits longitudinal fusion between ruffles along one side to form an axial tube on the axial blade (Fig. 1D). The holotype (Fig. 1E) exhibits the next stage with fusion and branching of ruffles to form a complex bed of lateral tubes supported upon the axial tube. Beyond the branching point, the axial blade and tube of both extremities arise *de-novo* from the lateral ruffles—continuity does not exist between axial components of the basal axis and the two distal shoots. By wall thickness, paratype CA6, 14.7 cm long, is next oldest of the series (Fig. 1F) but its gross morphology has apparently been simplified by abrasion. It consists of the axial tube bearing only the thick-walled bases of lateral tubes in alternating offset pairs. The marginal ruffles and tubes have apparently been torn off during

collection. The oldest specimen, not figured, is an extremely thick-walled and dense basal part, 6.6×4.9 cm, of a much larger specimen. That this constructed series of body shapes represents a sequence in growth of a single species is confirmed by identical loose spicules in all specimens.

Framework (Fig. 2, Table 1): The framework is an unchanneled dictyonal lattice, consisting of, in the thinnest-walled (young) specimens and at growing edges of thick-walled (older) specimens, a one-layer, two-dimensional lattice of somewhat irregular rectangular meshwork with easily recognizable longitudinal dictyonal strands (Fig. 2A). Most of the framework of all but the thinnest specimens is augmented by addition of secondary dictyonalia in irregular-mesh network mainly on dermal, but in some places on the atrial side to form a three-dimensional framework (Fig. 2B). Small hexactins attached to beams of primary and secondary dictyonalia are abundant. Wall thickening and increasing rigidity of the framework with aging is due to addition of both more secondary dictyonalia and small hexactins, but only slightly accompanied by thickening of primary dictyonal strands. Spurs are long, thin, rough

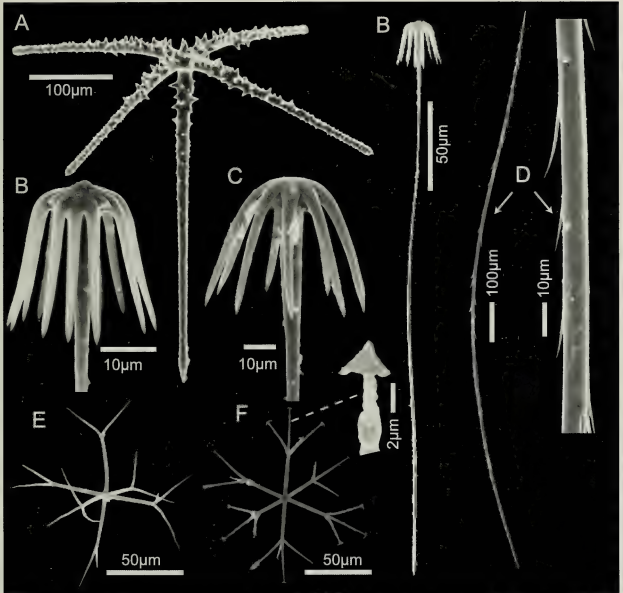


Fig. 3. *Farrea herdendorfi*, new species, spicules of holotype USNM 1001596 (SEM). A. Surface pentactin. B. Thimblate anchorate clavule, whole and head. C. Umbellate anchorate clavule head. D. Uncinete, whole and magnified segment. E. Oxyhexaster. F. Onychexaster with magnified ray tip.

and spine-like, usually straight but occasionally slightly curved.

Spicules (Fig. 3, Table 1): Pentactins (Fig. 3A), lining both dermal and atrial surfaces, have tangential rays heavily spined on outer surfaces, and long proximal ray with heavy spination only on upper third. Uncinates are very long, exceptionally thin and moderately barbed. Two forms of anchorate clavules occur intermixed on both surfaces, both forms having a thin, smooth shaft ending in a slightly rough, bluntly pointed tip. The thimblate (thimble-shaped)

form (Fig. 3B) has approximately 15 spines projecting down from a discoid cap, flaring slightly outward at the lower edge. The anchorate form (Fig. 3C) has approximately 10 spines projecting out and down from a smoothly rounded cap, continuing on the angle of curvature without reflexion. Microscleres consist of two types of smooth hexasters distributed throughout the specimen. Oxyhexasters (Fig. 3E) have six long primary rays, each bearing 2–3 secondary rays ending in sharp tips. Onychexasters (Fig. 3F), alternately interpretable as dis-

Table 1.—Spicule and framework dimensions (in μm) of *Farrea herdendorfii*, new species, holotype USNM 1001596, from off South Carolina, USA.

Item	Mean	St. dev.	Range	N
A. Surface pentactin:				
tangential ray length	231	29	179–299	50
tangential ray width	13.1	2.9	5.2–20.0	50
proximal ray length	298	81	141–464	50
proximal ray width	11.2	2.2	6.6–17.2	50
B. Thimble clavule length				
head length	32.7	5.5	20–45	50
head diameter	34.9	7.9	19.7–56.2	50
C. Umbellate clavule length				
head length	454	55	313–581	50
head diameter	36.9	4.4	29–49	50
	48.2	5.3	32–66	50
D. Uncinate length				
width	1368	308	830–2086	50
	6.1	1.4	3.5–9.9	50
E. Oxyhexaster diameter				
primary ray length	120	13	86–146	50
secondary ray length	30.7	4.6	21.6–43.1	50
	33.1	4.7	20.7–44.3	50
F. Onyhexaster diameter				
primary ray length	114	12	87–141	50
secondary ray length	27.9	3.6	22.2–39.7	50
	29.7	4.0	19.3–37.8	50
G. Framework beam length				
beam width	352	129	125–748	50
	28.2	9.2	14.5–57.7	50
H. Framework spur length				
	287.0	110	124–727	50

cohexasters with reduced discs, have 3–4 irregularly lumpy secondary rays (without sharp spines) each ending in a flat disc with 2–4 short blunt claws.

Etymology.—The species is named after the collector of the holotype, Prof. Charles E. Herdendorf, who also served as coordinator of the Adjunct Science and Education Program, S.S. 'Central America' Project, Columbus-America Discovery Group. Gender of the species name is female.

Remarks.—Herdendorf et al. (1995) reported this form as "*Farrea* new species" (p. 86) and figured the specimen designated here as holotype being collected (their Fig. 45). The species differs from all known *Farrea* in the form of its clavules. The distinctive thimble clavule head is most similar to that of form B of *F. kurilensis* (Okada, 1932), but those clavules have coarsely thorned shafts and are accompanied by a

pileate clavule not present in *F. herdendorfii*.

Farrea seiri, new species
(Figs. 4, 5; Table 2)

Holotype.—USNM 1001594, Southeast Indian Ridge, Indian Ocean, 39°12.83'S, 77°52.88'W, 22 Mar 1996, 1450 m depth, coll. D.S. Scheirer and K. Johnson, Boomerang Expedition, Leg 6, R/V 'Melville', biosample #7, Site 48, Dredge 58, dive# BMRG 06 MV.

Diagnosis.—*Farrea* with only anchorate clavules, all thimble in form without shaft spines. The most abundant clavule type has straight claws while the less common form has claws spiralled either dextrally or sinistrally.

Description.—Size and shape: The holotype and only sample consists of three

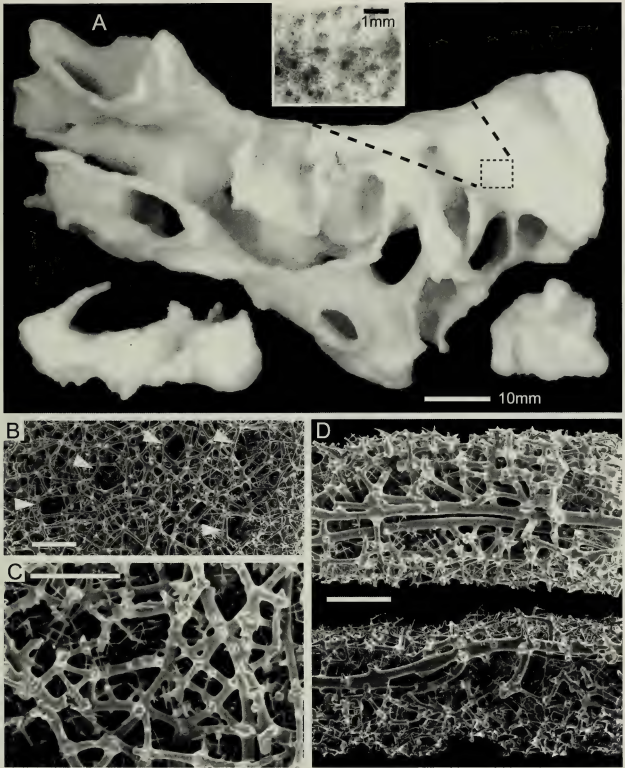


Fig. 4. *Farrea seiri*, new species, body form and framework of holotype USNM 1001594. A. Body form with epirhyses evident in magnified inset. B. Outer surface with shallow epirhyses indicated by arrowheads (SEM). C. Probable primary layer in middle frontal layer of framework exposed by dissection (SEM). D. Two transverse sections of body wall showing thickened main longitudinal strands deep within framework (SEM). Scale bars = 0.5 mm.

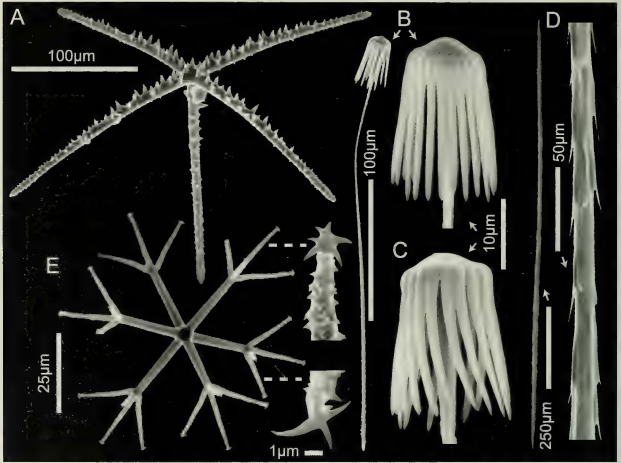


Fig. 5. *Farrea seiri*, new species, scicules of holotype USNM 1001594 (SEM). A. Surface pentactin. B. Straight thimble anchorate clavule, whole and head. C. Spiral umbellate anchorate clavule head. D. Uncinate, whole and magnified segment. E. Onyxexaster with magnified ray tips.

very stout fragments from the basal part of a single specimen (Fig. 4A). The specimen was severely damaged during dredge collection, all distal parts with thin body wall having been lost. The largest fragment measures 9.6×4.3 cm, the second largest 3.9×1.5 cm, and the smallest 1.8×1.7 cm. All fragments are white in colour, with fairly thick walls (for *Farreidae*), 2.08 ± 1.04 mm (range 0.95–3.80 mm, $n = 10$), though all are quite fragile, easily crushed and crumbled.

The main fragment is composed of two fused tubes, the younger attached obliquely along the side of the older. The older tubular element provided basal attachment for the specimen and was dead at the time of collection. The younger tube has a series of lateral openings arranged in sets of two in alternating offset pairs, aperture length 9.2

± 0.9 mm (range 8.3–10.4 mm, $n = 5$) width 5.1 ± 0.9 mm (range 4.1–7.0 mm, $n = 5$). Attempts to map dermal and atrial surface topology showed that there is no consistent distinction between surfaces relative to tubular walls.

Framework (Fig. 4, Table 2): The outer layers of the rigid dictyonal framework (Fig. 4B), are composed of a highly irregular mesh of hexactins, many with polyradial nodes, outlining shallow extradictyonal epirhyses and aporhyses as surface pits (Figs. 4A insert, 4B). Pits have ovoid apertures, length 0.33 ± 0.038 mm (range 0.26–0.38 mm, $n = 8$), width 0.24 ± 0.045 mm (range = 0.18–0.32 mm, $n = 8$). Distances between pits 0.66 ± 0.18 mm (range 0.33–1.20 mm, $n = 32$).

Beam thickening has occurred throughout the entire specimen, and there is no sin-

Table 2.—Spicule and framework dimensions (in μm) of *Farrea seiri*, new species, holotype USNM 1001594, from mid Indian Ocean.

Item	Mean	St. dev.	Range	N
A. Surface pentactin:				
tangential ray length	155	37	67–253	50
tangential ray width	8.1	2.6	3.9–12.5	50
proximal ray length	193	68	99–379	50
proximal ray width	7.9	2.3	3.1–13.3	50
B. Straight clavule length				
head length	27.3	4.9	16.3–39.3	50
head diameter	17.0	3.8	12.8–29.5	50
C. Spiral clavule length				
head length	29.7	4.3	21.0–39.3	50
head diameter	21.4	3.4	13.4–28.1	50
D. Uncinate length				
width	802	376	520–1610	8
	6.5	2.5	3.3–10.1	8
E. Onychexaster diameter				
primary ray length	91	11	72–117	50
secondary ray length	26.2	4.0	18.7–35.5	50
	21.9	3.7	13.2–29.0	50
F. Framework beam length				
beam width	287	107	89–503	50
	51	16	22–96	83

gle layer which can be identified as a buried farreoid two-dimensional grid (Fig. 4C). Long stretches of smooth dictyonal strands located deep within the wall (Fig. 4D) are hypersilicified, obscuring original hexactins. Both outer and inner meshes are further obscured by large numbers of small intercalated hexactins. Spurs are moderately common on both surfaces, and within the internal meshwork, but these are not directly comparable to spurs on the primary dictyonalia of other farreids.

Spicules (Fig. 5, Table 2): Pentactins have strong spination on outer surface of tangential rays, extending almost to the tips (Fig. 5A). The proximal ray is heavily spined near the centrum, and entirely rough throughout its length. Clavules are all anchorate and thimblate in form and occur in two types, a straight thimblate type (Fig. 5B) and spiro-thimblate type (Fig. 5D). Both have a thin, smooth shaft, ending in a bluntly pointed tip. The head of the straight thimblate type has approx. 25 claws projecting down from a discoid cap, either

straight and parallel or flaring slightly outward. The spiro-thimblate type has similar cap and claws, but claws curve distally either to the left (sinistral) or right (dextral). Pentactins and both clavule types occur on all surfaces without distinction. Uncinates are typically long and thin with moderately developed barbs but without a distinguishable centrum (Fig. 5D). The only microsclere type is an onychexaster (Fig. 5E) distributed evenly throughout the specimen. The finely rough primary rays each bear four similarly rough secondary rays, each of which ends in a button margined by 3–6 short, slightly reclined claws.

Etymology.—The species name, *seiri*, is formed from the acronym of its collection locale, the Southeast Indian Ridge. Gender of the species name is female.

Remarks.—This species is most similar and closely related to *F. herdendorfi* described above, but differs in having only thimblate anchorate clavules and lacking oxyhexaster microscleres. The unavailability of distal portions of the specimen, and

Table 3.—Spicule and framework dimensions (in μm) of *Asceptrulum axialis*, new genus, new species, holotype USNM 1001604, from NE Pacific.

Item	Mean	St. dev.	Range	N
A. Surface pentactin:				
tangential ray length	217	29	141–279	50
tangential ray width	16.8	4.4	7.9–25.1	50
proximal ray length	446	108	261–752	50
proximal ray width	15.1	4.5	8.6–27.1	50
B. Uncinate length				
width	1641	250	1173–1967	12
C. Discohexaster diameter				
primary ray length	66	7	53–81	50
secondary ray length	10.0	1.7	6.2–13.5	50
	25.4	3.0	19.8–31.2	50
D. Framework beam length ^a				
beam width ^a	346	75	204–584	50
	43.8	9.1	28.4–77.7	50
E. Spur length ^a				
	335	79	147–528	50

* In marginal areas of framework.

its presumable two-dimensional farreoid framework do not seriously compromise its placement in *Farrea* since its spiculation is compelling evidence of its relationship to other *Farrea* species. Thickness of the basal skeleton and presence of shallow epirhyses and aporhyses are rarely encountered in the genus but are not unique to this species.

Genus *Asceptrulum*, new genus

Type species.—*Asceptrulum axialis*, here designated.

Diagnosis.—Farreidae lacking sceptrules.

Etymology.—The genus name, *Asceptrulum*, is formed from Greek *a* = without, plus sceptrula, from Greek *skeptron* and Latin *sceptrum* (neuter) = royal wand or staff, in allusion to the absence of sceptrule spicules. Gender of the genus name is neuter.

Remarks.—See under species below.

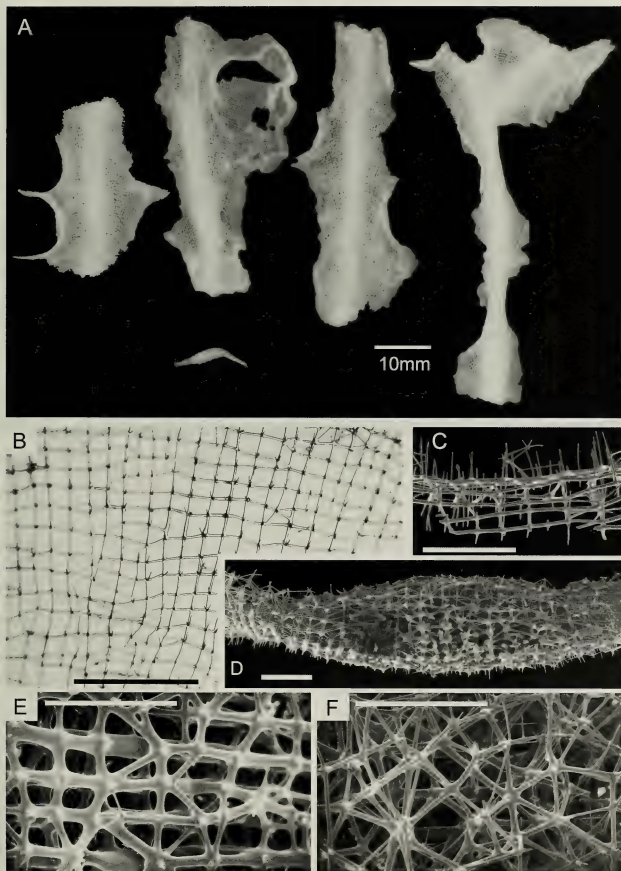
Asceptrulum axialis, new species (Figs. 6, 7; Table 3)

Holotype.—USNM 1001604: North CoAxial segment, Juan de Fuca ridge, northern Oregon, 46°29.83'N, 129°35.79'W, 19 Jul 1993, 2387 m depth, coll. V. Tunnicliffe, R/S 'ROPOS' dive HYS 221.

Diagnosis.—*Asceptrulum* with axial condensation of its farreoid framework.

Description.—Size and shape: The single specimen encountered and recorded in situ by video, was broken during collection; about one-half was recovered as four fragments (Fig. 6A). The intact specimen was attached to hard substrate in a region of recently formed basalt blocks sparsely clothed in bacterial mats and strands. Before collection, the organism was frond-like or Y-shaped, 14 cm tall, with a branch point 9 cm from the basal attachment. The four recovered pieces are all thin ribbons or blades with clear axial thickening, thin mar-

Fig. 6. *Asceptrulum axialis*, new genus, new species, body form and framework of holotype USNM 1001604. A. Body form of recovered fragments with cross-section of one fragment. B. Frontal view of single-layer primary framework in marginal area (LM). C. Same in slightly oblique transverse view showing long, straight spurs



(SEM). D. Cross-section of axial region of blade, atrial surface down, with longitudinal primary strands seen at extreme left (SEM). E. Atrial surface of axial region showing thickened primary longitudinal strands (SEM). F. Dermal surface of same (SEM). Scale bars of B-F = 0.5 mm.

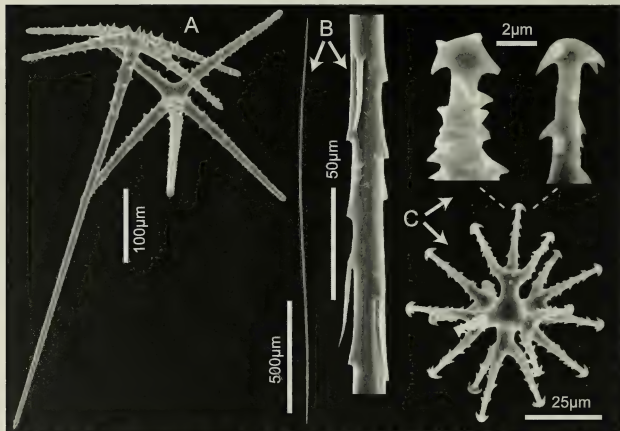


Fig. 7. *Asceptrulum axialis*, new genus, new species, spicules of holotype USNM 1001604 (SEM). A. Surface pentactins. B. Uncinatate, whole and magnified segment. C. Discohexaster with magnified ray tips.

ginal fringes with low-amplitude undulation or ruffles. At one point the curved lateral margins are extended and undergo self-fusion resulting in a short lateral tube 1.4 cm in diameter. Intact areas of blades are 9.2–26.2 mm wide and 1.63 ± 0.32 mm (range 0.86–1.88 mm, $n = 10$) thick at axis centers.

Framework (Fig. 6, Table 3): The primary framework is a typical farreoid one-layer, two-dimensional mesh of smooth beams (Figs. 6B, C) most obvious in the marginal areas. Blade thickness increases gradually toward the axis by addition of up to nine layers of secondary dictyonalia in irregular arrangement on one side, assumed dermal, of the primary framework (Fig. 6D). On the two surfaces of the blade axes, beams are twice as thick on the atrial side with exposed old primary frame (Fig. 6E), 81.3 ± 31.2 μm (range 54–134 μm , $n = 5$), than on the dermal side (Fig. 6F), 41.1

± 14.8 μm (range 28.0–64.5 μm , $n = 5$). Small hexactins fused to framework beams are present but sparse. Spurs of the primary frame are long and straight on both surfaces (Fig. 6C), but while those on the atrial side are rough, those of the dermal side are smooth and often extended and variable in texture. Many of the dermal spurs are fused to centres of secondary dictyonalia or tips of their rays. The secondary structures are a mixture of true and false nodes, with connections occurring between grid levels by synapticula. Channelization is absent.

Spicules (Fig. 7, Table 3): The species has both low diversity and density of loose spicules. Megascleres consist of large, robust pentactins (Fig. 7A) and long, thin uncinates (Fig. 7B). Pentactins, present on dermal and gastral surfaces, have tangential rays with heavy spination on outer and lateral surfaces and proximal rays with coarse tubercles on the upper third of the ray and

very sparse low spines over the remainder. Uncinates are typical with well-developed barbs, brackets, and no detectable central tyle. The only microsclere type is a relatively scarce, robust discohexaster (Fig. 7C), distributed evenly throughout the wall. The six primary rays are short, thick and smooth, each supporting three heavily spined secondary rays which end in hemispherically arched discs bearing 5–6 recurved marginal spines.

Etymology.—The species name, *axialis*, is originally derived from Latin *axis* = rod or pole. It is here formed from the English adjective *axial* to preserve its euphonious spelling and reflect the easily visible, dense, axial skeletal framework. Gender of the species name is neuter.

Remarks.—Absence of sceptrules in this specimen cannot be attributed to pathological condition, damage during collection or inadequate sampling of spicules. The specimen was almost certainly alive at collection, with surface pentactins arrayed in the normal rectangular lattice in places. It is extremely unlikely that disease or the collection process would result in loss of only the one spicule type had sceptrules been present. Occasionally sceptrules may be difficult to obtain in very small samples of farreids, but the use of filtration for spicule collection from cm-size fragments has never failed to find scopules. When the first searches for sceptrules in this specimen proved negative, the entire set of fragments was eventually extracted for spicules and examined; not one part of a sceptrule was found. We are very confident that sceptrules were neither lost nor overlooked. They must have been intrinsically absent.

Since sceptrules are lacking in *Asceptrulum*, its assignment to Farreidae rather than Euretidae is based its one-layered farreoid framework as its primary dictyonal skeleton. A farreoid framework (Reid 1964) consists of a two-dimensional primary grid-like scaffold with dictyonalia, fused in parallel longitudinal strands, cross-linked to adjacent strands by tangential rays fused side-

to-side, resulting in a grid-like layer of fused framework. It is the single layer, or two-dimensional, character of this structure that is considered by some authors to be distinctive for the family Farreidae. This alternate definition of Farreidae is extremely important for paleontologists, since loose spicules are unavailable in fossil material. Reiswig (2002) did not include the farreoid framework as a diagnostic feature of Farreidae since it is absent in one of its five extant genera, *Sarostegia* Topsent, 1904 (with euretoid framework). He did, however, note that it has historically been an important diagnostic feature, and thus it is included here in the emended diagnosis.

The alternative assignment of *Asceptrulum* to Euretidae is poorly supported by similar overall spiculation (excepting sceptrule) and presence of a farreoid framework in one of its genera, the monospecific genus, *Bathyxiphus* Schulze, 1899. Position of *Bathyxiphus* cannot be used to support assignment of *Asceptrulum* to Euretidae since its (*Bathyxiphus*) sceptrule type is not known with complete certainty and its own assignment is both provisional and precarious. Based upon the firm relationship of the farreoid framework with Farreidae, *Asceptrulum* is best assigned to that family.

Within Farreidae, *A. axialis* has no obvious close relatives. Axial thickening of a blade-form body is unknown in the family and absence of oxy-tip microscleres (presence of only disc- or onych-tip forms) is known only in four *Farrea*, all of which have a body form of branching and usually anastomosing tubes; *F. woodwardi* Kent, 1870; *F. sollasi* Schulze, 1886; *F. weltneri* Topsent, 1901; *F. occa polyclavula* Tabachnick, 1988. None of these are likely ancestral forms which could have given rise to *A. axialis* through the one-step loss of sceptrules.

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The origin of biological information and the higher taxonomic categories

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Introduction

In a recent volume of the Vienna Series in Theoretical Biology (2003), Gerd B. Müller and Stuart Newman argue that what they call the “origination of organismal form” remains an unsolved problem. In making this claim, Müller and Newman (2003:3–10) distinguish two distinct issues, namely, (1) the causes of form generation in the individual organism during embryological development and (2) the causes responsible for the production of novel organismal forms in the first place during the history of life. To distinguish the latter case (phylogeny) from the former (ontogeny), Müller and Newman use the term “origination” to designate the causal processes by which biological form first arose during the evolution of life. They insist that “the molecular mechanisms that bring about biological form in modern day embryos should not be confused” with the causes responsible for the origin (or “origination”) of novel biological forms during the history of life (p. 3). They further argue that we know more about the causes of ontogenesis, due to advances in molecular biology, molecular genetics and developmental biology, than we do about the causes of phylogenesis—the ultimate origination of new biological forms during the remote past.

In making this claim, Müller and Newman are careful to affirm that evolutionary biology has succeeded in explaining how pre-existing forms diversify under the twin influences of natural selection and variation of genetic traits. Sophisticated mathematically-based models of population genetics

have proven adequate for mapping and understanding quantitative variability and populational changes in organisms. Yet Müller and Newman insist that population genetics, and thus evolutionary biology, has not identified a specifically causal explanation for the origin of true morphological novelty during the history of life. Central to their concern is what they see as the inadequacy of the variation of genetic traits as a source of new form and structure. They note, following Darwin himself, that the sources of new form and structure must precede the action of natural selection (2003: 3)—that selection must act on what already exists. Yet, in their view, the “genocentricity” and “incrementalism” of the neo-Darwinian mechanism has meant that an adequate source of new form and structure has yet to be identified by theoretical biologists. Instead, Müller and Newman see the need to identify epigenetic sources of morphological innovation during the evolution of life. In the meantime, however, they insist neo-Darwinism lacks any “theory of the generative” (p. 7).

As it happens, Müller and Newman are not alone in this judgment. In the last decade or so a host of scientific essays and books have questioned the efficacy of selection and mutation as a mechanism for generating morphological novelty, as even a brief literature survey will establish. Thomson (1992:107) expressed doubt that large-scale morphological changes could accumulate via minor phenotypic changes at the population genetic level. Miklos (1993:29) argued that neo-Darwinism fails to provide a mechanism that can produce

large-scale innovations in form and complexity. Gilbert et al. (1996) attempted to develop a new theory of evolutionary mechanisms to supplement classical neo-Darwinism, which, they argued, could not adequately explain macroevolution. As they put it in a memorable summary of the situation: "starting in the 1970s, many biologists began questioning its [neo-Darwinism's] adequacy in explaining evolution. Genetics might be adequate for explaining microevolution, but microevolutionary changes in gene frequency were not seen as able to turn a reptile into a mammal or to convert a fish into an amphibian. Microevolution looks at adaptations that concern the survival of the fittest, not the arrival of the fittest. As Goodwin (1995) points out, 'the origin of species—Darwin's problem—remains unsolved' " (p. 361). Though Gilbert et al. (1996) attempted to solve the problem of the origin of form by proposing a greater role for developmental genetics within an otherwise neo-Darwinian framework,¹ numerous recent authors have continued to raise questions about the adequacy of that framework itself or about the problem of the origination of form generally (Webster & Goodwin 1996; Shubin & Marshall 2000; Erwin 2000; Conway Morris 2000, 2003b; Carrol 2000; Wagner 2001; Becker & Lönnig 2001; Stadler et al. 2001; Lönnig & Saedler 2002; Wagner & Stadler 2003; Valentine 2004:189–194).

What lies behind this skepticism? Is it warranted? Is a new and specifically causal theory needed to explain the origination of biological form?

This review will address these questions. It will do so by analyzing the problem of the origination of organismal form (and the

corresponding emergence of higher taxa) from a particular theoretical standpoint. Specifically, it will treat the problem of the origination of the higher taxonomic groups as a manifestation of a deeper problem, namely, the problem of the origin of the information (whether genetic or epigenetic) that, as it will be argued, is necessary to generate morphological novelty.

In order to perform this analysis, and to make it relevant and tractable to systematists and paleontologists, this paper will examine a paradigmatic example of the origin of biological form and information during the history of life: the Cambrian explosion. During the Cambrian, many novel animal forms and body plans (representing new phyla, sub-phyla and classes) arose in a geologically brief period of time. The following information-based analysis of the Cambrian explosion will support the claim of recent authors such as Müller and Newman that the mechanism of selection and genetic mutation does not constitute an adequate causal explanation of the origination of biological form in the higher taxonomic groups. It will also suggest the need to explore other possible causal factors for the origin of form and information during the evolution of life and will examine some other possibilities that have been proposed.

The Cambrian Explosion

The "Cambrian explosion" refers to the geologically sudden appearance of many new animal body plans about 530 million years ago. At this time, at least nineteen, and perhaps as many as thirty-five phyla of forty total (Meyer et al. 2003), made their first appearance on Earth within a narrow five- to ten-million-year window of geologic time (Bowring et al. 1993, 1998a:1, 1998b:40; Kerr 1993; Monastersky 1993; Aris-Brosou & Yang 2003). Many new sub-phyla, between 32 and 48 of 56 total (Meyer et al. 2003), and classes of animals also arose at this time with representatives of these new higher taxa manifesting signifi-

¹ Specifically, Gilbert et al. (1996) argued that changes in morphogenetic fields might produce large-scale changes in the developmental programs and, ultimately, body plans of organisms. Yet they offered no evidence that such fields—if indeed they exist—can be altered to produce advantageous variations in body plan, though this is a necessary condition of any successful causal theory of macroevolution.

cant morphological innovations. The Cambrian explosion thus marked a major episode of morphogenesis in which many new and disparate organismal forms arose in a geologically brief period of time.

To say that the fauna of the Cambrian period appeared in a geologically sudden manner also implies the absence of clear transitional intermediate forms connecting Cambrian animals with simpler pre-Cambrian forms. And, indeed, in almost all cases, the Cambrian animals have no clear morphological antecedents in earlier Vendian or Precambrian fauna (Miklos 1993, Erwin et al. 1997:132, Steiner & Reitner 2001, Conway Morris 2003b:510, Valentine et al. 2003:519–520). Further, several recent discoveries and analyses suggest that these morphological gaps may not be merely an artifact of incomplete sampling of the fossil record (Foote 1997, Foote et al. 1999, Benton & Ayala 2003, Meyer et al. 2003), suggesting that the fossil record is at least approximately reliable (Conway Morris 2003b:505).

As a result, debate now exists about the extent to which this pattern of evidence comports with a strictly monophyletic view of evolution (Conway Morris 1998a, 2003a, 2003b:510; Willmer 1990, 2003). Further, among those who accept a monophyletic view of the history of life, debate exists about whether to privilege fossil or molecular data and analyses. Those who think the fossil data provide a more reliable picture of the origin of the Metazoan tend to think these animals arose relatively quickly—that the Cambrian explosion had a “short fuse.” (Conway Morris 2003b:505–506, Valentine & Jablonski 2003). Some (Wray et al. 1996), but not all (Ayala et al. 1998), who think that molecular phylogenies establish reliable divergence times from pre-Cambrian ancestors think that the Cambrian animals evolved over a very long period of time—that the Cambrian explosion had a “long fuse.” This review will not address these questions of historical pattern. Instead, it will analyze whether the neo-Darwinian process of mu-

tation and selection, or other processes of evolutionary change, can generate the form and information necessary to produce the animals that arise in the Cambrian. This analysis will, for the most part,² therefore, not depend upon assumptions of either a long or short fuse for the Cambrian explosion, or upon a monophyletic or polyphyletic view of the early history of life.

Defining Biological Form and Information

Form, like life itself, is easy to recognize but often hard to define precisely. Yet, a reasonable working definition of form will suffice for our present purposes. Form can be defined as the four-dimensional topological relations of anatomical parts. This means that one can understand form as a unified arrangement of body parts or material components in a distinct shape or pattern (topology)—one that exists in three spatial dimensions and which arises in time during ontogeny.

Insofar as any particular biological form constitutes something like a distinct arrangement of constituent body parts, form can be seen as arising from constraints that limit the possible arrangements of matter. Specifically, organismal form arises (both in phylogeny and ontogeny) as possible arrangements of material parts are constrained to establish a specific or particular arrangement with an identifiable three dimensional topography—one that we would recognize as a particular protein, cell type, organ, body plan or organism. A particular

² If one takes the fossil record at face value and assumes that the Cambrian explosion took place within a relatively narrow 5–10 million year window, explaining the origin of the information necessary to produce new proteins, for example, becomes more acute in part because mutation rates would not have been sufficient to generate the number of changes in the genome necessary to build the new proteins for more complex Cambrian animals (Ohno 1996:8475–8478). This review will argue that, even if one allows several hundred million years for the origin of the metazoan, significant probabilistic and other difficulties remain with the neo-Darwinian explanation of the origin of form and information.

“form,” therefore, represents a highly specific and constrained arrangement of material components (among a much larger set of possible arrangements).

Understanding form in this way suggests a connection to the notion of information in its most theoretically general sense. When Shannon (1948) first developed a mathematical theory of information he equated the amount of information transmitted with the amount of uncertainty reduced or eliminated in a series of symbols or characters. Information, in Shannon’s theory, is thus imparted as some options are excluded and others are actualized. The greater the number of options excluded, the greater the amount of information conveyed. Further, constraining a set of possible material arrangements by whatever process or means involves excluding some options and actualizing others. Thus, to constrain a set of possible material states is to generate information in Shannon’s sense. It follows that the constraints that produce biological form also impart information. Or conversely, one might say that producing organismal form by definition requires the generation of information.

In classical Shannon information theory, the amount of information in a system is also inversely related to the probability of the arrangement of constituents in a system or the characters along a communication channel (Shannon 1948). The more improbable (or complex) the arrangement, the more Shannon information, or information-carrying capacity, a string or system possesses.

Since the 1960s, mathematical biologists have realized that Shannon’s theory could be applied to the analysis of DNA and proteins to measure the information-carrying capacity of these macromolecules. Since DNA contains the assembly instructions for building proteins, the information-processing system in the cell represents a kind of communication channel (Yockey 1992: 110). Further, DNA conveys information via specifically arranged sequences of nu-

cleotide bases. Since each of the four bases has a roughly equal chance of occurring at each site along the spine of the DNA molecule, biologists can calculate the probability, and thus the information-carrying capacity, of any particular sequence n bases long.

The ease with which information theory applies to molecular biology has created confusion about the type of information that DNA and proteins possess. Sequences of nucleotide bases in DNA, or amino acids in a protein, are highly improbable and thus have large information-carrying capacities. But, like meaningful sentences or lines of computer code, genes and proteins are also *specified* with respect to function. Just as the meaning of a sentence depends upon the specific arrangement of the letters in a sentence, so too does the function of a gene sequence depend upon the specific arrangement of the nucleotide bases in a gene. Thus, molecular biologists beginning with Crick equated *information* not only with complexity but also with “specificity,” where “specificity” or “specified” has meant “necessary to function” (Crick 1958:144, 153; Sarkar, 1996:191).³ Molecular biologists such as Monod and Crick understood biological information—the information stored in DNA and proteins—as something more than mere complexity (or improbability). Their notion of information associated both biochemical contingency and combinatorial complexity with DNA sequences (allowing DNA’s carrying capacity to be calculated), but it also affirmed that sequences of nucleotides and amino acids in functioning macromolecules possessed a high degree of *specificity* relative to the maintenance of cellular function.

The ease with which information theory applies to molecular biology has also created confusion about the location of infor-

³ As Crick put it, “information means here the *precise* determination of sequence, either of bases in the nucleic acid or on amino acid residues in the protein” (Crick 1958:144, 153).

mation in organisms. Perhaps because the information carrying capacity of the gene could be so easily measured, it has been easy to treat DNA, RNA and proteins as the sole repositories of biological information. Neo-Darwinists in particular have assumed that the origination of biological form could be explained by recourse to processes of genetic variation and mutation alone (Levinton 1988:485). Yet if one understands organismal form as resulting from constraints on the possible arrangements of matter at many levels in the biological hierarchy—from genes and proteins to cell types and tissues to organs and body plans—then clearly biological organisms exhibit many levels of information-rich structure.

Thus, we can pose a question, not only about the origin of genetic information, but also about the origin of the information necessary to generate form and structure at levels higher than that present in individual proteins. We must also ask about the origin of the “specified complexity,” as opposed to mere complexity, that characterizes the new genes, proteins, cell types and body plans that arose in the Cambrian explosion. Dembski (2002) has used the term “complex specified information” (CSI) as a synonym for “specified complexity” to help distinguish functional biological information from mere Shannon information—that is, specified complexity from mere complexity. This review will use this term as well.

The Cambrian Information Explosion

The Cambrian explosion represents a remarkable jump in the specified complexity or “complex specified information” (CSI) of the biological world. For over three billion years, the biological realm included little more than bacteria and algae (Brocks et al. 1999). Then, beginning about 570–565 million years ago (mya), the first complex multicellular organisms appeared in the rock strata, including sponges, cnidarians, and the peculiar Ediacaran biota (Grotzin-

ger et al. 1995). Forty million years later, the Cambrian explosion occurred (Bowring et al. 1993). The emergence of the Ediacaran biota (570 mya), and then to a much greater extent the Cambrian explosion (530 mya), represented steep climbs up the biological complexity gradient.

One way to estimate the amount of new CSI that appeared with the Cambrian animals is to count the number of new cell types that emerged with them (Valentine 1995:91–93). Studies of modern animals suggest that the sponges that appeared in the late Precambrian, for example, would have required five cell types, whereas the more complex animals that appeared in the Cambrian (e.g., arthropods) would have required fifty or more cell types. Functionally more complex animals require more cell types to perform their more diverse functions. New cell types require many new and specialized proteins. New proteins, in turn, require new genetic information. Thus an increase in the number of cell types implies (at a minimum) a considerable increase in the amount of specified genetic information. Molecular biologists have recently estimated that a minimally complex single-celled organism would require between 318 and 562 kilobase pairs of DNA to produce the proteins necessary to maintain life (Koonin 2000). More complex single cells might require upward of a million base pairs. Yet to build the proteins necessary to sustain a complex arthropod such as a trilobite would require orders of magnitude more coding instructions. The genome size of a modern arthropod, the fruitfly *Drosophila melanogaster*, is approximately 180 million base pairs (Gerhart & Kirschner 1997:121, Adams et al. 2000). Transitions from a single cell to colonies of cells to complex animals represent significant (and, in principle, measurable) increases in CSI.

Building a new animal from a single-celled organism requires a vast amount of new genetic information. It also requires a way of arranging gene products—proteins—into higher levels of organization.

New proteins are required to service new cell types. But new proteins must be organized into new systems within the cell; new cell types must be organized into new tissues, organs, and body parts. These, in turn, must be organized to form body plans. New animals, therefore, embody hierarchically organized systems of lower-level parts within a functional whole. Such hierarchical organization itself represents a type of information, since body plans comprise both highly improbable and functionally specified arrangements of lower-level parts. The specified complexity of new body plans requires explanation in any account of the Cambrian explosion.

Can neo-Darwinism explain the discontinuous increase in CSI that appears in the Cambrian explosion—either in the form of new genetic information or in the form of hierarchically organized systems of parts? We will now examine the two parts of this question.

Novel Genes and Proteins

Many scientists and mathematicians have questioned the ability of mutation and selection to generate information in the form of novel genes and proteins. Such skepticism often derives from consideration of the extreme improbability (and specificity) of functional genes and proteins.

A typical gene contains over one thousand precisely arranged bases. For any specific arrangement of four nucleotide bases of length n , there is a corresponding number of possible arrangements of bases, 4^n . For any protein, there are 20^n possible arrangements of protein-forming amino acids. A gene 999 bases in length represents one of 4^{999} possible nucleotide sequences; a protein of 333 amino acids is one of 20^{333} possibilities.

Since the 1960s, some biologists have thought functional proteins to be rare among the set of possible amino acid sequences. Some have used an analogy with human language to illustrate why this should be the case. Denton (1986, 309–311), for example,

has shown that meaningful words and sentences are extremely rare among the set of possible combinations of English letters, especially as sequence length grows. (The ratio of meaningful 12-letter words to 12-letter sequences is $1/10^{14}$; the ratio of 100-letter sentences to possible 100-letter strings is $1/10^{100}$.) Further, Denton shows that most meaningful sentences are *highly isolated* from one another in the space of possible combinations, so that random substitutions of letters will, after a very few changes, inevitably degrade meaning. Apart from a few closely clustered sentences accessible by random substitution, the overwhelming majority of meaningful sentences lie, probabilistically speaking, beyond the reach of random search.

Denton (1986:301–324) and others have argued that similar constraints apply to genes and proteins. They have questioned whether an undirected search via mutation and selection would have a reasonable chance of locating new islands of function—representing fundamentally new genes or proteins—within the time available (Eden 1967, Shützenberger 1967, Løvtrup 1979). Some have also argued that alterations in sequencing would likely result in loss of protein function before fundamentally new function could arise (Eden 1967, Denton 1986). Nevertheless, neither the extent to which genes and proteins are sensitive to functional loss as a result of sequence change, nor the extent to which functional proteins are isolated within sequence space, has been fully known.

Recently, experiments in molecular biology have shed light on these questions. A variety of mutagenesis techniques have shown that proteins (and thus the genes that produce them) are indeed highly specified relative to biological function (Bowie & Sauer 1989, Reidhaar-Olson & Sauer 1990, Taylor et al. 2001). Mutagenesis research tests the sensitivity of proteins (and, by implication, DNA) to functional loss as a result of alterations in sequencing. Studies of proteins have long shown that amino acid res-

idues at many active positions cannot vary without functional loss (Perutz & Lehmann 1968). More recent protein studies (often using mutagenesis experiments) have shown that functional requirements place significant constraints on sequencing even at non-active site positions (Bowie & Sauer 1989, Reidhaar-Olson & Sauer 1990, Chothia et al. 1998, Axe 2000, Taylor et al. 2001). In particular, Axe (2000) has shown that multiple as opposed to single position amino acid substitutions inevitably result in loss of protein function, even when these changes occur at sites that allow variation when altered in isolation. Cumulatively, these constraints imply that proteins are highly sensitive to functional loss as a result of alterations in sequencing, and that functional proteins represent highly isolated and improbable arrangements of amino acids—arrangements that are far more improbable, in fact, than would be likely to arise by chance alone in the time available (Reidhaar-Olson & Sauer 1990; Behe 1992; Kauffman 1995:44; Dembski 1998:175–223; Axe 2000, 2004). (See below the discussion of the neutral theory of evolution for a precise quantitative assessment.)

Of course, neo-Darwinists do not envision a completely random search through the set of all possible nucleotide sequences—so-called “sequence space.” They envision natural selection acting to preserve small advantageous variations in genetic sequences and their corresponding protein products. Dawkins (1996), for example, likens an organism to a high mountain peak. He compares climbing the sheer precipice up the front side of the mountain to building a new organism by chance. He acknowledges that this approach up “Mount Improbable” will not succeed. Nevertheless, he suggests that there is a gradual slope up the backside of the mountain that could be climbed in small incremental steps. In his analogy, the backside climb up “Mount Improbable” corresponds to the process of natural selection acting on random changes in the genetic text. What

chance alone cannot accomplish blindly or in one leap, selection (acting on mutations) can accomplish through the cumulative effect of many slight successive steps.

Yet the extreme specificity and complexity of proteins presents a difficulty, not only for the chance origin of specified biological information (i.e., for random mutations acting alone), but also for selection and mutation acting in concert. Indeed, mutagenesis experiments cast doubt on each of the two scenarios by which neo-Darwinists envision new information arising from the mutation/selection mechanism (for review, see Lönnig 2001). For neo-Darwinism, new functional genes either arise from non-coding sections in the genome or from preexisting genes. Both scenarios are problematic.

In the first scenario, neo-Darwinists envision new genetic information arising from those sections of the genetic text that can presumably vary freely without consequence to the organism. According to this scenario, non-coding sections of the genome, or duplicated sections of coding regions, can experience a protracted period of “neutral evolution” (Kimura 1983) during which alterations in nucleotide sequences have no discernible effect on the function of the organism. Eventually, however, a new gene sequence will arise that can code for a novel protein. At that point, natural selection can favor the new gene and its functional protein product, thus securing the preservation and heritability of both.

This scenario has the advantage of allowing the genome to vary through many generations, as mutations “search” the space of possible base sequences. The scenario has an overriding problem, however: the size of the combinatorial space (i.e., the number of possible amino acid sequences) and the extreme rarity and isolation of the functional sequences within that space of possibilities. Since natural selection can do nothing to help *generate* new functional sequences, but rather can only preserve such sequences once they have arisen, chance alone—random variation—must do the

work of information generation—that is, of finding the exceedingly rare functional sequences within the set of combinatorial possibilities. Yet the probability of randomly assembling (or “finding,” in the previous sense) a functional sequence is extremely small.

Cassette mutagenesis experiments performed during the early 1990s suggest that the probability of attaining (at random) the correct sequencing for a short protein 100 amino acids long is about 1 in 10^{65} (Reidhaar-Olson & Sauer 1990, Behe 1992:65–69). This result agreed closely with earlier calculations that Yockey (1978) had performed based upon the known sequence variability of cytochrome *c* in different species and other theoretical considerations. More recent mutagenesis research has provided additional support for the conclusion that functional proteins are exceedingly rare among possible amino acid sequences (Axe 2000, 2004). Axe (2004) has performed site directed mutagenesis experiments on a 150-residue protein-folding domain within a β -lactamase enzyme. His experimental method improves upon earlier mutagenesis techniques and corrects for several sources of possible estimation error inherent in them. On the basis of these experiments, Axe has estimated the ratio of (a) proteins of typical size (150 residues) that perform a specified function via any folded structure to (b) the whole set of possible amino acids sequences of that size. Based on his experiments, Axe has estimated this ratio to be 1 to 10^{77} . Thus, the probability of finding a functional protein among the possible amino acid sequences corresponding to a 150-residue protein is similarly 1 in 10^{77} .

Other considerations imply additional improbabilities. First, new Cambrian animals would require proteins much longer than 100 residues to perform many necessary specialized functions. Ohno (1996) has noted that Cambrian animals would have required complex proteins such as lysyl oxidase in order to support their stout body structures. Lysyl oxidase molecules in ex-

tant organisms comprise over 400 amino acids. These molecules are both highly complex (non-repetitive) and functionally specified. Reasonable extrapolation from mutagenesis experiments done on shorter protein molecules suggests that the probability of producing functionally sequenced proteins of this length at random is so small as to make appeals to chance absurd, even granting the duration of the entire universe. (See Dembski 1998:175–223 for a rigorous calculation of this “Universal Probability Bound”; See also Axe 2004.) Yet, second, fossil data (Bowering et al. 1993, 1998a:1, 1998b:40; Kerr 1993; Monastersky 1993), and even molecular analyses supporting deep divergence (Wray et al. 1996), suggest that the duration of the Cambrian explosion (between $5\text{--}10 \times 10^6$ and, at most, 7×10^7 years) is far smaller than that of the entire universe ($1.3\text{--}2 \times 10^{10}$ years). Third, DNA mutation rates are far too low to generate the novel genes and proteins necessary to building the Cambrian animals, given the most probable duration of the explosion as determined by fossil studies (Conway Morris 1998b). As Ohno (1996:8475) notes, even a mutation rate of 10^{-9} per base pair per year results in only a 1% change in the sequence of a given section of DNA in 10 million years. Thus, he argues that mutational divergence of pre-existing genes cannot explain the origin of the Cambrian forms in that time.⁴

⁴ To solve this problem Ohno himself proposes the existence of a hypothetical ancestral form that possessed virtually all the genetic information necessary to produce the new body plans of the Cambrian animals. He asserts that this ancestor and its “pananimalian genome” might have arisen several hundred million years before the Cambrian explosion. On this view, each of the different Cambrian animals would have possessed virtually identical genomes, albeit with considerable latent and unexpressed capacity in the case of each individual form (Ohno 1996:8475–8478). While this proposal might help explain the origin of the Cambrian animal forms by reference to pre-existing genetic information, it does not solve, but instead merely displaces, the problem of the origin of the genetic information necessary to produce these new forms.

The selection/mutation mechanism faces another probabilistic obstacle. The animals that arise in the Cambrian exhibit structures that would have required many new *types* of cells, each of which would have required many novel proteins to perform their specialized functions. Further, new cell types require *systems* of proteins that must, as a condition of functioning, act in close coordination with one another. The unit of selection in such systems ascends to the system as a whole. Natural selection selects for functional advantage. But new cell types require whole systems of proteins to perform their distinctive functions. In such cases, natural selection cannot contribute to the process of information generation until *after* the information necessary to build the requisite *system* of proteins has arisen. Thus random variations must, again, do the work of information generation—and now not simply for one protein, but for many proteins arising at nearly the same time. Yet the odds of this occurring by chance alone are, of course, far smaller than the odds of the chance origin of a single gene or protein—so small in fact as to render the chance origin of the genetic information necessary to build a new cell type (a necessary but not sufficient condition of building a new body plan) problematic given even the most optimistic estimates for the duration of the Cambrian explosion.

Dawkins (1986:139) has noted that scientific theories can rely on only so much “luck” before they cease to be credible. The neutral theory of evolution, which, by its own logic, prevents natural selection from playing a role in generating genetic information until after the fact, relies on entirely too much luck. The sensitivity of proteins to functional loss, the need for long proteins to build new cell types and animals, the need for whole new *systems* of proteins to service new cell types, the probable brevity of the Cambrian explosion relative to mutation rates—all suggest the immense improbability (and implausi-

bility) of any scenario for the origination of Cambrian genetic information that relies upon random variation alone unassisted by natural selection.

Yet the neutral theory requires novel genes and proteins to arise—essentially—by random mutation alone. Adaptive advantage accrues *after* the generation of new functional genes and proteins. Thus, natural selection cannot play a role *until* new information-bearing molecules have independently arisen. Thus neutral theorists envision the need to scale the steep face of a Dawkins-style precipice of which there is *no* gradually sloping backside—a situation that, by Dawkins’ own logic, is probabilistically untenable.

In the second scenario, neo-Darwinists envision novel genes and proteins arising by numerous successive mutations in the preexisting genetic text that codes for proteins. To adapt Dawkins’s metaphor, this scenario envisions gradually climbing down one functional peak and then ascending another. Yet mutagenesis experiments again suggest a difficulty. Recent experiments show that, even when exploring a region of sequence space populated by proteins of a single fold and function, most multiple-position changes quickly lead to loss of function (Axe 2000). Yet to turn one protein into another with a completely novel structure and function requires specified changes at many sites. Indeed, the number of changes necessary to produce a new protein greatly exceeds the number of changes that will typically produce functional losses. Given this, the probability of escaping total functional loss during a random search for the changes needed to produce a new function is extremely small—and this probability diminishes exponentially with each additional requisite change (Axe 2000). Thus, Axe’s results imply that, in all probability, random searches for novel proteins (through sequence space) will result in functional loss long before any novel functional protein will emerge.

Blanco et al. have come to a similar conclusion. Using directed mutagenesis, they have determined that residues in both the hydrophobic core and on the surface of the protein play essential roles in determining protein structure. By sampling intermediate sequences between two naturally occurring sequences that adopt different folds, they found that the intermediate sequences "lack a well defined three-dimensional structure." Thus, they conclude that it is unlikely that a new protein fold would evolve from a pre-existing fold via a series of folded intermediate sequences (Blanco et al. 1999: 741).

Thus, although this second neo-Darwinian scenario has the advantage of starting with functional genes and proteins, it also has a lethal disadvantage: any process of random mutation or rearrangement in the genome would in all probability generate nonfunctional intermediate sequences before fundamentally new functional genes or proteins would arise. Clearly, nonfunctional intermediate sequences confer no survival advantage on their host organisms. Natural selection favors *only* functional advantage. It cannot select or favor nucleotide sequences or polypeptide chains that do not yet perform biological functions, and still less will it favor sequences that efface or destroy preexisting function.

Evolving genes and proteins will range through a series of nonfunctional intermediate sequences that natural selection will not favor or preserve but will, in all probability, eliminate (Blanco et al. 1999, Axe 2000). When this happens, selection-driven evolution will cease. At this point, neutral evolution of the genome (unhinged from selective pressure) may ensue, but, as we have seen, such a process must overcome immense probabilistic hurdles, even granting cosmic time.

Thus, whether one envisions the evolutionary process beginning with a noncoding region of the genome or a preexisting functional gene, the functional specificity and complexity of proteins impose very strin-

gent limitations on the efficacy of mutation and selection. In the first case, function must arise first, before natural selection can act to favor a novel variation. In the second case, function must be continuously maintained in order to prevent deleterious (or lethal) consequences to the organism and to allow further evolution. Yet the complexity and functional specificity of proteins implies that both these conditions will be extremely difficult to meet. Therefore, the neo-Darwinian mechanism appears to be inadequate to generate the new information present in the novel genes and proteins that arise with the Cambrian animals.

Novel Body Plans

The problems with the neo-Darwinian mechanism run deeper still. In order to explain the origin of the Cambrian animals, one must account not only for new proteins and cell types, but also for the origin of new body plans. Within the past decade, developmental biology has dramatically advanced our understanding of how body plans are built during ontogeny. In the process, it has also uncovered a profound difficulty for neo-Darwinism.

Significant morphological change in organisms requires attention to timing. Mutations in genes that are expressed late in the development of an organism will not affect the body plan. Mutations expressed early in development, however, could conceivably produce significant morphological change (Arthur 1997:21). Thus, events expressed early in the development of organisms have the only realistic chance of producing large-scale macroevolutionary change (Thomson 1992). As John and Miklos (1988:309) explain, macroevolutionary change requires alterations in the very early stages of ontogenesis.

Yet recent studies in developmental biology make clear that mutations expressed early in development typically have deleterious effects (Arthur 1997:21). For example, when early-acting body plan mol-

ecules, or morphogens such as *bicoid* (which helps to set up the anterior-posterior head-to-tail axis in *Drosophila*), are perturbed, development shuts down (Nüsslein-Volhard & Wieschaus 1980, Lawrence & Struhl 1996, Müller & Newman 2003).⁵ The resulting embryos die. Moreover, there is a good reason for this. If an engineer modifies the length of the piston rods in an internal combustion engine without modifying the crankshaft accordingly, the engine won't start. Similarly, processes of development are tightly integrated spatially and temporally such that changes early in development will require a host of other coordinated changes in separate but functionally interrelated developmental processes downstream. For this reason, mutations will be much more likely to be deadly if they disrupt a functionally deeply-embedded structure such as a spinal column than if they affect more isolated anatomical features such as fingers (Kauffman 1995:200).

This problem has led to what McDonald (1983) has called "a great Darwinian paradox" (p. 93). McDonald notes that genes that are observed to vary within natural populations do not lead to major adaptive changes, while genes that could cause major changes—the very stuff of macroevolution—apparently do not vary. In other words, mutations of the kind that macroevolution doesn't need (namely, viable genetic mutations in DNA expressed late in development) do occur, but those that it does need (namely, beneficial body plan mutations expressed early in development)

apparently don't occur.⁶ According to Darwin (1859:108) natural selection cannot act until favorable variations arise in a population. Yet there is no evidence from developmental genetics that the kind of variations required by neo-Darwinism—namely, favorable body plan mutations—ever occur.

Developmental biology has raised another formidable problem for the mutation/selection mechanism. Embryological evidence has long shown that DNA does not wholly determine morphological form (Goodwin 1985, Nijhout 1990, Sapp 1987, Müller & Newman 2003), suggesting that mutations in DNA alone cannot account for the morphological changes required to build a new body plan.

DNA helps direct protein synthesis.⁷ It also helps to regulate the timing and expression of the synthesis of various proteins within cells. Yet, DNA alone does not determine how individual proteins assemble themselves into larger systems of proteins; still less does it solely determine how cell types, tissue types, and organs arrange themselves into body plans (Harold 1995:

⁶ Notable differences in the developmental pathways of similar organisms have been observed. For example, congeneric species of sea urchins (from genus *Helicidaris*) exhibit striking differences in their developmental pathways (Raff 1999:110–121). Thus, it might be argued that such differences show that early developmental programs can in fact be mutated to produce new forms. Nevertheless, there are two problems with this claim. First, there is no direct evidence that existing differences in sea urchin development arose by mutation. Second, the observed differences in the developmental programs of different species of sea urchins do not result in new body plans, but instead in highly conserved structures. Despite differences in developmental patterns, the endpoints are the same. Thus, even if it can be assumed that mutations produced the differences in developmental pathways, it must be acknowledged that such changes did not result in novel form.

⁷ Of course, many post-translation processes of modification also play a role in producing a functional protein. Such processes make it impossible to predict a protein's final sequencing from its corresponding gene sequence alone (Sarkar 1996:199–202).

⁵ Some have suggested that mutations in "master regulator" Hox genes might provide the raw material for body plan morphogenesis. Yet there are two problems with this proposal. First, Hox gene expression begins only after the foundation of the body plan has been established in early embryogenesis (Davidson 2001:66). Second, Hox genes are highly conserved across many disparate phyla and so cannot account for the morphological differences that exist between the phyla (Valentine 2004:88).

2774, Moss 2004). Instead, other factors—such as the three-dimensional structure and organization of the cell membrane and cytoskeleton and the spatial architecture of the fertilized egg—play important roles in determining body plan formation during embryogenesis.

For example, the structure and location of the cytoskeleton influence the patterning of embryos. Arrays of microtubules help to distribute the essential proteins used during development to their correct locations in the cell. Of course, microtubules themselves are made of many protein subunits. Nevertheless, like bricks that can be used to assemble many different structures, the tubulin subunits in the cell's microtubules are identical to one another. Thus, neither the tubulin subunits nor the genes that produce them account for the different shape of microtubule arrays that distinguish different kinds of embryos and developmental pathways. Instead, the structure of the microtubule array itself is determined by the location and arrangement of its subunits, not the properties of the subunits themselves. For this reason, it is not possible to predict the structure of the cytoskeleton of the cell from the characteristics of the protein constituents that form that structure (Harold 2001:125).

Two analogies may help further clarify the point. At a building site, builders will make use of many materials: lumber, wires, nails, drywall, piping, and windows. Yet building materials do not determine the floor plan of the house, or the arrangement of houses in a neighborhood. Similarly, electronic circuits are composed of many components, such as resistors, capacitors, and transistors. But such lower-level components do not determine their own arrangement in an integrated circuit. Biological systems also depend on hierarchical arrangements of parts. Genes and proteins are made from simple building blocks—nucleotide bases and amino acids—arranged in specific ways. Cell types are made of, among other things, systems of specialized

proteins. Organs are made of specialized arrangements of cell types and tissues. And body plans comprise specific arrangements of specialized organs. Yet, clearly, the properties of individual proteins (or, indeed, the lower-level parts in the hierarchy generally) do not fully determine the organization of the higher-level structures and organizational patterns (Harold 2001:125). It follows that the genetic information that codes for proteins does not determine these higher-level structures either.

These considerations pose another challenge to the sufficiency of the neo-Darwinian mechanism. Neo-Darwinism seeks to explain the origin of new information, form, and structure as a result of selection acting on randomly arising variation at a very low level within the biological hierarchy, namely, within the genetic text. Yet major morphological innovations depend on a specificity of arrangement at a much higher level of the organizational hierarchy, a level that DNA alone does not determine. Yet if DNA is not wholly responsible for body plan morphogenesis, then DNA sequences can mutate indefinitely, without regard to realistic probabilistic limits, and still not produce a new body plan. Thus, the mechanism of natural selection acting on random mutations in DNA cannot *in principle* generate novel body plans, including those that first arose in the Cambrian explosion.

Of course, it could be argued that, while many single proteins do not by themselves determine cellular structures and/or body plans, proteins acting in concert with other proteins or suites of proteins could determine such higher-level form. For example, it might be pointed out that the tubulin subunits (cited above) are assembled by other helper proteins—gene products—called Microtubule Associated Proteins (MAPS). This might seem to suggest that genes and gene products alone do suffice to determine the development of the three-dimensional structure of the cytoskeleton.

Yet, MAPS, and indeed many other nec-

essary proteins, are only part of the story. The location of specified target sites on the interior of the cell membrane also helps to determine the shape of the cytoskeleton. Similarly, so does the position and structure of the centrosome which nucleates the microtubules that form the cytoskeleton. While both the membrane targets and the centrosomes are made of proteins, the location and form of these structures is not wholly determined by the proteins that form them. Indeed, centrosome structure and membrane patterns *as a whole* convey three-dimensional structural information that helps determine the structure of the cytoskeleton and the location of its subunits (McNiven & Porter 1992:313–329). Moreover, the centrioles that compose the centrosomes replicate independently of DNA replication (Lange et al. 2000:235–249, Marshall & Rosenbaum 2000:187–205). The daughter centriole receives its form from the overall structure of the mother centriole, not from the individual gene products that constitute it (Lange et al. 2000). In ciliates, microsurgery on cell membranes can produce heritable changes in membrane patterns, even though the DNA of the ciliates has not been altered (Sonneborn 1970:1–13, Frankel 1980:607–623; Nanney 1983:163–170). This suggests that membrane patterns (as opposed to membrane constituents) are impressed directly on daughter cells. In both cases, form is transmitted from parent three-dimensional structures to daughter three-dimensional structures directly and is not wholly contained in constituent proteins or genetic information (Moss 2004).

Thus, in each new generation, the form and structure of the cell arises as the result of *both* gene products and pre-existing three-dimensional structure and organization. Cellular structures are built from proteins, but proteins find their way to correct locations in part because of pre-existing three-dimensional patterns and organization inherent in cellular structures. Pre-existing three-dimensional form present in the pre-

ceding generation (whether inherent in the cell membrane, the centrosomes, the cytoskeleton or other features of the fertilized egg) contributes to the production of form in the next generation. Neither structural proteins alone, nor the genes that code for them, are sufficient to determine the three-dimensional shape and structure of the entities they form. Gene products provide necessary, but not sufficient conditions, for the development of three-dimensional structure within cells, organs and body plans (Harold 1995:2767). But if this is so, then natural selection acting on genetic variation alone cannot produce the new forms that arise in history of life.

Self-Organizational Models

Of course, neo-Darwinism is not the only evolutionary theory for explaining the origin of novel biological form. Kauffman (1995) doubts the efficacy of the mutation/selection mechanism. Nevertheless, he has advanced a self-organizational theory to account for the emergence of new form, and presumably the information necessary to generate it. Whereas neo-Darwinism attempts to explain new form as the consequence of selection acting on random mutation, Kauffman suggests that selection acts, not mainly on random variations, but on emergent patterns of order that self-organize via the laws of nature.

Kauffman (1995:47–92) illustrates how this might work with various model systems in a computer environment. In one, he conceives a system of buttons connected by strings. Buttons represent novel genes or gene products; strings represent the law-like forces of interaction that obtain between gene products—i.e., proteins. Kauffman suggests that when the complexity of the system (as represented by the number of buttons and strings) reaches a critical threshold, new modes of organization can arise in the system “for free”—that is, naturally and spontaneously—after the manner of a phase transition in chemistry.

Another model that Kauffman develops is a system of interconnected lights. Each light can flash in a variety of states—on, off, twinkling, etc. Since there is more than one possible state for each light, and many lights, there are a vast number of possible states that the system can adopt. Further, in his system, rules determine how past states will influence future states. Kauffman asserts that, as a result of these rules, the system will, if properly tuned, eventually produce a kind of order in which a few basic patterns of light activity recur with greater-than-random frequency. Since these actual patterns of light activity represent a small portion of the total number of possible states in which the system can reside, Kauffman seems to imply that self-organizational laws might similarly result in highly improbable biological outcomes—perhaps even sequences (of bases or amino acids) within a much larger sequence space of possibilities.

Do these simulations of self-organizational processes accurately model the origin of novel genetic information? It is hard to think so.

First, in both examples, Kaufmann presupposes but does not explain significant sources of preexisting information. In his buttons-and-strings system, the buttons represent proteins, themselves packets of CSI, and the result of pre-existing genetic information. Where does this information come from? Kauffman (1995) doesn't say, but the origin of such information is an essential part of what needs to be explained in the history of life. Similarly, in his light system, the order that allegedly arises for "for free" actually arises only if the programmer of the model system "tunes" it in such a way as to keep it from either (a) generating an excessively rigid order or (b) devolving into chaos (pp. 86–88). Yet this necessary tuning involves an intelligent programmer selecting certain parameters and excluding others—that is, inputting information.

Second, Kauffman's model systems are not constrained by functional consider-

ations and thus are not analogous to biological systems. A system of interconnected lights governed by pre-programmed rules may well settle into a small number of patterns within a much larger space of possibilities. But because these patterns have no function, and need not meet any functional requirements, they have no specificity analogous to that present in actual organisms. Instead, examination of Kauffman's (1995) model systems shows that they do not produce sequences or systems characterized by *specified* complexity, but instead by large amounts of symmetrical order or internal redundancy interspersed with aperiodicity or (mere) complexity (pp. 53, 89, 102). Getting a law-governed system to generate repetitive patterns of flashing lights, even with a certain amount of variation, is clearly interesting, but not biologically relevant. On the other hand, a system of lights flashing the title of a Broadway play would model a biologically relevant self-organizational process, at least if such a meaningful or functionally specified sequence arose without intelligent agents previously programming the system with equivalent amounts of CSI. In any case, Kauffman's systems do not produce *specified* complexity, and thus do not offer promising models for explaining the new genes and proteins that arose in the Cambrian.

Even so, Kauffman suggests that his self-organizational models can specifically elucidate aspects of the Cambrian explosion. According to Kauffman (1995:199–201), new Cambrian animals emerged as the result of "long jump" mutations that established new body plans in a discrete rather than gradual fashion. He also recognizes that mutations affecting early development are almost inevitably harmful. Thus, he concludes that body plans, once established, will not change, and that any subsequent evolution must occur within an established body plan (Kauffman 1995:201). And indeed, the fossil record does show a curious (from a neo-Darwinian point of view) top-down pattern of appearance, in which high-

er taxa (and the body plans they represent) appear first, only later to be followed by the multiplication of lower taxa representing variations within those original body designs (Erwin et al. 1987, Lewin 1988, Valentine & Jablonski 2003:518). Further, as Kauffman expects, body plans appear suddenly and persist without significant modification over time.

But here, again, Kauffman begs the most important question, which is: what produces the new Cambrian body plans in the first place? Granted, he invokes "long jump mutations" to explain this, but he identifies no specific self-organizational process that can produce such mutations. Moreover, he concedes a principle that undermines the plausibility of his own proposal. Kauffman acknowledges that mutations that occur early in development are almost inevitably deleterious. Yet developmental biologists know that these are the only kind of mutations that have a realistic chance of producing large-scale evolutionary change—i.e., the big jumps that Kauffman invokes. Though Kauffman repudiates the neo-Darwinian reliance upon random mutations in favor of self-organizing order, in the end, he must invoke the most implausible kind of random mutation in order to provide a self-organizational account of the new Cambrian body plans. Clearly, his model is not sufficient.

Punctuated Equilibrium

Of course, still other causal explanations have been proposed. During the 1970s, the paleontologists Eldredge and Gould (1972) proposed the theory of evolution by punctuated equilibrium in order to account for a pervasive pattern of "sudden appearance" and "stasis" in the fossil record. Though advocates of punctuated equilibrium were mainly seeking to describe the fossil record more accurately than earlier gradualist neo-Darwinian models had done, they did also propose a mechanism—known as species selection—by which the large morphologi-

cal jumps evident in fossil record might have been produced. According to punctuationalists, natural selection functions more as a mechanism for selecting the fittest species rather than the most-fit individual among a species. Accordingly, on this model, morphological change should occur in larger, more discrete intervals than it would given a traditional neo-Darwinian understanding.

Despite its virtues as a descriptive model of the history of life, punctuated equilibrium has been widely criticized for failing to provide a mechanism sufficient to produce the novel form characteristic of higher taxonomic groups. For one thing, critics have noted that the proposed mechanism of punctuated evolutionary change simply lacked the raw material upon which to work. As Valentine and Erwin (1987) note, the fossil record fails to document a large pool of species prior to the Cambrian. Yet the proposed mechanism of species selection requires just such a pool of species upon which to act. Thus, they conclude that the mechanism of species selection probably does not resolve the problem of the origin of the higher taxonomic groups (p. 96).⁸ Further, punctuated equilibrium has not addressed the more specific and fundamental problem of explaining the origin of the new biological information (whether genetic or epigenetic) necessary to produce novel biological form. Advocates of punctuated equilibrium might assume that the new species (upon which natural selection acts) arise by known micro-evolutionary processes of speciation (such as founder ef-

⁸ Erwin (2004:21), although friendly to the possibility of species selection, argues that Gould provides little evidence for its existence. "The difficulty" writes Erwin of species selection, "... is that we must rely on Gould's arguments for theoretical plausibility and sufficient relative frequency. Rarely is a mass of data presented to justify and support Gould's conclusion." Indeed, Gould (2002) himself admitted that species selection remains largely a hypothetical construct: "I freely admit that well-documented cases of species selection do not permeate the literature" (p. 710).

fect, genetic drift or bottleneck effect) that do not necessarily depend upon mutations to produce adaptive changes. But, in that case, the theory lacks an account of how the specifically *higher* taxa arise. Species selection will only produce more fit species. On the other hand, if punctualists assume that processes of genetic mutation can produce more fundamental morphological changes and variations, then their model becomes subject to the same problems as neo-Darwinism (see above). This dilemma is evident in Gould (2002:710) insofar as his attempts to explain adaptive complexity inevitably employ classical neo-Darwinian modes of explanation.⁹

Structuralism

Another attempt to explain the origin of form has been proposed by the structuralists such as Gerry Webster and Brian Goodwin (1984, 1996). These biologists, drawing on the earlier work of D'Arcy Thompson (1942), view biological form as the result of structural constraints imposed upon matter by morphogenetic rules or laws. For reasons similar to those discussed above, the structuralists have insisted that these generative or morphogenetic rules do not reside in the lower level building materials of or-

⁹ "I do not deny either the wonder, or the powerful importance, of organized adaptive complexity. I recognize that we know no mechanism for the origin of such organismal features other than conventional natural selection at the organismic level—for the sheer intricacy and elaboration of good biomechanical design surely precludes either random production, or incidental origin as a side consequence of active processes at other levels" (Gould 2002:710). "Thus, we do not challenge the efficacy or the cardinal importance of organismal selection. As previously discussed, I fully agree with Dawkins (1986) and others that one cannot invoke a higher-level force like species selection to explain 'things that organisms do'—in particular, the stunning panoply of organismic adaptations that has always motivated our sense of wonder about the natural world, and that Darwin (1859) described, in one of his most famous lines (3), as 'that perfection of structure and coadaptation which most justly excites our admiration'" (Gould 2002:886).

ganisms, whether in genes or proteins. Webster and Goodwin (1984:510–511) further envision morphogenetic rules or laws operating ahistorically, similar to the way in which gravitational or electro-magnetic laws operate. For this reason, structuralists see phylogeny as of secondary importance in understanding the origin of the higher taxa, though they think that transformations of form can occur. For structuralists, constraints on the arrangement of matter arise not mainly as the result of historical contingencies—such as environmental changes or genetic mutations—but instead because of the continuous ahistorical operation of fundamental laws of form—laws that organize or inform matter.

While this approach avoids many of the difficulties currently afflicting neo-Darwinism (in particular those associated with its "genocentricity"), critics (such as Maynard Smith 1986) of structuralism have argued that the structuralist explanation of form lacks specificity. They note that structuralists have been unable to say just where laws of form reside—whether in the universe, or in every possible world, or in organisms as a whole, or in just some part of organisms. Further, according to structuralists, morphogenetic laws are mathematical in character. Yet, structuralists have yet to specify the mathematical formulae that determine biological forms.

Others (Yockey 1992; Polanyi 1967, 1968; Meyer 2003) have questioned whether physical laws could in principle generate the kind of complexity that characterizes biological systems. Structuralists envision the existence of biological laws that produce form in much the same way that physical laws produce form. Yet the forms that physicists regard as manifestations of underlying laws are characterized by large amounts of symmetric or redundant order, by relatively simple patterns such as vortices or gravitational fields or magnetic lines of force. Indeed, physical laws are typically expressed as differential equations (or algorithms) that almost by definition describe recurring phe-

nomena—patterns of compressible “order” not “complexity” as defined by algorithmic information theory (Yockey 1992:77–83). Biological forms, by contrast, manifest greater complexity and derive in ontogeny from highly complex initial conditions—i.e., non-redundant sequences of nucleotide bases in the genome and other forms of information expressed in the complex and irregular three-dimensional topography of the organism or the fertilized egg. Thus, the kind of form that physical laws produce is not analogous to biological form—at least not when compared from the standpoint of (algorithmic) complexity. Further, physical laws lack the information content to specify biology systems. As Polanyi (1967, 1968) and Yockey (1992:290) have shown, the laws of physics and chemistry allow, but do not determine, distinctively biological modes of organization. In other words, living systems are consistent with, but not deducible, from physical-chemical laws (1992:290).

Of course, biological systems do manifest some reoccurring patterns, processes and behaviors. The same type of organism develops repeatedly from similar ontogenetic processes in the same species. Similar processes of cell division re-occur in many organisms. Thus, one might describe certain biological processes as law-governed. Even so, the existence of such biological regularities does not solve the problem of the origin of form and information, since the recurring processes described by such biological laws (if there be such laws) only occur as the result of pre-existing stores of (genetic and/or epigenetic) information and these information-rich initial conditions impose the constraints that produce the recurring behavior in biological systems. (For example, processes of cell division recur with great frequency in organisms, but depend upon information-rich DNA and proteins molecules.) In other words, distinctively biological regularities depend upon pre-existing biological information. Thus, appeals to higher-level biological laws presuppose, but do not explain, the

origination of the information necessary to morphogenesis.

Thus, structuralism faces a difficult in principle dilemma. On the one hand, physical laws produce very simple redundant patterns that lack the complexity characteristic of biological systems. On the other hand, distinctively biological laws—if there are such laws—depend upon pre-existing information-rich structures. In either case, laws are not good candidates for explaining the origination of biological form or the information necessary to produce it.

Cladism: An Artifact of Classification?

Some cladists have advanced another approach to the problem of the origin of form, specifically as it arises in the Cambrian. They have argued that the problem of the origin of the phyla is an artifact of the classification system, and therefore, does not require explanation. Budd and Jensen (2000), for example, argue that the problem of the Cambrian explosion resolves itself if one keeps in mind the cladistic distinction between “stem” and “crown” groups. Since crown groups arise whenever new characters are added to simpler more ancestral stem groups during the evolutionary process, new phyla will inevitably arise once a new stem group has arisen. Thus, for Budd and Jensen what requires explanation is not the crown groups corresponding to the new Cambrian phyla, but the earlier more primitive stem groups that presumably arose deep in the Proterozoic. Yet since these earlier stem groups are by definition less derived, explaining them will be considerably easier than explaining the origin of the Cambrian animals *de novo*. In any case, for Budd and Jensen the explosion of new phyla in the Cambrian does not require explanation. As they put it, “given that the early branching points of major clades is an inevitable result of clade diversification, the alleged phenomenon of the phyla appearing early and remaining morphologically static is not seen to require

particular explanation" (Budd & Jensen 2000:253).

While superficially plausible, perhaps, Budd and Jensen's attempt to explain away the Cambrian explosion begs crucial questions. Granted, as new characters are added to existing forms, novel morphology and greater morphological disparity will likely result. But what causes new characters to arise? And how does the information necessary to produce new characters originate? Budd and Jensen do not specify. Nor can they say how derived the ancestral forms are likely to have been, and what processes, might have been sufficient to produce them. Instead, they simply assume the sufficiency of known neo-Darwinian mechanisms (Budd & Jensen 2000:288). Yet, as shown above, this assumption is now problematic. In any case, Budd and Jensen do not explain what causes the origination of biological form and information.

Convergence and Teleological Evolution

More recently, Conway Morris (2000, 2003c) has suggested another possible explanation based on the tendency for evolution to converge on the same structural forms during the history of life. Conway Morris cites numerous examples of organisms that possess very similar forms and structures, even though such structures are often built from different material substrates and arise (in ontogeny) by the expression of very different genes. Given the extreme improbability of the same structures arising by random mutation and selection in disparate phylogenies, Conway Morris argues that the pervasiveness of convergent structures suggests that evolution may be in some way "channeled" toward similar functional and/or structural endpoints. Such an end-directed understanding of evolution, he admits, raises the controversial prospect of a teleological or purposive element in the history of life. For this reason, he argues that the phenomenon of convergence has received less attention

than it might have otherwise. Nevertheless, he argues that just as physicists have reopened the question of design in their discussions of anthropic fine-tuning, the ubiquity of convergent structures in the history of life has led some biologists (Denton 1998) to consider extending teleological thinking to biology. And, indeed, Conway Morris himself intimates that the evolutionary process might be "underpinned by a purpose" (2000:8, 2003b:511).

Conway Morris, of course, considers this possibility in relation to a very specific aspect of the problem of organismal form, namely, the problem of explaining why the same forms arise repeatedly in so many disparate lines of descent. But this raises a question. Could a similar approach shed explanatory light on the more general causal question that has been addressed in this review? Could the notion of purposive design help provide a more adequate explanation for the origin of organismal form generally? Are there reasons to consider design as an explanation for the origin of the biological information necessary to produce the higher taxa and their corresponding morphological novelty?

The remainder of this review will suggest that there are such reasons. In so doing, it may also help explain why the issue of teleology or design has re-emerged within the scientific discussion of biological origins (Denton 1986, 1998; Thaxton et al. 1992; Kenyon & Mills 1996; Behe 1996, 2004; Dembski 1998, 2002, 2004; Conway Morris 2000, 2003a, 2003b; Lönnig 2001; Lönnig & Saedler 2002; Nelson & Wells 2003; Meyer 2003, 2004; Bradley 2004) and why some scientists and philosophers of science have considered teleological explanations for the origin of form and information despite strong methodological prohibitions against design as a scientific hypothesis (Gillespie 1979, Lenior 1982:4).

First, the possibility of design as an explanation follows logically from a consideration of the deficiencies of neo-Darwinism and other current theories as explana-

tions for some of the more striking "appearances of design" in biological systems. Neo-Darwinists such as Ayala (1994:5), Dawkins (1986:1), Mayr (1982:xi-xii) and Lewontin (1978) have long acknowledged that organisms appear to have been designed. Of course, neo-Darwinists assert that what Ayala (1994:5) calls the "obvious design" of living things is only apparent since the selection/mutation mechanism can explain the origin of complex form and organization in living systems without an appeal to a designing agent. Indeed, neo-Darwinists affirm that mutation and selection—and perhaps other similarly undirected mechanisms—are fully sufficient to explain the appearance of design in biology. Self-organizational theorists and punctuationalists modify this claim, but affirm its essential tenet. Self-organization theorists argue that natural selection acting on self-organizing order can explain the complexity of living things—again, without any appeal to design. Punctuationalists similarly envision natural selection acting on newly arising species with no actual design involved.

And clearly, the neo-Darwinian mechanism does explain many appearances of design, such as the adaptation of organisms to specialized environments that attracted the interest of 19th century biologists. More specifically, known micro-evolutionary processes appear quite sufficient to account for changes in the size of Galapagos finch beaks that have occurred in response to variations in annual rainfall and available food supplies (Weiner 1994, Grant 1999).

But does neo-Darwinism, or any other fully materialistic model, explain all appearances of design in biology, including the body plans and information that characterize living systems? Arguably, biological forms—such as the structure of a chambered nautilus, the organization of a trilobite, the functional integration of parts in an eye or molecular machine—attract our attention in part because the organized complexity of such systems seems reminiscent of our own designs. Yet, this review

has argued that neo-Darwinism does not adequately account for the origin of all appearances of design, especially if one considers animal body plans, and the information necessary to construct them, as especially striking examples of the appearance of design in living systems. Indeed, Dawkins (1995:11) and Gates (1996:228) have noted that genetic information bears an uncanny resemblance to computer software or machine code. For this reason, the presence of CSI in living organisms, and the discontinuous increases of CSI that occurred during events such as the Cambrian explosion, appears at least suggestive of design.

Does neo-Darwinism or any other purely materialistic model of morphogenesis account for the origin of the genetic and other forms of CSI necessary to produce novel organismal form? If not, as this review has argued, could the emergence of novel information-rich genes, proteins, cell types and body plans have resulted from actual design, rather than a purposeless process that merely mimics the powers of a designing intelligence? The logic of neo-Darwinism, with its specific claim to have accounted for the appearance of design, would itself seem to open the door to this possibility. Indeed, the historical formulation of Darwinism in dialectical opposition to the design hypothesis (Gillespie 1979), coupled with neo-Darwinism's inability to account for many salient appearances of design including the emergence of form and information, would seem logically to re-open the possibility of actual (as opposed to apparent) design in the history of life.

A second reason for considering design as an explanation for these phenomena follows from the importance of explanatory power to scientific theory evaluation and from a consideration of the potential explanatory power of the design hypothesis. Studies in the methodology and philosophy of science have shown that many scientific theories, particularly in the historical sciences, are formulated and justified as inferences to the best explanation (Lipton 1991:

32–88, Brush 1989:1124–1129, Sober 2000:44). Historical scientists, in particular, assess or test competing hypotheses by evaluating which hypothesis would, if true, provide the best explanation for some set of relevant data (Meyer 1991, 2002; Cleland 2001:987–989, 2002:474–496).¹⁰ Those

¹⁰Theories in the historical sciences typically make claims about what happened in the past, or what happened in the past to cause particular events to occur (Meyer 1991:57–72). For this reason, historical scientific theories are rarely tested by making predictions about what will occur under controlled laboratory conditions (Cleland 2001:987, 2002:474–496). Instead, such theories are usually tested by comparing their explanatory power against that of their competitors with respect to already known facts. Even in the case in which historical theories make claims about past causes they usually do so on the basis of pre-existing knowledge of cause and effect relationships. Nevertheless, prediction may play a limited role in testing historical scientific theories since such theories may have implications as to what kind of evidence is likely to emerge in the future. For example, neo-Darwinism affirms that new functional sections of the genome arise by trial and error process of mutation and subsequent selection. For this reason, historically many neo-Darwinists expected or predicted that the large non-coding regions of the genome—so-called “junk DNA”—would lack function altogether (Orgel & Crick 1980). On this line of thinking, the non-functional sections of the genome represent nature’s failed experiments that remain in the genome as a kind of artifact of the past activity of the mutation and selection process. Advocates of the design hypotheses on the other hand, would have predicted that non-coding regions of the genome might well reveal hidden functions, not only because design theorists do not think that new genetic information arises by a trial and error process of mutation and selection, but also because designed systems are often functionally polyvalent. Even so, as new studies reveal more about the functions performed by the non-coding regions of the genome (Gibbs 2003), the design hypothesis can no longer be said to make this claim in the form of a specifically future-oriented prediction. Instead, the design hypothesis might be said to gain confirmation or support from its ability to explain this now known evidence, albeit after the fact. Of course, neo-Darwinists might also amend their original prediction using various auxiliary hypotheses to explain away the presence of newly discovered functions in the non-coding regions of DNA. In both cases, considerations of *ex post facto* explanatory power re-emerge as central to assessing and testing competing historical theories.

with greater explanatory power are typically judged to be better, more probably true, theories. Darwin (1896:437) used this method of reasoning in defending his theory of universal common descent. Moreover, contemporary studies on the method of “inference to the best explanation” have shown that determining which among a set of competing possible explanations constitutes the best depends upon judgments about the causal adequacy, or “causal powers,” of competing explanatory entities (Lipton 1991:32–88). In the historical sciences, uniformitarian and/or actualistic (Gould 1965, Simpson 1970, Rutten 1971, Hooykaas 1975) canons of method suggest that judgments about causal adequacy should derive from our present knowledge of cause and effect relationships. For historical scientists, “the present is the key to the past” means that present experience-based knowledge of cause and effect relationships typically guides the assessment of the plausibility of proposed causes of past events.

Yet it is precisely for this reason that current advocates of the design hypothesis want to reconsider design as an explanation for the origin of biological form and information. This review, and much of the literature it has surveyed, suggests that four of the most prominent models for explaining the origin of biological form fail to provide adequate causal explanations for the discontinuous increases of CSI that are required to produce novel morphologies. Yet, we have repeated experience of rational and conscious agents—in particular ourselves—generating or causing increases in complex specified information, both in the form of sequence-specific lines of code and in the form of hierarchically arranged systems of parts.

In the first place, intelligent human agents—in virtue of their rationality and consciousness—have demonstrated the power to produce information in the form of linear sequence-specific arrangements of characters. Indeed, experience affirms that

information of this type routinely arises from the activity of intelligent agents. A computer user who traces the information on a screen back to its source invariably comes to a *mind*—that of a software engineer or programmer. The information in a book or inscription ultimately derives from a writer or scribe—from a mental, rather than a strictly material, cause. Our experience-based knowledge of information-flow confirms that systems with large amounts of specified complexity (especially codes and languages) invariably originate from an intelligent source—from a mind or personal agent. As Quastler (1964) put it, the “creation of new information is habitually associated with conscious activity” (p. 16). Experience teaches this obvious truth.

Further, the highly specified hierarchical arrangements of parts in animal body plans also suggest *design*, again because of our experience of the kinds of features and systems that designers can and do produce. At every level of the biological hierarchy, organisms require specified and highly improbable arrangements of lower-level constituents in order to maintain their form and function. Genes require specified arrangements of nucleotide bases; proteins require specified arrangements of amino acids; new cell types require specified arrangements of systems of proteins; body plans require specialized arrangements of cell types and organs. Organisms not only contain information-rich components (such as proteins and genes), but they comprise information-rich arrangements of those components and the systems that comprise them. Yet we know, based on our present experience of cause and effect relationships, that design engineers—possessing purposive intelligence and rationality—have the ability to produce information-rich hierarchies in which both individual modules and the arrangements of those modules exhibit complexity and specificity—information so defined. Individual transistors, resistors, and capacitors exhibit considerable complexity and specificity of design; at a higher level of organization,

their specific arrangement within an integrated circuit represents additional information and reflects further design. Conscious and rational agents have, as part of their powers of purposive intelligence, the capacity to design information-rich parts and to organize those parts into functional information-rich systems and hierarchies. Further, we know of no other causal entity or process that has this capacity. Clearly, we have good reason to doubt that mutation and selection, self-organizational processes or laws of nature, can produce the information-rich components, systems, and body plans necessary to explain the origination of morphological novelty such as that which arises in the Cambrian period.

There is a third reason to consider purpose or design as an explanation for the origin of biological form and information: purposive agents have just those necessary powers that natural selection lacks as a condition of its causal adequacy. At several points in the previous analysis, we saw that natural selection lacked the ability to generate novel information precisely because it can only act *after* new functional CSI has arisen. Natural selection can favor new proteins, and genes, but only after they perform some function. The job of generating new functional genes, proteins and systems of proteins therefore falls entirely to random mutations. Yet without functional criteria to guide a search through the space of possible sequences, random variation is probabilistically doomed. What is needed is not just a source of variation (i.e., the freedom to search a space of possibilities) or a mode of selection that can operate after the fact of a successful search, but instead a means of selection that (a) operates during a search—before success—and that (b) is guided by information about, or knowledge of, a functional target.

Demonstration of this requirement has come from an unlikely quarter: genetic algorithms. Genetic algorithms are programs that allegedly simulate the creative power of mutation and selection. Dawkins and

Küppers, for example, have developed computer programs that putatively simulate the production of genetic information by mutation and natural selection (Dawkins 1986:47–49, Küppers 1987:355–369). Nevertheless, as shown elsewhere (Meyer 1998:127–128, 2003:247–248), these programs only succeed by the illicit expedient of providing the computer with a “target sequence” and then treating relatively greater proximity to *future* function (i.e., the target sequence), not actual present function, as a selection criterion. As Berlinski (2000) has argued, genetic algorithms need something akin to a “forward looking memory” in order to succeed. Yet such foresighted selection has no analogue in nature. In biology, where differential survival depends upon maintaining function, selection cannot occur before new functional sequences arise. Natural selection lacks foresight.

What natural selection lacks, intelligent selection—purposive or goal-directed design—provides. Rational agents can arrange both matter and symbols with distant goals in mind. In using language, the human mind routinely “finds” or generates highly improbable linguistic sequences to convey an intended or *preconceived* idea. In the process of thought, functional objectives precede and constrain the selection of words, sounds and symbols to generate functional (and indeed meaningful) sequences from among a vast ensemble of meaningless alternative combinations of sound or symbol (Denton 1986:309–311). Similarly, the construction of complex technological objects and products, such as bridges, circuit boards, engines and software, result from the application of goal-directed constraints (Polanyi 1967, 1968). Indeed, in all functionally integrated complex systems where the cause is known by experience or observation, design engineers or other intelligent agents applied boundary constraints to limit possibilities in order to produce improbable forms, sequences or structures. Rational agents have repeatedly demonstrated the capacity to constrain the

possible to actualize improbable but initially unrealized future functions. Repeated experience affirms that intelligent agents (minds) uniquely possess such causal powers.

Analysis of the problem of the origin of biological information, therefore, exposes a deficiency in the causal powers of natural selection that corresponds precisely to powers that agents are uniquely known to possess. Intelligent agents have foresight. Such agents can select functional goals *before* they exist. They can devise or select material means to accomplish those ends from among an array of possibilities and then actualize those goals in accord with a *preconceived* design plan or set of functional requirements. Rational agents can constrain combinatorial space with distant outcomes in mind. The causal powers that natural selection lacks—almost by definition—are associated with the attributes of consciousness and rationality—with purposive intelligence. Thus, by invoking design to explain the origin of new biological information, contemporary design theorists are not positing an arbitrary explanatory element unmotivated by a consideration of the evidence. Instead, they are positing an entity possessing precisely the attributes and causal powers that the phenomenon in question requires as a condition of its production and explanation.

Conclusion

An experience-based analysis of the causal powers of various explanatory hypotheses suggests purposive or intelligent design as a causally adequate—and perhaps the most causally adequate—explanation for the origin of the complex specified information required to build the Cambrian animals and the novel forms they represent. For this reason, recent scientific interest in the design hypothesis is unlikely to abate as biologists continue to wrestle with the problem of the origination of biological form and the higher taxa.

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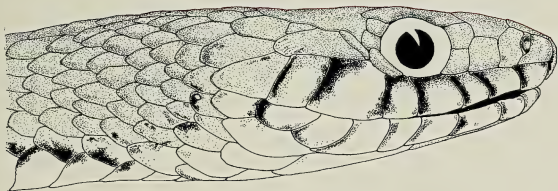


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STATEMENT FROM THE COUNCIL OF THE BIOLOGICAL SOCIETY OF WASHINGTON

The paper by Stephen C. Meyer, "The origin of biological information and the higher taxonomic categories," in vol. 117, no. 2, pp. 213–239 of the *Proceedings of the Biological Society of Washington*, was published at the discretion of the former editor, Richard v. Sternberg. Contrary to typical editorial practices, the paper was published without review by any associate editor; Sternberg handled the entire review process. The Council, which includes officers, elected councilors, and past presidents, and the associate editors would have deemed the paper inappropriate for the pages of the *Proceedings* because the subject matter represents such a significant departure from the nearly purely systematic content for which this journal has been known throughout its 122-year history. For the same reason, the journal will not publish a rebuttal to the thesis of the paper, the su-

periority of intelligent design (ID) over evolution as an explanation of the emergence of Cambrian body-plan diversity. The Council endorses a resolution on ID published by the American Association for the Advancement of Science (www.aaas.org/news/releases/2002/1106id2.shtml), which observes that there is no credible scientific evidence supporting ID as a testable hypothesis to explain the origin of organic diversity. Accordingly, the Meyer paper does not meet the scientific standards of the *Proceedings*.

We have reviewed and revised editorial policies to ensure that the goals of the Society, as reflected in its journal, are clearly understood by all. Through a web presence (www.biolsocwash.org) and improvements in the journal, the Society hopes not only to continue but to increase its service to the world community of systematic biologists.

A review of the North American subspecies of the Great Blue Heron (*Ardea herodias*)

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Abstract.—Geographic variation in the great Blue Heron (*Ardea herodias*) was comprehensively reviewed by H. C. Oberholser (1912), who recognized nine North American subspecies—excluding the so-called Great White Heron (*A. occidentalis* = *A. h. occidentalis*). Oberholser's revision provided the framework generally followed in subsequent subspecific treatments of this species. However, Payne's (1979) brief general summary of this species' geographic variation rejects most of these North American taxa, recognizing as valid only the nominate subspecies and those of the Pacific northwest [*A. h. fannini*] and Florida [*A. h. occidentalis*]. My studies verify that *A. h. herodias* and *A. h. fannini* are taxonomically distinct, along with *A. h. wardi* in which I include *A. h. treganzai*, *A. h. hyperonca*, and *A. h. sanctilucae*. In addition, I regard *A. h. lessoni*, *A. h. adoxa*, and *A. h. olgista* as synonymous with *A. h. herodias*, as all are based on migrant specimens of this form. In addition, I suspect Payne is justified as recognizing the Caribbean *A. h. occidentalis* as valid, based on its white plumage and shorter head plumes.

The Great Blue Heron (*Ardea herodias*) nests in North America from southeastern Alaska, southern British Columbia, northern Alberta, central Saskatchewan, northern Manitoba, northern Ontario, southern Quebec, New Brunswick, and Nova Scotia southward to the Gulf states, southern Florida; on the coastal lowlands of Mexico south to Tabasco, Nayarit, and Baja California; and locally in the Caribbean Basin (A.O.U. 1998). There are no nesting season specimens of Great Blue Herons taken between the Yucatan Peninsula of Mexico and Venezuela. Oberholser (1912) recognized nine subspecies over this extensive area, these being *A. h. herodias* L., 1758 (type locality: America [= Hudson Bay, Canada]); *A. h. wardi* Ridgway, 1882 (Oyster [= Estero] Bay, Florida); *A. h. treganzai* Court, 1908 (Egg Island, Great Salt Lake, Utah); *A. h. fannini* Chapman, 1901 (Skidegate [Graham Island], Queen Charlotte Islands, British Columbia); *A. h. hyperonca* Ober-

holser, 1912 (Baird [Shasta Co.], California); *A. h. sanctilucae* Thayer and Bangs, 1912 (Espiritu Santo Island, Baja California); *A. h. lessoni* Wagler, 1831 (Mexico); *A. h. adoxa* Oberholser, 1912 (Curacao); and *A. h. olgista* Oberholser, 1912 (San Clemente Island, California). Not included in Oberholser's revision was the so-called Great White Heron (*A. occidentalis*), which is now widely regarded as a white morph of *A. herodias* (e.g., A.O.U. 1998). In addition, he did include the endemic *A. h. cognatus* of the Galapago Islands, which is the only nesting population of this species outside North America.

Oberholser's (1912) subspecies were based on differences in plumage coloration and measurements among populations, which in some cases included migrants from other areas. In fact, although Oberholser was aware of both migration and other forms of dispersal in this species, he appears to have underestimated the extent of

this phenomenon. For example, Bond (1935) found that Oberholser's *A. h. adoxa* from Curacao is based on a series of eight specimens, all of which are southward migrants of *A. h. herodias*. In addition, the adult female holotype (examined) for Oberholser's (ibid.) *A. h. olgista* from San Clemente Island is also an example of the nominate form, based on its dark coloration and a wing chord of 433 mm, even though previously synonymized with the locally nesting *A. h. "hyperonca"* (= *A. h. wardi*) by Grinnell and Miller (1944) and Hellmayr and Conover (1948). Hellmayr and Conover (1948) also listed *A. lessoni* Wagler as a synonym of *A. h. herodias*, simply noting "type in Munich Museum examined."

Oberholser's revision provided the framework generally followed in subsequent subspecific treatments such as A. O. U. (1931, 1957), Peters (1931), Friedmann et al. (1950), Palmer (1962) and Hancock and Elliot (1978).

More recently, Payne (1979) has treated overall geographic variation in the *A. herodias* complex (including *A. occidentalis*), although he did so only briefly, generally, and without measurements or references to subspecific names. He recognized only three taxa in North America: the widespread *A. h. herodias*, *A. h. fannini* of the north Pacific Coast, and the white-plumaged *A. h. occidentalis* of the Caribbean Basin. My revisionary work on the Great Blue Heron began in an attempt to identify then recently collected Mexican specimens in the 1960's. Since then I have examined most of the available adult specimens in North American collections. My findings generally agree with those of Payne, except that I also recognize the populations of paler and larger birds of the southern and western North America as *A. h. wardi*. I did not examine plumage variation in nesting populations of the Caribbean Basin, but these may constitute a valid subspecies (*A. h. occidentalis*) based on the dominance of the white morph (rare elsewhere). If not recognizable, then these populations and those

of *A. h. wardi* should be merged under the older name of *A. h. occidentalis*.

Methods

Several caveats apply to the museum specimens used in this study, the first being the dearth of properly labeled and prepared adult nesting season skins for studies of geographic variation among Great Blue Herons in North America. For example, I found no nesting season adult males from Delaware, Virginia, West Virginia, and Kentucky; only single males from Maryland, Tennessee, South Carolina, and Alabama; and only two from North Carolina! Secondly, many specimens lack information on gonad size, weight, and fat condition, making it difficult to ascertain whether such birds are likely nesting or are migrants. As a result, one must often assume that birds are nesting on the basis of collection localities and dates, which can be complicated by (a) regional differences in the timing of breeding activities and (b) the migration and other forms of dispersal in this species. For example, we know post-nesting southern populations (*A. h. wardi*) can be dispersing northward in the northeastern U.S. while northern birds (*A. h. herodias*) are in the process of nesting (Dickerman 2002). Whereas coloration and measurements do distinguish these subspecies, some specimens overlap or intergrade between the two. As a result, these may be either included in or excluded from nesting samples, thus introducing some degree of bias into the data. In any case, I have arbitrarily set the nesting season for most North American populations of this species as April to July, subject to modification based on specimens' gonadal condition, weight, fat levels, coloration, and measurements.

A second caveat with Great Blue Heron specimens is that the plumage coloration can be altered by a variety of factors, including wear, bleaching, molt stage, chemicals used to preserve or protect skins, mu-

seum age, and especially staining due to the leakage and oxidation of body fat. In addition, winter-taken specimens in the north may be under greater nutritional stress, so that they may produce less powder down to coat the feathers. This in turn would greatly affect feather color, as the powder-down coating produces a pale bloom that makes the plumage appear lighter. In fact, this same effect can be extreme when the plumage is washed and the powder-down is removed (Dickerman 2004).

For my final comparisons of plumage coloration in Great Blue Heron populations, I borrowed 26 adult skins taken throughout North America, representing all of the mainland forms. All were clean but unwashed specimens, taken as early in the nesting season and chronologically recently as possible. As I found no differences in plumage color between males and females, I combined the sexes for these comparisons. In addition, I measured 214 males and 189 females for the following characters: wing chord, tail length, exposed culmen, and tarsus length (all in mm). After a preliminary analysis, I have variously grouped these measurements by subspecies, area, and sometimes type specimens (Table 1). I then calculated the sample sizes, ranges, means, and standard deviations for the four mensural characters, as well as performing two-sample t-tests to determine the significances ($P = 0.05$) of differences. I did not analyze either plumage or mensural variation in other age classes, because sample sizes were too small for juveniles and nestlings. Immatures were not analyzed.

Results

As did Oberholser (1912), I find Great Blue Herons can be aggregated into three distinct North American nesting populations on the basis of plumage coloration, exclusive of the white-phased birds of the Caribbean Basin (*A. h. occidentalis*). More specifically, this variation involves the coloration of the upper-parts, neck, and wing

feathers in adult birds, which ranges from pale to darker gray. The first of these aggregates consists of the moderately gray populations to which the name *A. h. herodias* can be applied. These nest in southern Canada west to interior southern British Columbia, then southward in the United States to eastern Washington, North Dakota, Wisconsin, Indiana, Maryland, and South Carolina. The second aggregate of paler populations in the southeastern, central, and western U.S. and Mexico that Oberholser (ibid.) assigned to four subspecies, of which the oldest name is *A. h. wardi* with *A. h. treganzai*, *A. h. hyperonca* and *A. h. sanctilucae* here considered synonyms. And the third is the darker gray *A. h. fannini*, whose range I have recommended be restricted to the coastal region of northwestern British Columbia and adjacent Alaska, specifically the Queen Charlotte Islands north to Prince William Sound (Dickerman 2004). However, as noted earlier, the slaty-black coloration of the holotype (Chapman 1901) is abnormally dark, apparently due to washing that removed the powder down coating and thus the paler bloom of the plumage (Dickerman 2004).

Oberholser (1912) further characterized nesting Great Blue Herons on the basis of measurements, which he particularly emphasized in allotting pale populations to four subspecies. Given this, I also assessed measurements in this species, in which males generally average larger than females in nesting populations (Table 1). For example, my overall samples reveal that males are 4.1% larger in wing chord, 3.5% in tail length, 6.5% in exposed culmen, and 6.5% in tarsus length (including only "typical populations of named forms, excluding *fannini* because of small sample size). However, the sexes overlap in all of these mensural characters, and t-tests often show the differences are not significant at the $P = 0.05$ level. Nonetheless, it is important to segregate the sexes when using measurements to allocate specimens to subspecies

and populations. As for the mensural characters themselves, I found the following:

Wing chord.—Nesting populations with the longest wings are 4.8% and 5.2% greater than those with the shortest in males and females, respectively. Means are smallest in *A. h. herodias*, generally becoming progressively larger through the populations of the interior western U.S., the Pacific Coast region, and Mexico to the southeastern U.S. (Table 1). However, a notable departure from this is that *A. h. occidentalis* has the wing chord intermediate, as opposed to being among the largest in the species. T-tests reveal that *A. h. herodias* averages significantly shorter in wing length than all but two other North American populations, the exceptions being males of *A. h. fannini* and *A. h. "treganzai."* By contrast, the latter is significantly shorter-winged than all but one of the *A. h. wardi* populations, that being the small Texas sample. All other population differences in this character are insignificant, with clinal intergradation being smoother among females than males.

Tail length.—Nesting populations with the longest tails are 7.7% and 8.8% greater than those with the shortest in males and females, respectively. Means are smallest in *A. h. herodias* and become progressively and significantly larger in Texas/Florida populations of *A. h. wardi*, *A. h. "hyperonca" × A. h. fannini*, and *A. h. fannini* (Table 1). All other population differences in this character are insignificant, with rather mosaic intergradation occurring among both males and females.

Exposed culmen.—Nesting populations with the longest culmens are 29.4% and 31.9% greater than those with the shortest in males and females, respectively. Means are smallest in *A. h. fannini* and then *A. h. "hyperonca" × A. h. fannini*, each of which has a significantly shorter culmen than all other populations of the species (Table 1). Elsewhere, males average smallest in *A. h. herodias*, which differ significantly from those with the longest culmens in Florida, Texas, and eastern Mexican *A.*

h. wardi and *A. h. occidentalis*. However, these extremes intergrade circuitously through *A. h. "treganzai," A. h. "hyperonca"* and *A. h. "sanctilucae"* with a similar pattern of geographic variation, except that *A. h. occidentalis* has a significantly longer culmen than all but one *A. h. wardi* (*sensu lato*) population—that in eastern Mexico, which has a sample size of only one!

Tarsus length.—Nesting populations with the longest tarsi are 33.2% and 27.3% greater than those with the smallest in males and females, respectively. Means in males are shortest in *A. h. fannini* and then *A. h. "hyperonca" × A. h. fannini*, each of which has a significantly shorter tarsus than all other populations of the species (Table 1). The same is true with females, except that the means of those two populations are essentially identical. Elsewhere, males and females average smallest in *A. h. herodias* and *A. h. "hyperonca"* which differ significantly from those with the longest tarsi in Florida *A. h. wardi* and *A. h. occidentalis*. However, these extremes intergrade circuitously through *A. h. "treganzai," A. h. "sanctilucae"* and Texas/eastern Mexican populations of *A. h. wardi*.

Discussion and Conclusions

Based on these findings, I recommend recognizing three subspecies among North American nesting populations of the Great Blue Heron, excluding the white-plumaged *A. h. occidentalis* of the Caribbean Basin.

The first is *Ardea herodias herodias* L., with its moderately gray plumage and a nesting range as outlined above (see Results section). This the most highly migratory of the subspecies, with birds regularly moving southward into Central America and the Caribbean and as far as Belize, Panama, Colombia, Venezuela, Curacao, and the Dominican Republic (also eastward to Bermuda). In addition, lesser numbers move elsewhere, including northward to Hudson Bay, northern Quebec, Anticosti Island, and Newfoundland (plus as a vagrant to Green-

Table 1.—Measurements in millimeters of mostly nesting season adult Great Blue Herons (*Ardea herodias*) from North America, with number, range (mean), and standard deviation.

Population	n	Wing chord	n	Tail	n	Culmen	n	Tarsus
<i>herodias</i> ¹	35	441-496 (470.0) SD 12.6	32	165-192 (177.4) SD 5.8	33	128-155 (144.1) SD 6.1	21	169-188 (179.8) SD 5.7
<i>wardi</i>	28	470-533 (493.0) SD 13.8	22	171-195 (182.7) SD 5.6	27	140-172 (154.6) SD 8.5	28	180-223 (202.8) SD 14.6
Florida		518		198		166		225
Type <i>wardi</i> ²	6	466-500 (485.5) SD 12.7	5	178-186 (182.8) SD (4.4)	6	148-165 (160.0) SD (6.9)	6	185-212 (199.0) SD (10.5)
Texas	7	475-498 (489.7) SD 9.7	7	176-189 (181.6) SD 4.5	7	154-164 (159.1) SD 3.0	7	184-212 (193.6) SD 8.7
Gulf Coast of Mexico	19	460-502 (485.6) SD 11.6	19	160-191 (179.7) SD 8.6	20	139-158 (149.7) SD 5.5	16	173-200 (188.7) SD 7.9
³ <i>sancitiluceae</i> ³	28	434-495 (476.0) SD 14.6	24	165-188 (178.9) SD 6.8	28	133-161 (146.5) SD 8.0	14	167-198 (183.9) SD 9.4
Baja California	31	474-516 (491.8) SD 11.4	29	174-201 (187.2) SD 6.4	31	133-160 (147.9) SD 6.6	29	164-203 (178.9) SD 7.7
⁴ <i>hyperonca</i> ⁴		500		193		156		195
Central and Southern California	29	460-508 (484.9) SD 12.2	25	180-208 (190.3) SD 6.4	30	120-149 (132.6) SD 7.2	26	147-180 (162.0) SD 7.2
Type <i>hyperonca</i> ²	7	458-488 (474.0) SD 10.8	7	182-198 (189.6) SD 5.4	7	116-133 (124.8) SD 6.2	7	142-164 (152.6) SD 9.7
<i>fannini</i> , <i>sensu stricto</i> ⁵	22	472-495 (480.1) SD 10.0	21	171-195 (182.5) SD 7.2	21	150-167 (159.7) SD 5.2	21	170-227 (201.2) SD 13.9
<i>occidentalis</i>								
<i>herodias</i>	35	431-480 (452.8) SD 9.2	34	161-188 (171.0) SD 6.0	32	124-145 (134.5) SD (5.0)	19	150-175 (166.5) SD 7.3

Table 1.—Continued.

Population	n	Wing chord	n	Tail	n	Culmen	n	Tarsus
<i>wardi</i>								
Florida	19	452–505 (476.2) SD 16.5	20	169–194 (178.4) SD 6.2	20	138–157 (144.0) SD 6.6	20	181–226 (193.8) SD 13.4
Texas	5	445–483 (470.6) SD 16.5	5	171–182 (177.2) SD 5.3	5	133–153 (142.6) SD 7.4	5	153–182 (170.4) SD 11.6
Gulf Coast of Mexico	1	465	1	171	1	157	1	182
" <i>sancitiluae</i> " ²	9	438–480 (461.2) SD 12.2	10	164–180 (173.0) SD 4.8	10	131–140 (138.1) SD 3.7	7	152–182 (170.8) SD 10.0
Baja California	47	432–491 (459.3) SD 13.7	46	160–192 (175.7) SD 6.9	47	123–156 (139.3) SD 6.7	22	155–185 (168.6) SD 7.3
" <i>hyperonca</i> " ²	29	450–485 (468.6) SD 10.3	26	168–190 (178.5) SD 5.7	30	123–152 (134.2) SD 7.2	28	152–184 (166.1) SD 7.2
Central, South California	22	445–495 (463.5) SD 11.8	22	167–190 (180.0) SD 5.6	21	118–132 (125.9) SD 4.9	22	142–163 (152.6) SD 7.1
<i>fannini</i>	7	459–489 (467.8) SD 11.0	7	184–195 (186.8) SD 5.4	7	104–126 (117.4) SD 7.1	7	146–157 (151.8) SD 3.3
<i>fannini, sensu strictu</i> ⁵	14	445–510 (466.4) SD 17.8	15	160–185 (172.8) SD 7.2	14	142–172 (154.0) SD 9.0	15	167–226 (192.9) SD 16.0
<i>occidentalis</i>								

¹ Connecticut, Maine, Massachusetts, New York, Indiana, Wisconsin, Michigan, North Dakota, Maryland, Virginia, North Carolina, South Carolina.

² Measurements from Oberholser (1912).

³ Idaho, Oregon, Utah, California, Arizona, New Mexico.

⁴ Southern British Columbia and coastal Washington.

⁵ Queen Charlotte Islands and coastal Alaska, north to Prince William Sound.

land), and west to California, Arizona, New Mexico, and Colorado. *A. h. adoxa* and *A. h. olgista* of Oberholser (1912) and *A. h. lessoni* Wagler were based on migrant *A. h. herodias*. Oberholser restricted the type locality of *A. lessoni* to the Valley of Mexico. However, there are no records of the species ever having nested in the Valley, and Payne (1979) was correct in just citing Mexico as the type locality. Hellmayr and Conover (1948) erroneously placed *A. h. olgista* in the synonymy of *A. h. hyperonca*. However, the wing chord of the type (433 mm) is far too short for that population and is even shorter for *A. h. herodias*! It is also darker, as in the nominate population.

The second subspecies recognized here is the pale *A. h. wardi*, which includes *A. h. "terganzai," A. h. "hyperonca,"* and *A. h. "santilucae."* Payne (1979) wrote in a footnote (p.198) "The type of *wardi* was taken on 5 January 1881. It is not known whether this was a local breeding bird or a wintering bird from a more northern population." There is no doubt that it was from the local population. The type of *A. h. wardi* is a very large bird (Oberholser 1912, Table 1), larger in all measurements than any male *A. h. herodias*, and it has longer tail, culmen, and tarsus measurements than any other male *A. h. wardi*. Size is largest in the southeast (Table 1) and smallest in the Great Basin region (*A. h. "terganzai"*), and only extremes can be identified based on measurements (Dickerman 1992, 2002). Oberholser described *A. h. "hyperonca"* as the color of *A. h. herodias*, but larger. The type is from northern California and is somewhat intermediate towards *A. h. fannini* and indeed inseparable from *A. h. herodias* in color, but it is larger than the largest male of *A. h. fannini* or of *A. h. herodias* (Table 1). However, specimens from central California in the California Academy of Science and the Museum of Vertebrate Zoology labeled *A. h. hyperonca* are inseparable in color from a topotype of *A. h. terganzai*, from early nesting season specimens from southern New Mexico and south

Texas, or from a midwinter specimen of *A. h. wardi* from Florida.

Contra Payne's comment on clinal variation in size in the east (1979), there are not enough nesting colony or even nesting season specimens yet available to fully document a cline. As mentioned earlier, there are no nesting season adult males from Delaware, Virginia, West Virginia or Kentucky; only single males from Maryland, Tennessee, South Carolina, and Alabama; and only two from North Carolina. Indeed the best clinal variation in size is on the west coast, with an increase in culmen and tarsal length from *A. h. fannini* in the north, through an intermediate population in southern British Columbia and Washington, to the long-billed, long-legged *A. h. "hyperonca"* population of California (Dickerman 2004).

A. h. wardi may be separated from *A. h. herodias* as follows:

1. Neck of *A. h. herodias* darker, colder "vinaceous" gray vs. "warmer," paler neck of *A. h. wardi*.
2. Chestnut of mid-ventral neck stripe is more extensive and darker in *A. h. herodias*, and usually extends to the area behind and below the eye, thus faintly outlining the white of the throat; in *A. h. wardi* the area behind and below the eye is always white; chestnut of mid-neck is reduced and paler.
3. Dorsum and wings are darker in *A. h. herodias* and paler in *A. h. wardi*.

The third subspecies recognized here is *A. h. fannini*, which differs from *A. h. herodias* in being darker gray in color and in having the exposed culmen and tarsus significantly shorter and tail longer (plus wing in males, Dickerman 2004). *A. h. fannini* differs in being notably much darker gray than *A. h. wardi* (sensu lato), and in having the exposed culmen and tarsus significantly shorter. In addition, males have significantly shorter wings than all *A. h. wardi* populations except *A. h. "terganzai"* on the interior western U.S. *A. h. fannini* seems to

differ from other Great Blue Herons in that it perforce fishes much of the time from rocks rather than wading, as do the other longer-legged subspecies. It appears to be largely resident within its nesting range (contra A.O.U. 1957), with the only extralimital specimen being an adult taken at Wainwright on the Arctic coast of Alaska (Brock 1959). I know of no specimens of *A. h. fannini* (as here defined) from south of the Queen Charlotte Islands. *A. h. fannini* intergrades southward with *A. h. "hyperonica"* and perhaps *A. h. "treganzai"* (both here = *A. h. wardi*) in southwestern British Columbia (including Vancouver Island) and western Washington (Dickerman 2004). For example, that population is paler gray as in *A. h. wardi* (sensu lato), but it is closer to *A. h. fannini* in the shorter exposed culmen, tarsus, and male wing chord.

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A new species of *Microgale* (Lipotyphla: Tenrecidae: Oryzorictinae) from the Forêt des Mikea of southwestern Madagascar

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Abstract.—A new species of *Microgale*, *M. jenkinsae* (Lipotyphla: Tenrecidae), is described based on two specimens taken during an early 2003 biological survey of the Forêt des Mikea in southwestern Madagascar. It is distinguished from other congeners by numerous pelage, cranial, and dental characters. *M. jenkinsae* is the fourth known species in this genus confirmed to occur in the dry western and southern forests of the island. The Forêt des Mikea, the only site *M. jenkinsae* is known from, is the last remaining block of a distinctive forest habitat and is under considerable threat from human habitat degradation. Action needs to be taken to protect this unique region.

Résumé.—Une nouvelle espèce de *Microgale*, *M. jenkinsae* (Lipotyphla: Tenrecidae), est décrite à partir de deux spécimens récoltés au cours d'un inventaire biologique mené au début de l'année 2003 dans la forêt des Mikea située au sud-ouest de Madagascar. On le distingue de ses autres congénères par divers caractères de pelage, crâniens et dentaires. *M. jenkinsae* est la quatrième espèce connue de ce genre dont la présence est confirmée dans les forêts sèches de l'ouest et du sud de l'île. La forêt des Mikea, le seul site d'où *M. jenkinsae* a été rapporté, est le dernier bloc d'un habitat forestier distinctif qui est cependant extrêmement menacé par la dégradation de l'habitat perpétrée par l'homme. Des actions doivent être prises pour protéger cette région unique.

On the island of Madagascar there is an endemic family of Lipotyphla, known as the Tenrecidae, that represents one of the most remarkable adaptive radiations found in living mammals (Olson & Goodman 2003). As currently circumscribed, *Microgale* (shrew tenrecs) a tenrecid genus in the subfamily Oryzorictinae, comprises 18 species (Jenkins 2003). On the basis of biological inventories and associated museum studies conducted over the past few decades, seven species of *Microgale* new to science have been named (Jenkins 1988, 1992, 1993; Jenkins et al. 1996, 1997; Goodman & Jenkins 1998; Jenkins &

Goodman 1999), although one of these, *M. pulla*, has since been synonymized (Jenkins et al. 1997). Subsequent to the publication of MacPhee's (1987) taxonomic revision of the genus *Microgale*, there has been a renewed interest in the small mammals of Madagascar. With the advent of pit-fall devices to trap these animals, there has been a massive increase in available shrew tenrec specimens. This has led to a series of publications refining some of MacPhee's taxonomic conclusions and a greater understanding of intra-specific, particularly age related, and inter-specific variation amongst these animals. As witnessed by the recent



Fig. 1. Map showing the collection locality of *Microgale jenkinsae* in the Forêt des Mikea, the forested zone between Morombe and Manombo, in southwestern Madagascar (expanded inset).

description of six new valid shrew tenrec taxa (an increase of 33%), *Microgale* taxonomy is in flux as a result of ongoing biological inventories and molecular and morphological studies.

Of the currently recognized 18 species of *Microgale*, 15 are restricted to the eastern and northern moister portions of Madagascar where they occur in either forests or marshes. Of the remaining three species, two have been collected over the past few decades in the dry western forests. These include *M. brevicaudata*, which occurs from the northern foothills of the Marojejy Massif in the northeast, a zone of humid forest but probably with a marked dry season, north to Vohemar and the region of Antsiranana at the north end of Madagascar, and then south along the west portion of the

island to at least the Onilahy River near Toliara (Goodman et al. unpublished; Fig. 1). The second species, *M. nasoloi*, is known from two inland isolated forests in southwestern Madagascar in the vicinity of Sakaraha—the Analavelona Massif and the Forêt de Vohihasia (Jenkins & Goodman 1999; Fig. 1). *M. longicaudata* is the third species falling into this group and has been collected from both eastern humid forests and western dry forests. However, *M. longicaudata*, as currently defined, includes several cryptic species and will soon be revised (Olson et al. in press).

MacPhee's (1987, Fig. 13) map of collecting localities for *Microgale* included 31 sites in the eastern humid forest where a total of nine species were trapped, two sites in the western dry deciduous each with sin-

gle species (one based on owl pellets), and three sites in the southern spiny-bush each with two species (all based on owl pellets). Although considerable advances have been made concerning the species richness and distribution of shrew tenrecs since MacPhee's important revision, these data indicate a greater diversity of this group in the more mesic portions of the island. Recent biological inventories of the western and southern forests of Madagascar have largely upheld this view. However, during a 2003 survey of the Forêt des Mikea, the region between Morombe and Manombo (Fig. 1), we captured a *Microgale* that represents a previously undescribed species of shrew tenrec.

Materials and Methods

Our small mammal collection made in the Forêt des Mikea contains two specimens of *Microgale*, and in order to determine their taxonomic identity, we have consulted material housed in several natural history museums, which include: **BMNH**—The Natural History Museum, London (formerly British Museum of Natural History); **FMNH**—Field Museum of Natural History, Chicago; **MNHN**—Muséum National d'Histoire Naturelle, Paris; and **UADBA**—Université d'Antananarivo, Département de Biologie Animale.

Five external measurements in millimeters were taken from our two specimens before preparation and included: total length, head and body length, tail length, hind foot length (not including claw), and ear length. Mass was measured with the use of a spring balance and recorded in grams.

An additional six cranial and two dental measurements were taken using a digital calipers accurate to the nearest 0.1 mm. These measurements, and their definitions, are: **breadth of braincase**: the greatest distance measured across the hamular processes of the squamosals to the mastoid bullae; **greatest length of skull**: the distance between the tips of the nasals and the poste-

rior most portion of the cranium; **interorbital breadth**: the minimum distance across the frontal bones between the orbital fossae; **length of mandibular tooth row**: the maximum distance from distal surface of the third molar to anterior surface of the first incisor; **length of nasal**: the maximum distance from the posterior extension of the nasals to their anterior tip; **length of palate**: the shortest distance between the tip of the postpalatal spine and anterior surface of the first upper incisor; **length of maxillary tooth row**: the maximum distance from distal surface of the third molar to anterior surface of the first incisor; and **zygomatic breadth**: the maximum span between the zygomatic processes of the maxillae.

Tooth abbreviations include: I = incisor, d = deciduous, C = canine, PM = premolar, and M = molar. Upper case tooth abbreviations with superscript are used for upper teeth and lower case abbreviations with subscript for lower teeth. Cranial and dental nomenclature follows Hershkovitz (1977) and MacPhee (1987).

After comparison of the two specimens collected in the Forêt des Mikea to all described forms of *Microgale*, these individuals could not be allocated to any known form and are therefore described as a new species.

Microgale jenkinsae, new species

Fig. 2, 3, Tables 1, 2

Holotype.—FMNH 176215, sub-adult male, collected on 18 February 2003 by Steven M. Goodman and Voahangy Soarimalala, field number SMG 13489. The specimen was preserved as a round study skin, with associated skull and partial postcranial skeleton. Tissue samples were preserved in EDTA. The skin is in good condition with a small hole in the left thigh. The skull and partial postcranial skeleton are intact. Dental age is sub-adult with I³ still erupting and matches MacPhee's (1987) eruption pattern stage 1. The basispenoid-basioccipital sutures are unfused.



Fig. 2. Photograph of the holotype of *Microgale jenkinsae* (FMNH 176215), a sub-adult male collected on 18 February 2003 in the Forêt des Mikea, 9.5 km west Ankioloaka, 22°46.7'S, 43°31.4'E. (Photograph taken by S. M. Goodman.)

Table 1.—External measurements (in millimeters) and weight (in grams) of *Microgale jenkinsae* and other species of small *Microgale*. Measurements presented as mean \pm standard deviation (minimum–maximum, n). For samples of two or fewer specimens only the measurements are presented.

Species	Total length	Head and body length	Tail length	Hind foot length	Ear length	Weight
<i>M. jenkinsae</i> (Holotype FMNH 176215)	143	62	79	15	18	4.9
<i>M. jenkinsae</i> (FMNH 176154)	147	59	81	14	18	5.3
<i>M. nasoloi</i> (Holotype FMNH 156187)	141	81	53	13	16	14.0
<i>M. pusilla</i>	127.4 \pm 6.16 119–136, n = 7	51.4 \pm 2.70 47–56, n = 7	69.9 \pm 4.18 65–77, n = 7	11.4 \pm 0.53 11–12, n = 7	11.4 \pm 0.98 10–13, n = 7	3.5 \pm 0.40 3.1–4.2, n = 7
<i>M. parvula</i>	117.7 \pm 5.83 110–128, n = 11	57.2 \pm 4.17 51–64, n = 11	58.4 \pm 4.39 53–66, n = 11	9.6 \pm 0.50 9–10, n = 11	8.6 \pm 0.45 8–9, n = 11	3.2 \pm 0.56 2.1–4.1, n = 11
<i>M. brevicaudata</i>	115.7 \pm 6.68 107–129, n = 13	41.9 \pm 0.35 63–74, n = 13	41.9 \pm 5.92 35–41, n = 13	12.4 \pm 0.96 11–14, n = 13	13.7 \pm 1.32 12–16, n = 13	8.9 \pm 1.59 6.3–12, n = 11
<i>M. fotsifotsy</i>	159.3 \pm 6.34 150–169, n = 11	70.8 \pm 6.71 64–85, n = 10	85.8 \pm 3.98 80–93, n = 12	15.9 \pm 0.90 15–17, n = 12	16.1 \pm 0.67 15–17, n = 12	9.4 \pm 2.97 6.8–15, n = 10

External measurements are: total length 143 mm, head and body length 62 mm, tail length 79 mm, hind foot length (without claw) 15 mm, and ear length 18 mm. The animal weighed 4.9 gm (Table 1).

Type locality.—Madagascar: Province de Toliara, Forêt des Mikea, 9.5 km west Ankiloaka, 22°46.7'S, 43°31.4'E, elevation about 80 m above sea level (Fig. 1). The site is about 17 km inland from the Mozambique Channel.

Habitat.—The holotype was obtained in partially disturbed dry transitional deciduous forest growing on red sands. It was captured in a pitfall trap placed in relatively dense understory composed primarily of *Xerophyta* (Velloziaceae), small bushes, and succulent Euphorbiaceae.

Diagnosis.—A relatively small member of the genus *Microgale* with a head and body length of 59–62 mm, tail length of 79–81 mm, and greatest skull length of 18.7–18.8 mm. Deciduous PM² is simple, caniniform, and single-rooted. The color of the dorsal pelage is mixed agouti and the venter is gray with white-tipped fur. The ears are notably long (18 mm) for a shrew tenrec of this size.

Paratype.—FMNH 176154 (SMG 13492), sub-adult female from the same locality as the holotype, collected 19 February 2003, and prepared as fluid preserved specimen with extracted skull. The dental eruption pattern fits MacPhee's (1987) stage 1. Tissues saved in EDTA.

Distribution.—*Microgale jenkinsae* is known only from the type locality in the Forêt des Mikea, southwestern Madagascar.

Description.—A small species of *Microgale* having a tail longer than the head and body (Fig. 2). The dorsal fur is relatively dense and soft. Pelage from the level of the ears to the base of the tail (including the flanks), is a mixture of completely black and tannish-brown hairs, or those that are tannish-brown along most of their length and black-tipped, imparting an agouti appearance. The agouti pattern runs anteriorly from the level of the ears to the eyes. An-

Table 2.—Cranial and dental measurements (in millimeters) and weight (in grams) of *Microgale jenkinsae* and other species of small *Microgale*. Measurements presented as mean \pm standard deviation (minimum – maximum, n). For samples of two or less specimens only the measurements are presented.

Species	Greatest length of skull	Zygomatic breadth	Interorbital minimum
<i>M. jenkinsae</i> (Holotype FMNH 176215)	18.8	6.9	4.0
<i>M. jenkinsae</i> (FMNH 176154)	18.7	6.9	4.0
<i>M. nasoloi</i> (Holotype FMNH 156187)	23.2	8.3	5.1
<i>M. pusilla</i>	16.6 \pm 0.71	6.1 \pm 0.24	3.4 \pm 0.17
	15.7–17.5, n = 7	5.6–6.3, n = 8	3.1–3.7, n = 9
<i>M. parvula</i>	16.5 \pm 0.47	5.1 \pm 0.23	3.7 \pm 0.19
	15.5–17.0, n = 12	4.7–5.4, n = 12	3.3–4.0, n = 12
<i>M. brevicaudata</i>	20.7 \pm 0.79	8.0 \pm 0.51	4.8 \pm 0.27
	19.0–21.9, n = 13	7.2–8.8, n = 13	4.3–5.2, n = 14
<i>M. fotsifotsy</i>	21.1 \pm 0.76	8.2 \pm 0.32	5.0 \pm 0.18
	20–22, n = 12	7.7–8.7, n = 11	4.6–5.2, n = 12

terior and lateral to this band, the pelage is distinctly paler in coloration, with the majority of hairs being pale tan to silvery-white. Individual hairs along the dorsum measure 4–5 mm. Guard hairs are medium gray in color. The ventral pelage, with the exception of the portion surrounding the gular to mental regions, is gray based with off-white tips. The difference between the ventral and dorsal color pattern is pronounced, but grade into each other laterally instead of forming a well-demarcated line. Upper surfaces of fore feet and hind feet are covered with short silver-white fur, which on the hind feet extends slightly beyond the claws as unguis tufts. The color of mystacial and rhinarial vibrissae vary from either completely beige-white or black, to black at the base and gradually becoming beige-white at the tips. Mystacial vibrissae reaching up to 20 mm and rhinarial vibrissae about 5 mm in length. Pinnae are notably long (18 mm) for a small *Microgale*, dark brown in color, and covered internally and externally with fine, silvery-gray fur.

The hind foot is relatively long (14–15 mm) for a small species of *Microgale* (Table 1). The first digit of the hind foot is less than one-third the length of the second dig-

it. The second and third digits are subequal in length, with the fourth digit slightly longer. The fifth digit is about two-thirds the length of the fourth. There are five plantar tubercles and, based on FMNH 176154 (SMG 13492), these are located at the base of digit 1 and digit 5, in intermediate positions between the base of digits 2 and 3 and digits 3 and 4, and notably reduced as distal hypothenar and proximal thenar pads.

The skin of the tail is dark brown dorsally and tannish-brown ventrally, and forming a relatively well-demarcated line laterally separating these two surfaces. The tail is clothed with very fine silvery-white fur, which becomes slightly denser at the tip. In FMNH 176154 (SMG 13492) the last 10 mm of the tail is mottled dark-white.

The skull is relatively short (Table 2), slightly flattened dorsolaterally, with a constricted interorbital region. The rostrum is relatively short and tapers anteriorly. The anterior portion of frontals consist of two slightly concave plates divided at the mid-dorsal line and the posterior portion is slightly-domed. The braincase has a slightly bulbous parietal and interparietal, a rounded supraoccipital and occipital, and a weakly defined occipital crest. Dentally the holotype is a sub-adult with the erupting crown

Table 2.—Extended.

Braincase width	Length of nasal	Length of palate	Length of maxillary toothrow	Length of mandibular toothrow
8.4	8.9	8.1	8.2	8.0
8.2	8.0	7.7	8.2	8.1
9.2	10.3	9.8	10.1	9.7
6.9 ± 0.11	7.0 ± 0.37	7.3 ± 0.34	7.4 ± 0.40	7.0 ± 0.36
6.8–7.1, n = 7	6.4–7.5, n = 8	6.8–7.8, n = 8	6.7–7.7, n = 8	6.5–7.4, n = 7
6.8 ± 0.18	7.3 ± 0.22	7.3 ± 0.23	7.4 ± 0.28	7.2 ± 0.19
6.5–7.0, n = 12	6.9–7.7, n = 12	6.9–7.6, n = 11	6.7–7.6, n = 12	7.0–7.6, n = 12
8.7 ± 0.27	9.3 ± 0.62	9.3 ± 0.57	9.3 ± 0.51	8.8 ± 0.35
8.2–9.1, n = 13	8.4–10.5, n = 14	8.2–10.2, n = 14	8.3–10.2, n = 14	8.1–9.4, n = 14
9.3 ± 0.26	9.4 ± 0.45	9.8 ± 0.39	10.0 ± 0.43	9.6 ± 0.47
8.9–9.7, n = 12	8.9–10.3, n = 12	9.1–10.2, n = 12	9.3–10.7, n = 12	9.0–10.5, n = 12

of P³ present and all antemolars are deciduous, fitting stage 1 in MacPhee's (1987) tooth eruption pattern. The upper toothrows from dI¹ to dPM² slightly converge anteriorly. The lingual margins of dPM³ and M¹ to M³ are roughly parallel. Palatal foramina are present. Pterygoids are relatively short and broad, and the pterygoid processes winged-shape and curved mid-ventrally. The glenoid fossa is shallow and narrowly curved. The mandibles are slender, the coronoid processes are relatively narrow at their bases and pointed dorsally, and the angular processes are short and narrow, and the dorsal surface is not expanded (Fig. 3).

The dentition is not markedly robust (Fig. 3). There is a gap between the dI¹ and dI² and between the dpm₂ and dpm₃. The first upper incisor (dI¹) is small, bicuspid (bidentate), and the distostyle moderately well developed; the dI² with approximately the same crown height as dI¹, the tricuspid (tridentate) has the anterior accessory cusp more developed than distostyle; the dI³ is one-half crown the height of dI² and reaching just beyond the level of the distostyle of the dI², the bicuspid with small distostyle; the dC¹ robust with crown height reaching that of the dI², with small accessory anterior cusp and pronounced distos-

tyle; the dP² small, equal in crown height to distostyle of the dC¹; the dP³ is large, slightly greater in crown height than the dC¹, lingual ledge with well-developed protocone, and the parastyle, mesiostyle, anterior ectostyle, and distostyle present; the dP⁴ is large, longer in crown length than M¹ to M³, with elongated paracone, the lingual ledge with a protocone more developed than M¹ to M³, anterior ectostyle approximately same length as paracone, and the parastyle, mesiostyle, and distostyle present; the M¹ and M² large, parastyle, mesiostyle, anterior ectostyle, and distostyle present, and centro-buccal cleft slightly more prominent in M² than M¹; the M³ is reduced in size and compressed anterioposteriorly. The first lower incisor (di₁) is large, slightly shorter in crown length to the di₂, the posterior accessory cusp well-developed; the di₂ is large, the posterior accessory cuspid well-developed; the di₃ is small, about one-half the crown length of lower (deciduous) canine; the dc is large, posterior accessory cuspid present, no anterior accessory cuspid; the dpm₂ is small, slightly shorter than posterior accessory cuspid of lower canine, poorly developed anterior accessory cuspid and posterior accessory cuspid, and single-rooted; the dpm₃ is moder-



Fig. 3. Views of the cranium and mandible of the holotype of *Microgale jenkinsae* (FMNH 176215): upper left, dorsal view; upper right, ventral view; lower center lateral view of cranium and mandible. (Photograph taken by J. Weinstein, image number Z94379_05d.)

ate in size, slightly longer in crown height than the pm_2 , moderately developed anterior accessory cuspid and posterior accessory cuspid; the dpm_4 is large, equal in crown height (formed by prominent protoconid) to m_1 , the anterior accessory cuspid and posterior accessory cuspid present; the m_1 and m_2 are large, the m_1 slightly subequal in crown height to the m_2 , both with well-developed protoconid, anterior accessory cuspid, and posterior accessory cuspid, and slightly elongated anterobuccal cingulum; the m_3 is large and equal to m_3 in crown height, and with a well-developed protoconid, anterior accessory cuspid, and prominent posterior accessory cuspid, and slightly elongated anterobuccal cingulum. Given that the individuals of *M. jenkinsae* are stage 1 sub-adults, no information can be provided on the adult dentition or antemolar replacement pattern of this species.

Comparisons.—The fact that our two specimens of *Microgale jenkinsae* are stage 1 sub-adults complicates comparisons to a certain degree. However, sub-adult members of this genus, at this stage of dental eruption, exhibit the pelage coloration of adults and, in general are similar to adults in external measurements (MacPhee 1987; Jenkins et al. 1996, 1997).

M. jenkinsae is readily distinguished externally from other relatively small members of this genus by pelage coloration and measurements. The contrasting agouti dorsum and grizzled-gray venter is unique among small shrew-tenrecs. The pelage pigmentation in *M. nasoloi* is a relatively uniform gray; *M. fotsifotsy* has less gray in the dorsum than *M. jenkinsae* and is notably darker; *M. parvula* has a dark brown dorsum and dark grayish-brown ventrum; *M. brevicaudata* is medium-brown dorsally and dull grayish-brown ventrally; and in *M. longicaudata* and *M. pusilla* the dorsum is a mixed light brown and medium brown and ventrum gray broadly edged with dark tan-brown. Further, there is no overlap in tail measurements between *M. jenkinsae* and any of these taxa, with the exception of

M. fotsifotsy, but *M. jenkinsae* can be differentiated from it based on pelage characteristics, a non-white-tipped tail, upper surfaces of the feet clothed with short silver-white fur, and several external measurements (Table 1).

The presence of a single-rooted second lower premolar separates *M. jenkinsae* from all other named small members of the genus *Microgale*, with the exception of *M. pusilla*. In the latter species the root form is identical in individuals with deciduous and permanent antemolar dentitions. *M. pusilla* is notably smaller than *M. jenkinsae* in all external, cranial, and dental measurements (Tables 1 and 2), and is separable based on pelage characters.

A generic revision of all members of *Microgale* is currently in preparation and includes molecular characters (Olson and Goodman, in prep.). The results of this study will be presented elsewhere and will address aspects of the phylogenetic position and sister-taxa relationships of *M. jenkinsae*.

Etymology.—This new species of *Microgale* is named after Paulina D. Jenkins of The Natural History Museum, London, for her important contributions to Tenrecidae systematics.

Discussion

Ecology.—*Microgale jenkinsae* is currently known only from the Forêt des Mikea, between Morombe and Manombo (Fig. 1), in the southwestern portion of Madagascar, a zone of transitional dry deciduous and spiny bush habitat (Seddon et al. 2000; Goodman and Soarimalala in press). This region receives, on average, about 400–500 mm of rainfall per year (Chaperon et al. 1993), with probably more rainfall in the inland higher ground than along the coastal plain. Differences in forest types within the Forêt des Mikea tend to follow this pattern, with more deciduous forest on the slightly higher ground away from the coast and spiny bush along the coastal plain.

The climax vegetation of the dry deciduous forest has been characterized as being dominated by the genera *Dalbergia*, *Commiphora*, and *Hildegardia* (Humbert 1965). The formation has a canopy 10 to 15 m high, sometimes reaching 20 m, with a open medium stratum and diffuse undergrowth. All trees and most of the shrubs shed their leaves in the dry season.

The vertebrate communities inhabiting the Forêt des Mikea are similar to other arid portions of the island, although there are apparently several strict and regional endemic vertebrates (e.g., the reptiles *Furcifer belalandaensis* and *Paroedura vahiny*, the birds *Uratelornis chimaera* and *Monias benschi*). The known small mammal community consists of six Lipotyphla (*Tenrec ecaudatus*, *Setifer setosus*, *Echinops telfairi*, *Geogale aurita*, *Microgale jenkinsae*, and *Suncus madagascariensis*), one introduced murine rodent (*Rattus rattus*), and two endemic Nesomyinae (*Macrotarsomys* sp. and *Eliurus myoxinus*) (Carleton and Schmidt 1990; Soarimalala and Goodman 2004; Goodman and Soarimalala in press).

Trapping.—During the survey of the Forêt des Mikea, six sites were visited and systematically trapped using standard live and pit-fall traps (for more details on techniques see Goodman & Carleton 1996; Goodman et al. 1996). Pit-fall devices have been particularly useful for sampling Lipotyphla difficult to trap by other methods. For example, the only known specimens of another western *Microgale*, *M. nasoloi*, were captured with this technique (Jenkins and Goodman 1999). Three pit-fall lines, each composed of 11 12-liter buckets placed 10 m apart, were installed at each of the six survey sites. There was considerable variation between sites in trap success and species diversity. At site 1, 20 individuals (*Tenrec*, *Setifer*, *Echinops*, *M. jenkinsae*, and *Geogale*) were caught in 198 bucket nights between 14 and 19 February 2003. At site 2, 10 individuals (*Echinops* and *Geogale*) were obtained in 198 bucket nights between 21 and 27 February 2003.

At site 3, 5 individuals (*Tenrec*, *Echinops*, *Rattus rattus*, and *Geogale*) were taken in 132 bucket nights between 2 and 5 March 2003. At site 4, only 4 individuals (*Tenrec*, *Geogale*, and *Suncus madagascariensis*) were trapped in 165 bucket nights between 8 and 12 March 2003. At site 5, nothing was captured in 198 bucket nights between 14 and 19 March 2003. At site 6, 7 individuals (*Geogale*) were captured in 132 bucket nights between 22 and 25 March 2003. This level of faunal heterogeneity (as reflected by trapping-success) may be related to microhabitat differences between the sites, but further research is needed to test this hypothesis.

Natural history.—Little definitive information can be gleaned on the natural history of *Microgale jenkinsae* on the basis of two specimens, and the following extrapolations are tentative. Using foot structure and the context in which this species was trapped, it is terrestrial. Both specimens were taken in a portion of the Forêt des Mikea dominated by more dry deciduous forest than by spiny bush habitat. Several of the other sites inventoried during the Forêt des Mikea survey tended to be dominated by spiny bush habitat. The two *M. jenkinsae* were obtained in different pitfall lines installed in portions of the forest having a relatively dense understory—one line was dominated by Gramineae associated with the regeneration of an old forest exploitation track and the other line in a microhabitat with a dense growth of *Xerophyta* (Velloziaceae) mixed with other low-growing plants and some succulent Euphorbiaceae.

An analysis of soil samples taken at each of the 18 pitfall lines installed during the Forêt des Mikea survey indicate that at site 1, where the two specimens of *M. jenkinsae* were collected, the average percent carbon in the soil was higher (1.9%, range 0.98–2.3%) than four of the other five sites (all less than 0.9% carbon). The outlier is site 2 which had a slightly higher soil carbon content (2.4%, range 0.08–4.5%) than site

1. Given that shrew tenrecs are believed to be primarily insectivorous, one may expect that their distribution would be correlated with soils relatively rich in organic material, which in turn would support a higher density and diversity of invertebrates.

Both specimens are dentally sub-adults, and, thus, it is not unexpected that they did not show any signs of reproductive activity. However, shrew tenrecs with deciduous antemolar dentitions can be reproductive (e.g., Jenkins et al. 1996). Our survey was conducted during the rainy season, a period of the year that normally coincides with breeding activity in small mammals in this area of the island (Ganzhorn et al. 1996; Randrianjafy 2003).

Paleoecological implications.—Remains of *Microgale pusilla* have been reported in disintegrated owl pellets of unknown age, but by extrapolation almost certainly Holocene, from the sites of Lelia and Anjohipaty in southwestern Madagascar (MacPhee 1986, 1987), a zone of xerophytic spiny bush habitat on an exposed limestone substrate. *M. pusilla* is considered to be an inhabitant of the more mesic portions of the island, including the eastern humid forest and central highlands. More recently bone remains of *M. pusilla* have been identified in owl pellets collected in the capital city of Antananarivo, at least 80 km from the nearest intact natural forest block, and it is assumed that this species may live in surrounding marshlands and rice fields (Goodman et al. 1997a). At several sites in the central highlands it has been captured in marshlands within close vicinity to natural forest (Goodman et al. 2000a, Soarimalala et al. 2001). Thus, its occurrence in owl pellets in southwestern Madagascar can be interpreted in at least two ways: this species is a generalist and is able to live in a variety of ecological conditions from humid forests to marshlands to xerophytic bush—however, on the basis of recent inventories of the drier portions of the island there is no evidence of its occurrence in this latter habitat—or the undated owl

pellets collected in the southwest are from a past geological period when this region of Madagascar was distinctly more mesic.

The specimens of *M. pusilla* described by MacPhee (1986, 1987) from Lelia and Anjohipaty were deposited in the Service de Paléontologie collection at the Université d'Antananarivo. A detailed search of that collection, however, did not uncover these specimens. Nevertheless, a comparison of our material of *M. jenkinsae* to the illustrations and description of these specimens (MacPhee 1986) indicates considerable similarity in size, morphology, and dental structure. Most important in this regard is that dpm_2 (in *M. jenkinsae* and *M. pusilla*) and pm_2 (in *M. pusilla*) are simple in coronal structure and single-rooted, characters used to separate *M. pusilla* from all other small members of this genus before our recognition of *M. jenkinsae*. Further, on the basis of a scale provided with the line drawing of the Anjohipaty mandible (MacPhee 1986, Fig. 5), the approximate lower tooth-row length is 18.2 mm, which is within the range of *M. jenkinsae*, but notably larger than *M. pusilla* (Table 2). We strongly suspect that these specimens, reported as *M. pusilla*, may be referable to *M. jenkinsae*.

Recent biological surveys of the Parc National de Tsimanampetsotsa (Fig. 1), formerly under the statute of a Réserve Naturelle Intégrale, did not find any species of *Microgale* living in this protected area (Goodman et al. 2002), which is relatively close to Lelia and Anjohipaty. Our small mammal surveys in the Forêt des Mikea at six different sites, with a minimum of 132 pit-fall nights per site, yielded a total of 1023 pit-fall nights, yet only two individuals of *M. jenkinsae* were captured, both at the first site. This would indicate that this species is either rare or difficult to capture and presumably occupies specific microhabitats. The important point here is that before significant paleoenvironmental inferences can be made associated with the presence of certain taxa known only as subfossils, it is critical that detailed biological in-

ventories be conducted in the general region of the paleontological site to thoroughly document the extant fauna.

Conservation.—Historically, most field efforts associated with the exploration and documentation of Madagascar's unique fauna have been in the humid forests on the eastern, central, and northern portions of the island. Further, there is a preponderance of reserves and parks protecting this biome as compared to the drier western and southern regions of the island (ANGAP 2001). On the basis of several recent biogeographic analyses of small mammals and birds, species turnover along the nearly 1200 km long eastern humid forests of the island is relatively low (Goodman et al. 1997b, 2000b). A number of endemic species in this biome have broad distributions, many extending the complete length of this habitat. More recent biological surveys of Madagascar's western deciduous forests and southern spiny bush lands have revealed a previously unrecognized biota, including numerous terrestrial vertebrates. The growing realization is that levels of plant and animal species turnover along a latitudinal transect of western Madagascar is notably higher than the east, and this is probably related to a greater geological complexity and associated botanical communities in the west (Du Puy & Moat 2003).

The recent surveys of the Forêt des Mikea, which has no official protection, and forested regions to the north and south of this zone, are a case in point. Two undescribed species of mammals (*Microgale jenkinsae* and *Macrotarsomys* nov. sp.) have been discovered in the Forêt des Mikea that are unknown from any other region in the west. Further to the north, in the vicinity of the Bemaraha Plateau, there are at least two species of rodents that appear to be endemic to the region (Carleton et al. 2001). The recent discovery and description of *Microgale nasoloi* from unique forest formations in southwestern central Mada-

gascar seems to indicate another regional endemic with a very limited distribution.

The drier western and southern forests of Madagascar have been subjected to considerable anthropogenic degradation, perhaps greater than in the humid east (see Smith 1997, Dufils 2003). In areas such as the Forêt des Mikea, which was estimated in 1999 to contain forest cover in excess of 3700 km², habitat loss rates have increased over the past few decades associated with pressures in the form of selective logging, cattle pasture, hunting, and clearing for agricultural crops (Seddon et al. 2000). Given the levels of habitat heterogeneity and microendemism in the west, action needs to be taken to protect the remaining large blocks of natural habitat in this region. On the basis of recent exploration of the Forêt des Mikea this area should be given priority amongst the zones in need of rapid protection.

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Appendix 1

List of specimens of *Microgale* spp. examined during the course of this study.

Microgale parvula.—Province d'Antsiranana, Parc National de Marojejy [formerly Réserve Naturelle Intégrale de Marojejy], along tributary of Manantenina River, 8 km NW Manantenina, 14°26.2'S, 49°46.5'E, 450 m (FMNH 159681); Parc National de Marojejy [formerly Réserve Naturelle Intégrale de Marojejy], along tributary of Manantenina River, 10 km NW Manantenina, 14°26.0'S, 49°45.7'E, 775 m (FMNH 159682, 159683, 159684); Parc National de Marojejy [formerly Réserve Naturelle Intégrale de Marojejy], 11 km NW Manantenina, Antranohofa, 14°26.2'S, 49°44.5'E, 1225 m (FMNH 159685); Parc National de Marojejy [formerly Réserve Naturelle Intégrale de Marojejy], 10.5 km NW Manantenina, along tributary at head of Andranomifototra River, 14°26.4'S, 49°44.5'E, 1625 m (FMNH 159686). Province de Fianarantsoa, approx. 45 km S. Ambalavao, east bank Iantara River, along Ambalamanenjana-Ambatoboay trail, edge of Parc National d'Andringitra [formerly Réserve Naturelle Intégrale], 22°13'20"S, 47°01'29"E, 720 m (FMNH 151621); Parc National d'Andringitra [formerly Réserve Naturelle Intégrale d'Andringitra], approx. 43 km S. Ambalavao, junction of Sahavivarakay and Sahavatovy Rivers, 22°13'40"S, 47°00'13"E, 810 m (FMNH 151622); Parc National d'Andringitra [formerly Réserve Naturelle Intégrale d'Andringitra], approx. 38 km S. Ambalavao, on ridge east of Volotsangana River, 22°11'39"S, 46°58'16"E, 1625 m (FMNH 151623, 151723, 151794, 151801).

Microgale nasoloi.—Province de Toliara, Forêt de Vohibasia, 59 km northeast Sakaraha, 780 m,

22°27.5'S, 44°50.5'E (FMNH 156187); Forêt d'Analavelona, Antanimena, 12.5 km NW Andranoh-eza, 22°40.7'S, 44°11.5'E, 1050 m (FMNH 161576).

Microgale fotsifotsy.—Province de Fianarantsoa, Parc National d'Andringitra, 8.5 km SE Antanifotsy, Campement Andohan'Ambola, 22°10.273'S, 46°56.758'E, 1960 m (FMNH 165694, 165778, 165779); 2 km W. Andrambovato, along Tatamaly River, 21°30.7'S, 47°24.6'E, 1075 m (FMNH 170749); Forêt de Vinantelo, at foot of Mt. Ambodivohitra, 15.5 km SE Vohitrafeno, 21°46.6'S, 47°20.8'E, 1100 m (FMNH 170750); approx. 40 km S. Ambalavao, along Volotsangana River, 22°13'22"S, 46°58'18"E, 1210 m (FMNH 151646, 151647); Province de Mahajanga, western side of Anjanaharibe-Sud, 13.5 km SW Befin-gotra, 14°47.0'S, 49°26.5'E, 1200 m (FMNH 167428). Province de Toliara, Parc National d'Andohahela [formerly Réserve Naturelle Intégrale d'Andohahela], par-

cel I, 8 km NW Eminiminy, 24°37.55'S, 46°45.92'E, 440 m (FMNH 156569); Parc National d'Andohahela [formerly Réserve Naturelle Intégrale d'Andohahela], parcel I, 13.5 km NW Eminiminy, 24°35.04'S, 46°44.08'E, 1200 m (FMNH 156424); Parc National d'Andohahela [formerly Réserve Naturelle Intégrale d'Andohahela], parcel I, 15.0 km NW Eminiminy, 24°35.15'S, 46°43.85'E, 1500 m (FMNH 156570).

Microgale pusilla.—Province d'Antananarivo, 13 km NE Antananarivo, in *Tyto alba* pellets (FMNH 151606, 151607); 10 km SE Tsinjoarivo, Forêt de Mahatsinjo, Andasivodihazo, 19°40.7'S, 47°46.2'E, 1550 m (FMNH 166123, 166124, 166125); Réserve Spéciale d'Ambohitantely, 24 km NE Ankazobe, 18°10.1'S, 47°16.6'E, 1450 m (FMNH 165489). Province de Fianarantsoa, Manambolo Forest, Ambavafatra, along Andohabatotany River, 17.5 km SE Sendri-soa, 22°8'58"S, 47°1'25", 1300 m (FMNH 167612, 167619, 167621).

Designation of the type species of *Musaraneus* Pomel, 1848 (Mammalia: Soricomorpha: Soricidae)

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Abstract.—The genus name *Musaraneus* often is attributed to Brisson (1762), however, most of Brisson's names are unavailable. Pomel (1848) subsequently made the name *Musaraneus* available, but did not designate a type species. The 18 species that Pomel listed under *Musaraneus* currently are distributed among five modern genera, two of which (*Cryptotis* Pomel, 1848 and *Diplomesodon* Brandt, 1852) are predated by *Musaraneus*. Because *Cryptotis* and *Diplomesodon* potentially could be considered junior synonyms of *Musaraneus*, I propose *Sorex leucodon* Hermann, 1780 (= *Crocidura leucodon*) as the type species for *Musaraneus*, thereby establishing *Musaraneus* as a junior synonym of *Crocidura* Wagler, 1832.

The generic name *Musaraneus* Pomel, 1848 derives from *mus araneus* ("spider mouse"), one of the terms commonly used alongside *sorex* and *mus caecus* by classical Latin writers (e.g., Plinius n.d.; Columella n.d.; Serenus n.d.) to refer to small mammals now generally interpreted as shrews (family Soricidae). The classical name *mus araneus* has a long history of use in early zoological literature. It was adopted and used widely by Renaissance natural historians and made the transition from a Latin common name to being incorporated into more formal taxonomies. The vernacular *mus araneus* generally was applied to the small mammal called locally by a variety of names that included "muzeraigne," "spitzmus," "shrew," "erd shrew," or "shrew-mouse" (Gesner 1551, 1560, 1602; Marggraf 1648; Jonston 1657; Topsell 1658; Ray 1693). A number of early taxonomists attempted to establish the name as *Mus Araneus* or *Musaraneus* within hierarchical classifications (Charleton 1668; Klein 1751; Brisson 1756, 1762). It is of interest that Gesner (1551, 1560, 1602) and subsequent writers (e.g., Topsell 1658, Charleton 1668) interpreted *sorex* as dis-

tinct from *mus araneus*, in some cases as a broader category that might include *mus araneus* (e.g., Klein 1751), or as a separate set of animals, typified by *mus avellanarum*, the "haselmus" or "hasel-mouse" (Gesner 1560, Topsell 1658), or by the "rat" (Charleton 1668). Gesner's (1551, 1560, 1602) print of *mus araneus* is an illustration of a soricid (Fig. 1A), possibly a white-toothed shrew of the genus *Crocidura*, whereas his picture of a *sorex* is identifiable as a garden dormouse (*Eliomys quercinus*—Fig. 1B). His illustrations were copied and republished by subsequent writers (e.g., Topsell 1658) and likely influenced later interpretations of the names. In contrast, Linné (1746, 1748, 1758) explicitly and consistently applied *Sorex* to those mammals that previous authors had called *mus araneus* or *Musaraneus*, and *Sorex* Linné, 1758 is the name that survived in the taxonomic literature. *Musaraneus* continues to be reflected in modern words for shrew in a number of romance languages, e.g., *musaraña* (Spanish), *musaraigne* (French), *musaranho* (Portuguese), *musaragno* (Italian). It also survives, in part, in

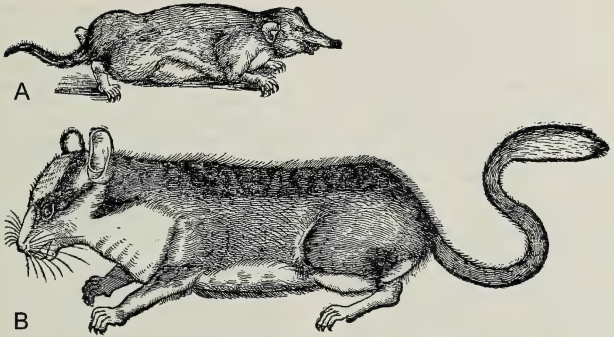


Fig. 1. Gesner's (1602) illustrations of (A) *mus araneus* and (B) *mus avellanarum* from *Historiae Animalium*. Photographs courtesy of the Smithsonian Institution Libraries, Joseph F. Cullman 3rd Library of Natural History, Washington D.C. Reproduced with permission.

the scientific name for the European common shrew, *Sorex araneus* Linné, 1758.

As a genus-level name, *Musaraneus* is often attributed to Brisson (1762; see Pomel 1848, Sherborn 1902, Palmer 1904, McKenna and Bell 1997, Kretzoi and Kretzoi 2000). Because Brisson (1762) did not consistently apply binomial nomenclature in his work, however, most of his names are unavailable in accordance with Article 11.4 of the *International Code of Zoological Nomenclature* (ICZN 1999; but see Hopwood 1947; ICZN 1998). In a subsequent classification of insectivores, Pomel (1848) re-described Brisson's *Musaraneus* as one of four genera (with *Talposorex* Pomel, *Sorex* Linnaeus, and *Galemys* Pomel) within the tribe Soriciens in his family Spalacogalae. Pomel (1848) made the name *Musaraneus* available, and therefore, he is the author of this name, as noted by Sherborn (1928). Hopwood (1947) recorded a number of other generic names used by Brisson (1762) that similarly were made available by later authors (see also ICZN 1998).

Pomel's (1848) *Musaraneus* comprised

18 species distributed among three "sections" (subgenera): *Cryptotis*, a new taxon with a single North American species; *Myosorex* Gray, 1838, an existing taxon comprising three African species; and *Crocidura* Wagler, 1832, an existing taxon containing 14 Old World species. Based on the list of included species, the genus *Musaraneus* included representatives from five modern genera. In addition to those genera representing Pomel's (1848) three sections (*Cryptotis*, *Myosorex*, *Crocidura*), one species (*Musaraneus puchellus*) represents *Diplomesodon* Brandt, 1852, and three others (*M. crassicaudatus*, *M. vulgaris*, *M. Bachmani*) represent *Sorex* Linné, 1758.

Pomel (1848) was uneven in designating species that he considered to be typical of the genera he described. In his classification of insectivores, Pomel noted a "typical species" for his newly-described *Talposorex*, but not for his names *Galemys* or *Musaraneus*. For these latter genera, he provided lists of species divided among several sections (subgenera). Pomel (1848) wrote the latter name as, "Genre *Musaraneus* Briss,

Pom.,” clearly indicating the influence of Brisson (1762). It is curious, however, that his version of *Musaraneus* did not explicitly include any of the three “species” (*Musaraneus*, *Musaraneus aquaticus*, *M. brasiliensis*) that Brisson (1762) had allocated to his genus *Musaraneus*. Pomel (1848) may have considered Brisson’s (1762) unimomial “species” *Musaraneus* to be represented by what Pomel called *Musaraneus* (*Crocidura*) *vulgaris*, which he equated with *araneus* of authors.

The type species of *Musaraneus* Pomel, 1848 is important to modern taxonomists because *Musaraneus* Pomel, 1848 predates *Cryptotis* Pomel, 1848 and *Diplomesodon* Brandt, 1852, and *Musaraneus* could be interpreted as a senior synonym of one of these genera. Kretzoi and Kretzoi (2000: 241) indicated that the type species for *Musaraneus* Pomel is “*Crocidura* (*M.*) *priscus* Pomel” (sic). There are a number of important and confusing errors in their account for this name, however. Both the original description of the genus and the designation of *Crocidura priscus* as the type species are credited by them to “Pomel 1853,” which is referenced as “Arch. Sci. Phys. Nat., Bibl. Univ. Genève, 9: 249,” but this reference is a conflation of several different publications. Pomel (1853a, 1853b) are parts of his “Catalogue des Vertébrés Fossiles,” which was published in at least three sections in *Annales Scientifiques, Littéraires et Industrielles de L’Auvergne*: the first in October and November of 1852 (Pomel 1852), the second in March and April of 1853 (Pomel 1853a), and the last in May and June of 1853 (Pomel 1853b). Insectivores, including the description of the fossil species *Musaraneus* (*Crocidura*) *priscus*, appear in the first part of this work, and the correct citation for that name is Pomel (1852:351). Pomel’s original description of *Musaraneus* is in an earlier publication (Pomel 1848) that was published in Volume 9 of *Archives des Sciences Physiques et Naturelles*, Genève. In order for a species to be designated a type species

by a subsequent author, it must have been included in the genus by the original author (ICZN 1999: art. 69.2). However, Pomel (1848) did not include the name *priscus* among the species he listed under *Musaraneus*, as he had not yet described the species. Therefore, the selection by Kretzoi and Kretzoi (2000) is invalid.

Pomel’s (1848:249) original description of *Musaraneus* reads:

Trois intermédiaires en haut, deux en bas, estomac oblong avec poche bien marquée sous le boyau pylorique.

My translation of this description is:

Three upper intermediary teeth, two lowers, stomach oblong with well-marked pouch below the pyloric constriction.

I interpret Pomel’s upper “intermédiaires” to represent the simplified upper dentition between the large, hooked first incisor and the roughly molariform fourth premolar (P4) that commonly are referred to as “unicuspids” (Choate 1970). The lower “intermédiaires” are the teeth designated the lower unicuspid and lower fourth premolar (p4). Among the five modern genera Pomel (1848) included within *Musaraneus*, all but *Myosorex* have a single lower unicuspid and p4; *Myosorex* typically has two lower unicuspid in addition to p4. In the upper dentition, *Sorex* has five unicuspid, *Cryptotis* and *Myosorex* each have four, and *Diplomesodon* has two. Only *Crocidura* has three upper unicuspid in accord with Pomel’s (1848) description. Although it is not required that the type species match the original description for a genus, it is highly desirable.

Among the modern species of *Crocidura* that Pomel (1848) included in *Musaraneus*, the majority are African, one is from Japan, and one, *Crocidura leucodon*, is widespread in continental Europe, including France, where Pomel lived. Among the recommendations for selecting a type species for subsequent designation are that the species be common and that it be well known to the

original author (ICZN 1999: Recommendations 69.A1, 69.A7). Therefore, I select *Sorex leucodon* Hermann, 1780, as used in the name combination *Musaraneus (Crociodura) leucodon* by Pomel (= *Crociodura leucodon*), as the type species of *Musaraneus* Pomel, 1848. By designating this taxon as the type species, *Musaraneus* Pomel, 1848 becomes a junior synonym of *Crociodura* Wagler, 1832, thereby stabilizing the generic names *Cryptotis* and *Diplomesodon* in accordance with their long-established usage.

Acknowledgments

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The mammals of Palawan Island, Philippines

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Abstract.—The mammal fauna of Palawan Island, Philippines is here documented to include 58 native species plus four non-native species, with native species in the families Soricidae (2 species), Tupaiidae (1), Pteropodidae (6), Emballonuridae (2), Megadermatidae (1), Rhinolophidae (8), Vespertilionidae (15), Molossidae (2), Cercopithecidae (1), Manidae (1), Scuriidae (4), Muridae (6), Hystricidae (1), Felidae (1), Mustelidae (2), Herpestidae (1), Viverridae (3), and Suidae (1). Eight of these species, all microchiropteran bats, are here reported from Palawan Island for the first time (*Rhinolophus arcuatus*, *R. macrootis*, *Miniopterus australis*, *M. schreibersi*, and *M. tristis*), and three (*Rhinolophus* cf. *borneensis*, *R. creaghi*, and *Murina* cf. *tubinaris*) are also the first reports from the Philippine Islands. One species previously reported from Palawan (*Hipposideros bicolor*) is removed from the list of species based on re-identification as *H. ater*, and one subspecies (*Rhinolophus anderseni aequalis* Allen 1922) is placed as a junior synonym of *R. acuminatus*. Thirteen species (22% of the total, and 54% of the 24 native non-flying species) are endemic to the Palawan faunal region; 12 of these are non-flying species most closely related to species on the Sunda Shelf of Southeast Asia, and only one, the only bat among them (*Acerodon leucotis*), is most closely related to a species endemic to the oceanic portion of the Philippines. Of the 28 insectivorous bats, 18 species are somewhat to highly widespread in Indo-Australia, 2 are shared only with the Sunda Shelf and Indochina, 1 with the Sunda Shelf alone, 3 occur on the Sunda Shelf and the oceanic Philippines, 1 occurs in Palawan, Sulawesi, and the oceanic Philippines, 2 occur only on Palawan and in the oceanic Philippines, and 1 occurs on Borneo, Sulawesi, and throughout the Philippines. Though the insectivorous bats tend to be widely distributed, these data, particularly the distributions of the non-volant species, strongly reinforce the perception of Palawan Island (and associated smaller islands) as a biogeographic unit of the Sunda Shelf, with only limited similarity to other portions of the Philippine Islands.

The Philippine archipelago is remarkable for the large number of indigenous land mammal species (ca. 175), and especially for the number of endemic species (ca. 112). Given its relatively small land area, the Philippines has perhaps the greatest concentration of endemic mammals in the

world (Heaney et al. 1998, Heaney & Regalado 1998, Mittermeier et al. 1997). These species, especially the endemics, are not distributed homogeneously over the country; rather, there is a large number of discrete biogeographic units, and these correspond to the limits of the islands that ex-

isted during periods of low sea level during the late Pleistocene (Heaney 1986, 1991a, 1991b, 2000). With a single exception, current geological evidence indicates that none of these "Pleistocene islands" has had dry-land connections to the Asian mainland or to other areas. Rather, each arose as a *de novo* oceanic island, some from a combination of oceanic crust and volcanic materials, and some as uplifted areas of continental rock that had been submerged for long periods, and all of these have remained isolated by sea channels (Hall 1998, 2002; Heaney 1985, 1986, 1991a). The sole exception is the Palawan faunal region, which generally has been considered to be a portion of the Sunda Shelf, both geologically and biogeographically, with many species shared with Borneo (Dickerson 1928, Everett 1889, Heaney 1986). Although Palawan was initially also a *de novo* oceanic island, its biogeographic affinity to the Sunda Shelf has been thought to be due to the presence of a shallow shelf between Borneo and Palawan with an intervening depth of ca. 145 m (Heaney 1986, 1991a). Previously, evidence indicated that sea levels dropped to about 165 m below present levels during the penultimate glacial episode (Gascoyne et al. 1979), which would have resulted in a dry-land connection of Palawan to Borneo at about 165,000 BP (Heaney 1985, 1986, 1991a). However, recent evidence suggests that sea level dropped only to about 135 m (Rohling et al. 1998) or perhaps as little as 115 m below present levels (Siddall et al. 2003, Voris 2000) during that glacial episode, leaving open the question of when Palawan was connected to Borneo, or if the gap simply became very narrow.

The mammals of Palawan Island, the largest part of the faunal region at 11,785 km², and the associated smaller islands have been documented over the course of more than a century (Allen 1910, Allen 1922, Everett 1889, Heaney et al. 1998, Hoogstraal 1951, Kuntz 1969, Reis & Garong 2001, Sanborn 1952, Taylor 1934, Timm & Bir-

ney 1980), but the fauna is still poorly known in many respects. Little information has been available for most species on ecology and distribution, including habitat requirements, and only a few studies have considered phylogenetic relationships (e.g., shrews: Heaney & Ruedi 1994; bats: Musser et al. 1982; squirrels: Heaney 1979; murid rodents: Musser 1979, Musser & Newcomb 1983, Musser & Heaney 1992; pangolin: Feiler 1998; leopard cats: Groves 1997). In particular, microchiropteran bats have been only superficially documented. The limitations of available data have thus limited understanding of the Southeast Asian fauna, and the Philippine fauna in particular, from both biogeographic and ecological perspectives, and hence limited conservation planning in a nation that is often cited as one of the most in need of effective conservation action (Mittermeier et al. 1999, Ong et al. 2002, Wildlife Conservation Society of the Philippines 1997).

Two of us (Esselstyn and Widmann) recently conducted extensive surveys of the mammals of Palawan Island, focusing on the 15 sites described below. Esselstyn worked from December 1999 to November 2000 at Sites 1–11, emphasizing (though not exclusively) insectivorous bats, which are the mammals most poorly known in the Philippines (Heaney et al. 1998, Heaney & Mallari 2002), and Widmann conducted studies of bats, rodents, and larger mammals from 1997 to 2002 at Sites 12–15; Heaney visited briefly in April 2000. In this paper, we report information collected during these studies, emphasizing new data on bats, and we include additional unpublished records of mammals. We summarize information on all additional species that were not taken during this study but have been documented on the island, and re-examined some key specimens from prior studies. We include descriptions of the habitats where we conducted our surveys because of a general paucity of such information, and use all available information to evaluate conservation status of the mammals. We include

measurements of the skulls of selected species of insectivorous bats that have been especially poorly known.

Methods

At Sites 1–11, small non-volant mammals were captured using locally made live (cage) traps and Victor (snap) rat traps. Approximately 90% of live traps used measured $11 \times 11 \times 24$ cm, and 10% measured $13 \times 16 \times 13$ cm. Trap lines consisting of approximately 70 traps (50 live traps and 20 snap traps) were placed in areas of traversable terrain. Individual traps were placed in locations of likely capture (e.g., near holes, along fallen logs, near root buttresses, etc.) along the line spaced at 5–15 m intervals. Most traps were set at ground level, but in forest habitats we placed 5–15% of the traps in elevated locations up to 2 m above ground level on fallen logs, horizontal vines, etc. All but two trap lines were set for three nights; the exceptions at Sites 3 and 7 were set for five and two nights, respectively. At Sites 12–14, a mixture of live traps were used (see Site descriptions). Most trap lines were baited with fresh grilled coconut coated with peanut butter. Other trap lines were baited with live earthworms or bananas. All traps were checked in the early morning and late afternoon. Baits were changed at least once daily, usually in the afternoon, and as necessary in the early morning. Most live animals were released at the site of capture.

We captured bats using a harp trap (ca. 2×2 m, 4 bank), mist nets (2×6 m, 16 mm mesh), butterfly nets, and hand capture at Sites 1–11; only nets were used at Sites 12–15. Harp trap and net locations were selected to be locations of likely capture (e.g., natural canopy breaks, over streams and trails, around fruiting trees, and near potential roosting locations). The harp trap and mist nets were usually set in a location for three nights, and occasionally for only one or two nights. During surveys of caves, we primarily used the harp trap, and its loca-

tion was frequently changed. Mist nets were continuously monitored during peak activity periods from 1800 to 2000 h (at Sites 12 and 13, until 2400 h) and then checked again in the early morning. The harp trap was checked periodically between 1800 and 2100 h and again in the early morning. In forested areas, we searched for bats in potential roosting locations (e.g., hollow trees, rock formations, new banana leaves, etc.). Most bats were released at the site of capture. For many of the bats, we report the proportion of adult females that were pregnant on certain dates. These were palpated externally to determine the presence or absence of an embryo before being released.

Forearm and cranial measurements were taken by L. R. Heaney and D. S. Balete at the Field Museum of Natural History (FMNH). All voucher specimens from Essetstyn, which are cited below as specimens examined, were preserved in fluid (with skulls later removed and cleaned) and cataloged at the FMNH; half of the vouchers have been deposited at the National Museum of the Philippines (NMP). Additionally, data on several previously unreported specimens housed in the University of Michigan Museum of Zoology (UMMZ) and United States National Museum of Natural History (USNM) are included here.

Site Descriptions

See Fig. 1 for approximate locations of study sites. The province of Palawan includes the main island called Palawan and many smaller, nearby islands. The island is politically divided into 13 municipalities, one of which is Puerto Princesa City; the municipalities and the city are subdivided into barangays, and barangays into sitios.

Site 1 ($10^{\circ}03'00''N$, $119^{\circ}00'44''E$) was in lowland primary forest located along the Taraban River in northern Puerto Princesa Municipality, at elevations ranging between ca. 100 and 200 m. Slope in the area was generally moderate, rising from the river to the ridge-tops. Forest in the area was

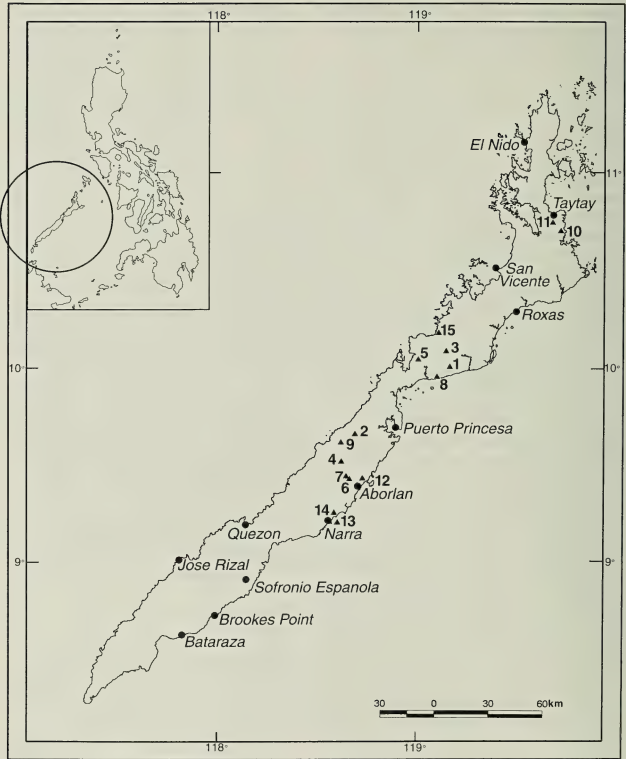


Fig. 1. Map of Palawan Island, showing the locations of the primary towns (solid circles) and research sites (solid triangles), and the position of Palawan in the Philippines (inset).

nearly undisturbed, which is uncommon at this low elevation. We were aware of only one small human-made clearing (ca. 0.5 ha) in the area; other disturbances included col-

lection of minor forest products and hunting of *Sus barbatus* and *Macaca fascicularis*. Canopy ranged from 20 to 30 m in height and was multi-layered. Canopy trees ranged

in diameter from 40–80 cm and had light buttress development. Leaf litter was thin. We surveyed small volant and non-volant mammals for 13 days in January 2000. Four trap lines were run for three nights, yielding 3 *Tupaia palawanensis*, 21 *Maxomys panglima*, and 1 juvenile *Viverra zibetha* in 792 trap-nights. Three of the lines were baited with coconut and peanut butter, while one line was baited with live earthworms. Forty-eight net-nights produced 1 *Cynopterus brachyotis* and 12 harp-nights produced 3 *Rhinolophus acuminatus*, 3 *R. arcuatus*, and 1 *R. creaghi*, plus other means produced 11 *Megaderma spasma* and 1 *R. acuminatus*.

Site 2 (9°42'14"N, 118°32'01"E) was in lowland primary forest located mid-way up Mt. Salakot, between 300 and 700 m elevation. Slope was rolling to moderately steep. Several small streams dissected the area. The only major human-caused disturbance in the area was an unused helicopter landing pad and an abandoned road; the road had a dense regrowth of ferns and small trees. *Sus barbatus* was hunted, and some almaciga trees (*Agathis* sp.) near the upper reaches of the site had fallen due to over-collection of resin. Agohe trees (*Casuarina* sp.) gradually became more common as elevation increased. Canopy ranged from 15 to 30 m in height and was multi-layered. Canopy trees ranged in diameter from 35–60 cm with the largest emergents reaching 80–90 cm. Buttress systems were only slightly developed and stilt root systems were present above 600 m, but rare. Leaf litter was slightly deeper than at lower elevations. We surveyed small volant and non-volant mammals at this site for 20 days during March and July 2000. Six trap lines (three coconut and peanut butter-baited lines, one banana-baited line, and two earthworm-baited lines) yielded 16 *Tupaia palawanensis*, 55 *Maxomys panglima*, and 1 *Sundamys muelleri* from 1272 trap nights. Fifty-six net-nights yielded 1 *Cynopterus brachyotis*, 1 *Hipposideros diadema*, 8 *Rhinolophus arcuatus*, and 1 *R. creaghi*.

Ten harp-nights yielded 1 *Hipposideros diadema*, 16 *Rhinolophus arcuatus*, 10 *R. creaghi*, 2 *R. virgo*, and 2 *Kerivoula hardwickii*.

Site 3 (10°07'28"N, 118°59'36"E) was in primary montane and mossy forest located near the peak of Cleopatra's Needle (maximum elevation 1603 m), at elevations ranging from 1300 to 1600 m. Slope was moderate to extreme. Other than a trail to the peak occasionally traveled by tourists, there was little human-caused disturbance in the area. No above-ground sources of water were found near the site, but mist was frequently present: during our stay of two weeks during dry season, the area was almost continuously shrouded by a dense fog. Vegetation type was montane forest up to ca. 1500 m. At this elevation, the vegetation began a transition to mossy forest. In montane forest, the canopy reached a height of approximately 10 m. Trees, rocks, fallen logs, and other stable surfaces were covered with a thin layer of moss; epiphytic ferns and orchids were abundant. Many trees had an adventitious root system, but maintained straight boles. The canopy was more open here than at lower elevations. Above 1500 m, trees were shorter (2–4 m in height) and took on a shrub form above 1550 m. Moss growth was heavier at this elevation, and vegetation became extremely dense at the upper reaches. Pitcher plants (*Nepenthes*) began to appear at about 1500 m and were abundant by 1550 m. We surveyed small volant and non-volant mammals at this site for 12 days during February and March 2000. Three trap lines yielded 1 *Tupaia palawanensis*, 33 *Maxomys panglima*, and 3 *Rattus tiomanicus* in 740 trap-nights. Two lines were run for three nights each and one line was run for five nights; all three lines were baited with coconut and peanut butter. Forty-eight net-nights produced 2 *Rhinolophus arcuatus*, and 12 harp-nights produced no captures; 2 *Pipistrellus javanicus* were captured by hand.

Site 4 (9°33'45"N, 118°27'54"E) is a cave known locally as "Ma-ngit". It is located

along the Iraan River near Sitio Pamolkoan, Barake, Aborlan, at ca. 430 m elevation. The cave is in a small valley, restricted by mountains to the east and west. A small, seasonal stream flows through the cave. At least six entrances to the cave were evident, and many small tunnels connected medium to small caverns, which ranged from well-lit to completely dark. Very little disturbance was evident in or around the cave due to its isolated location (ca. 10 hour hike from the nearest road). The cave was surrounded by a large expanse of primary lowland forest, but some agricultural areas were present within ca. 5 km. Disturbances to local vegetation included collection of rattan (*Calamus* spp.). We surveyed bats in Ma-ngit Cave for six days during December 1999. We captured 819 bats belonging to seven species (9 *Eonycteris spelaea*, 43 *Hipposideros diadema*, 367 *Rhinolophus creaghi*, 4 *R. virgo*, 9 *Miniopterus australis*, 386 *M. schreibersi*, and 1 *M. tristis*) inside the cave.

Site 5 (10°05'00"N, 118°51'06"E) is a complex area of limestone karst containing probably greater than 100 caves in Barangays Tagabinet and Cabayugan, Puerto Princesa; elevation is ca. 50 m. Caves in the area ranged from tiny cracks too small to enter, to large complexes of multiple caverns with multiple entrances. Local terrain was generally flat except for the sometimes-massive limestone outcrops, which form high-rising cliffs throughout the area. Caves probably are present all over these complex formations, but only the very few found near ground level were accessible. We captured bats in and around five different caves/cave complexes. These represented some of the most accessible caves in the area. Disturbance at the caves was moderate, with vandalism and guano excavation evident at most caves. Most of the caves were surrounded immediately by agricultural development. Both primary and secondary lowland forests were present in the surrounding hills. We surveyed bats at these caves for 14 days between March and May

2000. A total of 575 bats belonging to 10 species (18 *Cynopterus brachyotis*, 1 *Megaderma spasma*, 100 *Hipposideros ater*, 239 *H. diadema*, 14 *Rhinolophus arcuatus*, 33 *R. creaghi*, 10 *R. macrotis*, 86 *R. virgo*, 15 *Miniopterus australis*, and 59 *M. schreibersi*) were captured.

Site 6 (9°28'25"N, 118°30'21"E) was a mostly abandoned agricultural area located in Barake, Aborlan Municipality, at elevation ranging from 40–80 m. A small stream flowed through the area and topography was flat to rolling. Vegetation was a mosaic of grassland (primarily *Imperata cylindrica*) with sparse trees (mostly *Vitex* sp.), cashew plantations, dense brush, and very small (<1 ha) areas of secondary growth. Frequent fires appeared to maintain this area as a grassland. We surveyed small volant and non-volant mammals for four days during June 2000. A single trap-line baited with live earthworms yielded 17 *Rattus exulans* in 186 trap-nights. We captured 7 *Cynopterus brachyotis* in 6 net nights, and 1 *Kerivoula whiteheadi* in 3 harp-nights.

Site 7 (9°29'15"N, 118°29'24"E) was in a narrow band of secondary forest in Barake, Aborlan Municipality, located between disturbed habitat at lower elevation (*Site 6*) and primary and good secondary forest at higher elevation. Elevation ranged from 80–140 m; slope was rolling to moderately steep, and two small streams dissected the area. Canopy height varied from 5–20 m. Woody vines and lianas were common and vegetation was quite dense in areas. Wild bananas (*Musa* spp.) were abundant, but patchy in distribution; leaf litter depth was highly variable. We surveyed this site for small volant and non-volant mammals for four days during June 2000. A single trap line baited with live earthworms yielding 120 trap-nights produced 1 *Rattus exulans*. Six net-nights produced 27 *Cynopterus brachyotis* and 1 *Macroglossus minimus*, and 3 harp-nights yielded 1 *Hipposideros diadema* and 1 *Kerivoula pellucida*.

Site 8 (9°59'47"N, 118°56'43"E) is a large cave complex located in a limestone

karst formation on top of the first ridge up from San Rafael, Puerto Princess, at an elevation of ca. 250 m. The cave complex is known locally as "Taraw". The cave system appeared to be quite large; we were unable to explore much of it due to a lack of climbing equipment and expertise. Some caverns exceeded 20 m in height, while others were quite small. We found no permanent water in or around the cave, but evidence of storm flow was present. Evidence of vandalism and guano collection was present. A mixture of habitats surrounded the cave complex: between the cave and the community of San Rafael, the vegetation was dominated by brushland and agricultural developments, while on the other side of the cave secondary and primary forest dominated, with mixed areas of slash-and-burn fields. We surveyed bats at this cave for five days during July 2000. We captured 2775 bats representing 10 species (7 *Hipposideros ater*, 43 *H. diadema*, 90 *Rhinolophus acuminatus*, 240 *R. arcuatus*, 239 *R. creaghi*, 25 *R. macrotis*, 151 *R. virgo*, 1257 *Miniopterus australis*, 711 *M. schreibersi*, 4 immature *M. sp.*, and 8 *Myotis macrotarsum*).

Site 9 (9°39'40"N, 118°27'48"E) is a small cave located in Sitio Labtay, Napsan, Puerto Princessa City. The cave, which consisted of a single chamber 1–2 m wide, 3–6 m high, and ca. 30 m long, was in a narrow canyon along the Panagurian River at ca. 280 m. Vegetation in the area consisted of good-quality secondary forest, second-growth forest, and agricultural developments. We trapped bats with a harp trap, mist nets, and a butterfly net in the cave and surrounding forest for five days during August 2000. We captured 73 bats (4 *Cynopterus brachyotis*, 68 *Hipposideros diadema*, and 1 *Rhinolophus arcuatus*).

Site 10 (10°44'00", 119°34'23") is a cave located near sea level in Sitio Sader, Bantulan, Taytay Municipality. The cave consisted of a single chamber (ca. 3–8 m wide, 3–7 m high, and 40 m long) with a large (>2.5 m diameter) entrance at each end.

Minor damage had been done by both treasure hunters and guano collectors. The surrounding vegetation was dominated by agricultural areas with some strips and patches of residual forest. Large expanses of secondary and logged-over forest were found nearby in the vicinity of Lake Manguao. We captured 115 bats belonging to 4 species (48 *Eonycteris spelaea*, 1 *Rousettus amplexicaudatus*, 64 *Hipposideros diadema*, and 2 *Miniopterus tristis*) using a harp trap and butterfly net at one of the entrances to the cave during three days in October 2000.

Site 11 (10°46'34"N, 119°31'52"E) was located around the perimeter of Lake Manguao, in Barangays Poblacion and Bantulan, Taytay Municipality. The area was dominated by secondary and logged-over forest, with disturbance from slash and burn agriculture being found throughout the area. The area retained ca. 60% forest cover. Slope was generally moderate to steep, and elevation ranged from ca. 40–250 m. We trapped for small volant and non-volant mammals in forest, agricultural habitats, and two small caves near the lake for 14 days during October and November 2000. We totalled 471 trap-nights in three lines baited with coconut and peanut butter, and captured 3 *Tupaia palawanensis*, 23 *Maxomys panglima*, and 1 *Rattus exulans*. Forty-two net-nights yielded 53 *Cynopterus brachyotis*, 2 *Macroglossus minimus*, and 1 *Rousettus amplexicaudatus*, and 13 harp-nights produced 1 *Megaderma spasma*, 1 *Rhinolophus acuminatus*, 2 *Kerivoula hardwickii*, and 5 *Tylonycteris pachypus*. Additionally, we captured 4 *Megaderma spasma* and 4 *R. acuminatus* by hand.

Site 12 (9°27'48"N, 118°32'16"E) was located at the "rainforestation" site in Sitio Kandis, Aborlan Municipality, in forest/grassland mosaic at ca. 40 m above sea level, about seven km away from the next good secondary forest in the foothills of the Victoria Range. Charcoal making, logging, rattan collection, grazing and burning were common until 1994 when such activities were made illegal. The terrain was flat to

rolling, dissected by two creeks. The site consisted of 5.5 ha *Imperata cylindrica* grassland interspersed with single shrubs and trees, predominantly *Antidesma ghae-sembilla*, which forms the fire climax in more open situations, with *Vitex pubescens*, *Guioa pleuropteris*, *Tarenna stenantha*, *Fagraea fragrans*, *Lantana camara*, and *Mussaenda philippica* in protected areas not affected by fire in the last ten to fifteen years. About 4.5 ha consisted of regenerating forest, close to two seasonal creeks, dominated by *Garcinia benthami*, *G. parviflora*, *Canarium asperum*, *Polyscias nodosa*, and *Barringtonia curranii*. Undergrowth was moderate to very dense. Canopy height was on average eight meters, with some taller emergents such as *Nephelium* sp. and *Dipterocarpus gracilis*. The most conspicuous vine was *Gnetum latifolium*. Macrophytic epiphytes were virtually absent. Leaf litter layer was usually not closed, except in very dry years. Surveys were conducted regularly from 1997–2000 with 10 medium-sized Sherman live traps, 10 commercial live rat traps, and 55 wire mesh traps (measurements equal to medium Shermans). Baits were roasted coconut with peanut butter, but mostly fruits available in the area. A total of 3514 trap-nights yielded 169 small mammals (28 *Tupaia palawanensis*, 8 *Sundasciurus juvencus*, 11 *Rattus exulans*, 16 *Rattus tiomanicus*, 104 *Maxomys panglima*, and 2 *Sundamys muelleri*). Mist nets (2 × 6 m) were set along trails in forest, in grassland, gaps in the shrub cover, and rarely in the canopy (ca. 8 m high). Capture sites were often near or in fruiting shrubs or trees, since the main focus of the study was on frugivores. From 1997 to 2000, a total of 482 net-nights yielded 1257 bats (1 *Acrodon leucotis*, 829 *Cynopterus brachyotis*, 394 *Macroglossus minimus*, 5 *Eonycteris spelaea*, 4 *Rousettus amplexicaudatus*, 18 *Megaderma spasma*, 1 *Hipposideros diadema*, 4 *Scotophilus kuhlii*, and 1 *Murina* cf. *tubinaris*); all but the *M.* cf. *tubinaris* were released.

Site 13 (09°13'N, 118°26'E) was on Rasa

Island, Narra Municipality, a small (8.3 km²) shallow coral island, 1.8 km offshore in the Sulu Sea. Approximately two-thirds of the island was covered with mangrove and one-third with coastal forest over limestone. About five percent of the latter had been converted into coconut plantation. Selective logging was done until the early 1990s, resulting in the complete loss of mature *Intsia bijuga*. The mangrove consisted of nine species of the genera *Rhizophora*, *Sonneratia*, *Avicennia*, *Bruguiera*, *Aegicer- as*, and *Ceriops*. Canopy height was variable, usually between 8 and 15 m. Emergent trees (e.g., *Garuga floribunda* and *Pterocymbium taluto*) ranged up to 42 m. Leaf litter layer was not closed, except under very dry conditions. Barren coral rocks and crevices were ubiquitous. Buttresses were a common feature of all emergent forest trees. Under open conditions, an herbal layer consisting of *Impatiens* sp. was present. Vines were abundant, including climbing bamboo *Dinochloa* sp., often forming dense tangles. Macrophytic orchids were present, but relatively scarce. Traps and nets were set along a trail within the coastal forest. Traps were baited with roasted coconut with peanut butter, and a few with crickets. Most traps caught hermit crabs. Nets were set in the understory, which was very open from January to April 2002 and only provided very few fruits due to an extended dry spell. Trapping totaled 104 trap-nights, and produced 3 *Rattus tanezumi* and 2 *R. tiomanicus*. Netting totaled 28 net nights, and yielded 2 *Cynopterus brachyotis*, 5 *Macroglossus minimus*, and 5 *Megaderma spasma*; all bats were released, and the rats preserved as vouchers.

Site 14 (9°17'N, 118°27'E) was in fresh-water swamp forest in Narra Municipality, in about 5 ha of remnant forest along Tarityen River. The habitat was dominated by two woody species, *Nauclea orientalis* and *Pandanus* sp., at lower elevations, which are flooded for at least six months. The herb layer was not extensive and was dominated by *Acrostichum* sp. The higher portions

were dominated by pioneering species of early to medium successional stages, such as *Trema orientalis*, *Vitex pubescens*, and *Commersonia bartramia*. Even during extreme dry spells like that in the first half of 2002, there were isolated open water bodies left, which connected to several creeks during the rainy season. The swamp forest is bordered by ricefields and grassland. Twenty trap-nights yielded 1 *Rattus exulans* and 1 *R. tiomanicus*. Twelve net-nights yielded 27 *Cynopterus brachyotis*, 5 *Macroglossus minimus*, and 1 *Megaderma spasma*; all bats were released and the rats preserved as vouchers.

Site 15 (10°12'N, 118°55'E) was along the "jungle trail" near the Central Park Station in Puerto Princesa (formerly St. Paul) Subterranean River National Park (PPSRNP). Primary lowland forest on steep slopes ascended from sea level to about 40 m. Five net-nights on 15 September 1996 yielded 1 *Cynopterus brachyotis*, 2 *Rhinolophus arcuatus*, 3 *Rhinolophus virgo*, and 2 *Rhinolophus* sp.; all were released. Additionally, all three authors made visual observations at various times.

Accounts of Species

Order Insectivora

Family Soricidae—Shrews

Crocidura palawanensis.—We never encountered this poorly known species. It is endemic to the Palawan faunal region and has been taken in old-growth rain forest and shrubby second growth (Heaney & Ruedi 1994); the holotype came from "deep forest near the sea at . . . Brooke's Point" (Taylor 1934), a second from near sea level in Babuyan, Puerto Princesa (Hoogstraal 1951, Sanborn 1952), and a third from 3600–4350 ft (ca. 1100–1300 m) on Mt. Mantalingajan (USNM); two additional specimens are from Balabac (Heaney & Ruedi 1994). IUCN (2002) lists this species as Vulnerable, but current definitions suggest that Data Deficient would be more appropriate.

Crocidura sp.—Reis & Garong (2001)

reported a single humerus of a shrew, substantially smaller in size than *C. palawanensis*, from undated sediments in a small rock-shelter cave near Tabon Cave on Lipuun Point, near Malunut Bay, in Quezon Municipality (near the location of the town of Quezon as shown in Fig. 1). They described the specimen as being similar in size to *C. monticola* from Borneo. We tentatively include it in our tallies of native species of Palawan, but we recommend that it be sought by trapping with small snaptraps baited with live earthworms and pit-fall traps.

Suncus murinus.—This introduced commensal is abundant in urban and agricultural areas (Rabor 1986); in forest, it is rarely present, but occasionally is common (Heaney et al. 1989, Heaney & Tabaranza 1997). It is found throughout Asia and Indo-Australia, including the Philippines (Heaney et al. 1998). We observed this species frequently in houses in Puerto Princesa City and the State Polytechnic College of Palawan in Aborlan Municipality.

Order Scandentia

Family Tupaiidae—Tree Shrews

Tupaia palawanensis.—This common species is endemic to the Palawan faunal region (Wilson 1993); it is related to *T. glis*, which is widespread on the Sunda Shelf (Corbet & Hill 1992). It is widespread on Palawan (Taylor 1934), and is usually common in secondary and primary lowland forest, though local densities may be highly variable between apparently similar habitats (Dans 1993, Hoogstraal 1951, Sanborn 1952). It is rare in montane forest, and common but patchy in agricultural areas. We captured and/or observed this species in coconut and cashew plantations, brushy areas with a few small trees (Sites 6, 11, and 12), secondary and logged-over forest (Sites 7 and 11), and primary forest (Sites 1, 2, 3, and 15) from near sea level to 1400 m. IUCN (2002) lists this species as Vulnerable, but we concur with Heaney et al.

(1998) that the species should be delisted due to the variety of habitats used and its apparent abundance. Specimens examined: 2: Site 1 (1), Site 2 (1).

Order Chiroptera

Family Pteropodidae—Fruit Bats

We follow Ingle & Heaney (1992) and Heaney et al. (1998) in regarding reports of *Haplonycteris fischeri* (Kock 1969) and *Ptenochirus minor* (Yoshiyuki 1979) from Palawan as erroneous, probably originating in mislabeled specimens. *Pteropus hypomelanus* is known from Cuyo Island, at the northeast edge of the Palawan faunal region (Heaney et al. 1998), as well as in the oceanic Philippines and on islets around Borneo, and should be sought on Palawan.

Acerodon leucotis.—This poorly known species is endemic to the Palawan faunal region. Hoogstraal (1951) found the species in an area with patches of "much disturbed remnants of original forest and dense second growth forest" on Busuanga Island, and two specimens were taken at Santiago, Iwahig (in Puerto Princesa) on Palawan (Sanborn 1952). A specimen from Bat Island (Barangay Tagburos, in Honda Bay), taken by P. O. Glass in 1978, is housed in the UMMZ. Heaney sighted large numbers of medium-sized, pale-furred flying foxes at Site 15 in April 2000, in the clearing of the old park headquarters near the center of the park ("Central Park"), that were probably this species. Widmann captured one at Site 12 at a height of 5 m, and saw others feeding in the canopy at ca. 8 m height. The IUCN (2002) lists this species as Vulnerable; we regard it as Data Deficient.

Cynopterus brachyotis.—Found throughout Southeast Asia; in the Philippines, it is common to abundant in secondary forest and agricultural areas, and rare in primary forest (Heaney et al. 1998); Sanborn (1952) reported many from Palawan. We netted this species frequently in secondary forest and agricultural areas at Sites 6, 7, 11, and 12, in freshwater swamp forest at Site 14,

and in coastal forest on Rasa Island (Site 13). We also captured this species in primary forest in a tree fall gap (Site 1), over a stream (Site 2), and at a place with no visible disturbance (Site 15). We found them roosting in various-sized groups in three caves at Sites 5 (there appeared be less than 50 in each of two caves) and 9 (ca. 300 individuals); although this species occasionally roosts in caves on Borneo (Payne et al. 1985), there are no previous records of such roosts in the Philippines. On several occasions we captured them carrying whole green figs (*Ficus* sp.) during flight; two of these individuals were returning to a cave at Site 5 between 1900–2000 h.

Out of 20 adult females caught at Site 14 on 20 March 2002, 15 were pregnant and 5 were carrying a single suckling young. On 1 and 2 April 2000, we captured three adult females at Site 5; all were carrying a single suckling infant during flight. On 17 May 2000 we captured eight adult females at Site 5; one was pregnant, one was carrying a suckling infant during flight, and two were emaciated and may have recently weaned their young. On this date, we also captured a male with enlarged mammarys (see Francis et al. 1994). On 30 October 2000, among 25 adult females, none were pregnant but one was lactating. Specimens examined: 4, Site 1 (1), Site 5 (3).

Eonycteris spelaea.—This widespread Southeast Asian species is common in agricultural areas in the Philippines, where all known roosts are in caves (Heaney et al. 1998, Rickart et al. 1993). Sanborn (1952) reported a large series from a cave above Tanabog, Palawan. We netted five individuals at Site 12, but most of our records came from caves in lowland forest. We found this species roosting in caves at Sites 4 and 10; at Site 4, the roosting population appeared to exceed 2000. At Site 10, there was an extremely large population (probably >50,000) of small pteropodids roosting inside the cave. We captured 49 pteropodids at the entrance to the cave, 48 of which

were *E. spelaea* and one was a *Rousettus amplexicaudatus*. On 19 December 1999, all three adult females we captured at Site 4 were pregnant. On 21 October 2000 at Site 10, we captured 11 adult female *E. spelaea*, four of which were carrying an infant during flight and five of which were pregnant. This species is heavily hunted in some areas of the Philippines (Rickart et al. 1993, Uzzurum 1992), but we observed no evidence of that being the case on Palawan. Specimens examined: 5, Site 4 (3), Site 10 (2).

Macroglossus minimus.—In the Philippines, this widespread Australasian species is common in secondary forest and agricultural areas and uncommon in primary forest up to more than 2000 m (Heaney et al. 1998, 1999). We captured this species in secondary lowland forest (Sites 7 and 12) and agricultural clearings (Site 11), usually near wild or domestic banana plants (*Musa* spp.), and in freshwater swamp forest in Narra Municipality and Rasa Island (Sites 13 and 14). Specimens examined: 3, Site 7 (1), Site 11 (2).

Pteropus vampyrus.—In the Philippines, this widespread Southeast Asian species occurs in primary lowland forest and adjacent agricultural areas (Heaney et al. 1998; Rabor 1955, 1986; Rickart et al. 1993; Sanborn 1953; Taylor 1934). Widmann estimated 400 individuals on Malinau Island, Aborlan Municipality in 1998, 570 on Rasa Island on 12 November 1999, and a small colony (ca. 40 individuals) at Lagan on Dumaran Island on 27 October 2001, based on departure counts. Flying foxes commonly sighted in Puerto Princesa City around mango and guyabano (= sour sop) trees are probably this species. In 1998, we found two individuals of this species that appeared to have been electrocuted on power lines, one at the Provincial Agriculture Center in Irawan, Puerto Princesa, and the other at the State Polytechnic College, Aborlan. We believe this species to be common overall, but under moderate pressure due to

hunting and perhaps to electrocution on power lines.

Rousettus amplexicaudatus.—Within the Philippines, this widespread Southeast Asian species is commonly found in agricultural habitats up to 500 m and rarely in primary lowland forest (Heaney et al. 1998). All known roosting sites are in caves (Heaney et al. 1989, 1991, 1998, 1999; Heidemman & Heaney 1989; Rickart et al. 1993). According to Payne et al. (1985), *R. amplexicaudatus* often roosts in association with *Eonycteris spelaea*. We netted one individual from a cave at Site 10 containing a large population of *E. spelaea*, one in an agricultural clearing in Site 11, and four in forest-grassland mosaic at Site 12; all of these sites are in heavily disturbed areas below 60 m. Specimens examined: 2, Site 10 (1), Site 11 (1).

Family Emballonuridae—Sheath-tailed Bats

There are no known records of *Saccolaimus saccolaimus* from Palawan, but its widespread distribution from India to New Guinea, including the oceanic Philippines (Heaney et al. 1998), suggests that it may be present and should be sought.

Emballonura alecto.—The Philippine sheath-tailed bat is known from Borneo, the Philippines, and Sulawesi (Heaney et al. 1998); we never encountered this species on Palawan, but Taylor (1934:200) captured five individuals “under an overhanging rock along Iwahig River, near the base of Thumb Peak”.

Taphozous melanopogon.—The bearded tomb bat is widespread in southern Asia (Heaney et al. 1998). In the Philippines, it is common in urban areas and lowland areas with limestone caves and rare in forest (Rickart et al. 1993, Sanborn 1952). There is a previous record from the vicinity of Puerto Princesa (Allen 1922), and A. C. Alcalá collected 6 specimens from Sitio Malabusog, Tinitian, Roxas Municipality in

1984 which are deposited in the UMMZ. We never encountered this species.

Family Megadermatidae—False Vampire and Ghost Bats

Megaderma spasma.—This widespread southern Asian species is common in primary lowland forest and disturbed forest in the Philippines (Heaney et al. 1991, 1998, 1999; Rickart et al. 1993). We captured this species from sea level to ca. 500 m in secondary forest (Site 7), primary forest (Sites 1 and 2), in a bamboo thicket (Site 11), and in or near caves (Sites 5 and 11). It was the most common insectivorous bat netted in forest-grassland-mosaic (Site 12), in swamp forest (Site 14), and in coastal forest (Site 13). At Site 1, we found this species roosting in small groups (<10) in four hollow trees distributed throughout the area. At Site 11 we found ca. 12 individuals roosting in a small cave (ca. 0.5–3 m wide, 0.3–1.5 m high, and 10 m long) along with *Rhinolophus acuminatus*. We also found two individuals roosting in a small cave (also Site 11) that had been severely disturbed by treasure hunters three years earlier. Cranial measurements of three individuals (Table 1) are slightly smaller than those of specimens from Leyte and Biliran (Rickart et al. 1993) and southern Luzon (Heaney et al. 1999). Specimens examined: 3, Site 1 (3).

Family Rhinolophidae—Horseshoe and Roundleaf Bats

Several poorly known but apparently widespread species in this family occur on the Sunda Shelf and in the oceanic Philippines and should be sought on Palawan; these include *Hipposideros cervinus* and *H. lekaguli* (Balet et al. 1995, Heaney et al. 1998, Ingle & Heaney 1992).

Hipposideros ater.—Occurs from India to Australia (Heaney et al. 1998). Known from lowland and montane forest and caves (Heaney et al. 1991, 1998; Payne et al. 1985, Rickart et al. 1993). We found this species to be uncommon to abundant in

three caves in disturbed lowland forest at 50 to 250 m elevation at Sites 5 (17% of 575 captures) and 8 (<1% of captures). During March to April 2000, none of the 26 females we captured at Site 5 were pregnant or lactating, but on 19 and 20 May 2000, 25 of 30 adult females were pregnant. We have re-examined a specimen from Palawan in the UMMZ identified by Allen (1922) as *H. bicolor*, and a series from the Tigoplan River, Palawan in FMNH reported by Sanborn (1952), and now consider them to be *H. ater*; thus, we now know of no records of *H. bicolor* from Palawan. Cranial measurements of 5 individuals (Table 1) are smaller than those of *H. bicolor* (Heaney et al. 1999, Ingle & Heaney 1992) but match those of *H. ater* (Ingle & Heaney 1992, Rickart et al. 1993). Specimens examined: 5, Site 5 (4), Site 8 (1).

Hipposideros diadema.—The diadem roundleaf bat is widespread from Myanmar to the Solomon Islands, with many previous records from Palawan (Allen 1922, Heaney et al. 1998). In the Philippines, it is common in disturbed forest, agricultural areas (Ingle 1992, Rickart et al. 1993), and primary forest (Heaney et al. 1998, Rickart et al. 1993). Reis & Garong (2001) reported specimens from sediments in a rock-shelter near Tabon Cave, Quezon Municipality dated to 11,130 BP. We captured this species from sea level to 600 m in disturbed grassland-forest mosaic (Sites 6 and 12), secondary forest (Site 7), primary forest (Site 2), and at nearly all caves we visited (Sites 4, 5, 8, 9, and 10), and we observed large numbers (probably thousands) in the underground river cave at PPSRNP. All of the roosts we identified held groups of *H. diadema* numbering greater than 200. Thirteen adult females captured in December 1999 included none that were pregnant or lactating. At Site 5 in March to April 2000, none of the 54 adult females were pregnant or lactating, but between 15 and 20 May 2000 26 of 43 were pregnant and one was carrying a suckling infant during flight. One of 21, one of 12, and none of 13 adult females

Table 1.—Means and ranges of cranial measurements of adults of Megadermatidae and Rhinolophidae from Palawan Island, Philippines.

Species	Sex	n	Condylobasic length	Zygomatic width	Mastoid width	Orbital length	Canine to molar	Molariform toothrow	Palalet breadth	Palalet length	Forearm length
<i>Megaderma spasma</i>	m	2	—	14.54 (14.52-14.55)	11.27 (11.26-11.28)	7.37 (7.3-7.43)	8.79 (8.67-8.91)	7.07 (6.95-7.18)	3.77 (3.5-4.04)	—	55.7 (55.4-56.0)
	f	1	—	14.17	11.32	7.57	9.0	7.06	3.79	—	54.3
<i>Hipposideros ater</i>	m	3	14.29 (14.21-14.37)	7.83 (7.74-7.90)	8.28 (8.26-8.30)	4.46 (4.3-4.56)	4.8 (4.68-4.93)	3.94 (3.72-4.21)	3.28 (3.22-3.33)	4.87 (4.83-4.94)	39.7 (39.4-39.9)
	f	2	14.54 (14.31-14.77)	7.82 (7.76-7.88)	8.31 (8.23-8.39)	4.78 (4.61-4.94)	4.86 (4.75-4.97)	4.05 (4.0-4.1)	3.43 (3.41-3.45)	5.21 (4.95-5.47)	40.3 (40.1-40.4)
<i>Rhinolophus acuminatus</i>	m	1	20.35	10.89	9.81	6.23	7.65	6.15	4.77	7.14	46.2
	f	4	19.44 (1)	10.70	9.68	6.17	7.59	6.01	4.76	6.56 (1)	47.7
<i>Rhinolophus anderseni</i> <i>semi aequilis</i> (holotype)	m	1	—	10.46	9.86	6.19	7.58	6.00	4.51	—	46.39
	m	2	18.78 (18.3-19.26)	9.79 (9.72-9.86)	9.52 (9.51-9.52)	5.21 (5.01-5.41)	7.54 (7.52-7.56)	5.52 (5.46-5.57)	4.12 (4.03-4.21)	6.74 (6.51-6.97)	46.5 (45.2-47.7)
<i>Rhinolophus arcuatus</i>	f	3	18.68 (18.41-18.91)	9.53 (9.41-9.62)	9.06 (8.64-9.36)	5.08 (5.02-5.18)	7.14 (6.95-7.47)	5.48 (5.29-5.63)	4.15 (4.08-4.27)	6.31 (6.05-6.48)	46.0 (45.6-46.5)
	f	1	16.86	8.64	8.57	4.88	6.65	5.07	4.13	5.84	42.8
<i>Rhinolophus borneensis</i>	m	1	22.26	11.77	11.12	6.7	8.96	6.62	5.34	6.85	54.4
	f	4	20.87 (2) (20.7-21.03)	11.03 (10.83-11.27)	10.62 (10.51-10.78)	6.25 (5.87-6.59)	8.45 (8.39-8.51)	6.45 (6.37-6.52)	4.83 (4.55-5.06)	6.87 (2) (6.76-6.98)	52.4 (51.5-54.6)
<i>Rhinolophus macrootis</i>	m	3	17.3 (2) (17.21-17.38)	8.63 (8.62-8.64)	9.37 (9.32-9.44)	4.37 (4.33-4.42)	6.51 (6.49-6.53)	4.87 (4.84-4.91)	3.39 (3.36-3.43)	5.7 (2) (5.64-5.76)	45.5 (45.1-45.8)
	f	2	17.68 (17.28-18.08)	8.66 (8.61-8.70)	9.48 (9.39-9.56)	4.20 (4.17-4.22)	6.63 (6.48-6.78)	4.93 (4.9-4.95)	3.58 (3.41-3.75)	6.37 (1)	47.7 (46.9-48.5)
<i>Rhinolophus creaghi</i>	m	3	16.13 (2) (15.99-16.26)	8.87 (8.78-8.95)	8.55 (8.41-8.72)	4.84 (4.7-4.94)	6.16 (6.04-6.23)	4.71 (4.59-4.85)	3.57 (3.5-3.66)	5.08 (2) (4.85-5.31)	40.5 (39.2-41.3)
	f	3	16.16 (15.72-16.48)	8.72 (8.68-8.78)	8.48 (8.45-8.51)	4.87 (4.84-4.89)	6.27 (6.15-6.36)	4.72 (4.67-4.76)	3.46 (3.3-3.56)	5.12 (4.43-5.63)	41.5 (40.8-41.9)

from July, August, and October were pregnant (Sites 8, 9, and 10, respectively). Specimens examined: 5, Site 4 (2), Site 5 (2), Site 9 (1).

Rhinolophus acuminatus.—This poorly known species occurs from Thailand to Lombok and Palawan, but not elsewhere in the Philippines (Heaney et al. 1998; specimens from Negros reported by Csorba et al. (2003) as this species were mislabelled). It is found in lowland forest on Borneo (Payne et al. 1985) and in secondary lowland dipterocarp forest on Banggi (Md. Nor 1995). We captured this species in caves from ca. 60 to 250 m in caves (Sites 8 and 11), a bamboo thicket (Site 11), and primary forest (Site 1). At Site 8, we captured 90 individuals out of 2775 captures. At Site 11 we found ca. 20 individuals roosting in a small cave (ca. 0.5–3 m wide, 0.3–1.5 m high and 10 m long) with ca. 12 *Megaderma spasma*. At Site 1, we took two individuals over a small stream just below a rock outcrop containing many fissures suitable for roosting bats. We also captured a single individual in our temporary living quarters at Site 1 after we observed for several days a bat feeding inside our semi-enclosed tent for several minutes daily between 0430 and 0600 h. Of 15 adult females taken in July 2000 at Site 8, one was pregnant and one was lactating. Cranial measurements (Table 1) match those previously available (Ingle & Heaney 1992) that are based on series from Balabac and Busuanga reported by Kuntz (1969) and housed in the USNM. We also refer two specimens collected by A. C. Alcalá on 13 July 1984, at Malabusog, Roxas Municipality housed at UMMZ (162885 and 162886) to this species, and include them in Table 1.

Sanborn (1952) reported a single specimen from Palawan (housed in FMNH) that he regarded as the first record from Palawan. However, we have determined that a single specimen (UMMZ 53112) collected in the late 1800s by the Beal/Steere Expedition and subsequently named *R. anderseni*

seni aequalis (Allen 1922) was this species. Heaney compared this specimen, which is the holotype and only known specimen, to series of all species currently known from Palawan. It was unambiguously identified as *R. acuminatus*; as noted by Medway (1977:32), a dorsal connecting process with a prominent triangular point (as shown by Medway 1977 fig. 6a and by Ingle and Heaney 1992 fig. 13a) is present, the base of the sella is not expanded into a cup, the median groove of the horseshoe is not broadened, and papillae are not present. The ears (18 mm) are less than half of the length of head plus body, and the forearm is 46.4 mm. The skull (measurements in Table 1) is virtually identical to those in the series from Sites 1 & 8, including overall size and shape, nasal swellings, braincase breadth and inflation, tooththrows, palatal bridge, foramina in the roof of the posterior portion of the nasal passage, and bullae. Because *R. acuminatus* was named by Peters in 1871 (from Gadok, Java), we therefore recognize *R. anderseni aequalis* as its junior synonym. We note that Cabrera (1909) described *Rhinolophus anderseni* “probably from Luzon”. Aside from the holotype of *R. anderseni aequalis*, no specimens have subsequently been referred to this species. Csorba et al. (2003) tentatively assigned *R. anderseni* Cabrera as a junior synonym of *R. arcuatus* on the basis of the original description plus new drawings of the noseleaf and measurements of the skull, but without examining the holotype. We provisionally accept this, but point out the need for direct examination and comparisons. IUCN (2002) lists *R. acuminatus* as Data Deficient. Specimens examined: 8, Site 1 (4), Site 8 (1), Malabusog (2), and the holotype of *R. anderseni aequalis*.

Rhinolophus arcuatus.—Widespread from Sumatra to New Guinea (Heaney et al. 1998). Specimens from the Philippines currently identified as *R. arcuatus* may consist of two or more species (Heaney et al. 1991, 1999; Ingle & Heaney 1992; Rickart et al. 1993). Individuals referred to this

"species" have been found in agricultural areas, secondary forest, and primary lowland, montane, and mossy forest (Heaney et al. 1991, 1999; Ingle 1992; Rickart et al. 1993). We regularly captured this species at elevations from sea level to 1400 m in lowland primary forest (Sites 1 and 2), montane forest (Site 3), and caves (Sites 5 and 8). We also captured a single individual in the understory of mature but disturbed forest near a cave at Site 9, and we tentatively identified two individuals from Site 15 (which were released) as belonging to this species. Of 8 adult females taken between 15 and 20 May 2000 at Site 5, 5 were pregnant and one was lactating. Of 22 adult females taken in July 2000 at Site 2, one was lactating, and of 189 captured in July at Site 8, none were pregnant but 14 were lactating. These are the first specimens of this species from the Palawan faunal region. Cranial measurements (Table 1) closely match those of specimens from Leyte (Rickart et al. 1993) and southern Luzon (Heaney et al. 1999). Specimens examined: 5, Site 1 (2), Site 2 (1), Site 3 (2).

Rhinolophus cf. borneensis.—A single specimen taken by P. O. Glass on 31 January 1978 at "Sabang, Buenavista" (in Barangay Cabayugan, near Ulugan Bay in Puerto Princesa Municipality, ca. 10°05'N, 118°49'E; UMMZ 161395) appears to be this species. It was previously known from Indochina, the Malay Peninsula, Java, and Borneo, as well as some smaller islands in the southern South China Sea (Corbet & Hill 1992, Csorba et al. 2003); this is the first record from Palawan and from the Philippines. Cranial measurements and features (Table 1) closely match specimens in FMNH from Sarawak, the Natuna Islands, and Sabah, and external features are similar, but because we have only a single specimen, the identification is tentative. On Borneo, "the species roosts in caves, sometimes in colonies of several hundred individuals" (Payne et al. 1985). P. O. Glass (*in litt.*) noted that he captured the specimen in a mist net in a small banana grove in an

area of mixed agricultural/second growth forest within 1 km of mature forest. Specimens examined: 1, from Sabang.

Rhinolophus creaghi.—This species was previously known from Borneo and Madura Islands, where it often roosts in caves (Corbet & Hill 1992, Csorba et al. 2003, Koopman 1993, Medway 1977, Payne et al. 1985). This is the first record of this species from Palawan Island and the Philippines. On Palawan, we found it to be common in primary lowland forest from near sea level to at least 700 m. We captured one individual at Site 1 and 11 individuals at Site 2. It roosts in caves, often in large numbers; we captured 368 (45% of captures) at Site 4, 239 (9% of captures) at Site 8, and 33 (6% of captures) at Site 5. Of 135 adult females captured in December 1999 at Site 4, 8 were pregnant. Of 16 captured at Site 5 in March to April, none were reproductively active; of 11 at Site 2 and 151 at Site 8 (July 2000), none were pregnant but one and 12 were lactating, respectively. Cranial measurements (Table 1) show this to be the largest member of the genus on Palawan; our specimens are not distinguishable from a small series from Borneo (FMNH 47071–47075). Two previously unidentified specimens from Mt. Salicod, 2300 ft. (which may be the same mountain as Mt. Salakot, Site 2; P. O. Glass, *in litt.*), taken by P. O. Glass in 1978 and housed in the UMMZ, were taken earlier but were not reported; cranial measurements from these specimens are included in Table 1. This species is listed as Near-Threatened by IUCN (2002). Specimens examined: 7, Site 4 (3), Site 5 (1), Site 8 (1), Mt. Salicod (2).

Rhinolophus macrotis.—This poorly known species ranges from India to Sumatra and the Philippines, where it is known from lowland forest with some records from caves (Heaney et al. 1998, Ingle 1992). Our specimens represent the first record from Palawan. We captured this species in or near three caves in disturbed lowland forest at 50–250 m at Sites 5 (10 captures) and 8 (25 captures). The species ap-

pears to be uncommon. At Sites 5 and 8 it represented less than 5% and 1% of our captures, respectively. At Site 5 on 20 May 2000, we captured and examined two adult females; both were pregnant. Of 8 adult females captured in July at Site 8, none were pregnant or lactating. Cranial measurements of 5 individuals (Table 1) fall within or near the range for the species in Ingle and Heaney (1992). Specimens examined: 5, Site 5 (4), Site 8 (1).

Rhinolophus virgo.—This Philippine endemic is widely distributed within the Philippines (Heaney et al. 1998). It is known from secondary forest, primary lowland forest, reaching mossy forest on small, low-lying islands, and often roosts in caves (Heaney et al. 1991, Ingle 1992, Rickart et al. 1993); Sanborn (1952) reported a series from Tanabog, Palawan. This species appeared to be rare in the cave at Site 4 (0.5% of captures), common at Site 8 (151 captures, about 6% of total) and abundant in some caves at Site 5 (15% of captures). We also captured this species in primary forest at Sites 2 and 15. Of 29 adult females captured between 27 March and 4 April 2000, none were pregnant or lactating. Of 35 females captured at Site 5 between 15 and 20 May 2000, 16 were pregnant and 5 were lactating. Of 78 females taken at Site 8 in July 2000, 6 were pregnant and 2 were lactating. Cranial measurements (Table 1) fall within the range (Ingle & Heaney 1992) or very near the range (Rickart et al. 1993) of previously available individuals. IUCN (2002) lists this species as Near-Threatened. Specimens examined: 6, Site 4 (2), Site 5 (4).

Family Vespertilionidae—Vesper and Evening Bats

This diverse family of bats is generally poorly documented, and more species should be sought on Palawan, including such widespread taxa as *Harpiocephalus harpia*, *Murina cyclotis*, *Myotis ater* (which Hill 1983 and Corbet & Hill 1992 have

shown to be distinct from *Myotis muricola* and to be present on Culion Island in Palawan faunal region), *Philetor brachypterus*, and *Pipistrellus tenuis*.

Glischropus tylopus.—This poorly known species is found from Myanmar to the Molucca Islands and Palawan (Heaney et al. 1998). In Peninsular Malaysia it roosts in rock crevices, bamboo, and in new banana leaves (Payne et al. 1985). We never encountered this species, but it is represented by a specimen in the USNM (Holister 1913).

Kerivoula hardwickii.—This species is widespread from India and southern China to the Lesser Sunda Islands and the Philippines (Heaney et al. 1998). It was previously known from lowland, montane, and ridge-top mossy forest from 500 to 1600 m in the Philippines (Heaney et al. 1999, Rickart et al. 1993). Everett (1889) included mention of this species from Palawan. A previous record from UMMZ (Heaney et al. 1998) has been re-identified as *K. whiteheadi*, as noted below. Payne et al. (1985) reported the species to "frequent the understory of tall forest" on Borneo, and Md. Nor (1995) caught one in primary lowland dipterocarp forest on Banggi Island "in the axil of a leaf on a rattan vine 1 m above ground", and netted them in the understory of primary forest on Balambangan Island. We captured two adult females, one of which was lactating, in a bamboo thicket at Site 11 (ca. 60 m asl), and two individuals in the understory (ca. 2–4 m above the ground) of primary lowland forest at ca. 650 m elevation at Site 2, all in harp-traps. Specimens examined: 3, Site 2 (1), Site 11 (2).

Kerivoula pellucida.—This poorly known species is known from the Malay Peninsula, the Sunda Shelf, Jolo, and Palawan (Heaney et al. 1998). Known only from lowland forest (Payne et al. 1985). Taylor (1934) reported two specimens from Palawan (no locality given) that he obtained from a group of seven that he found flying together in daylight: his map (Fig. 13),

shows the locality in the vicinity of Brooke's Point. On 21 June 2000, using a harp-trap we captured an adult female carrying a suckling infant in secondary lowland forest (ca. 80 m) over a small stream at Site 7. Cranial measurements of the adult female (Table 2) are smaller than the one specimen from Davao del Norte, Mindanao available to Ingle and Heaney (1992), but they are otherwise very similar; additional specimens are badly needed to examine patterns of variation. Specimens examined: 2, Site 7 (2).

Kerivoula whiteheadi.—This poorly known species is widely distributed from southern Thailand to Borneo and the Philippines (on Luzon, Mindanao, and Palawan; Heaney et al. 1998). In the Philippines, it is known only from near sea level in disturbed forest and agricultural areas (Sanborn 1952). A single specimen in the UMMZ captured by P. O. Glass on 29 Sept. 1978 at Irawan, Puerto Princesa Municipality (noted as 2 km N Irawan, at the base of Mt. Beaufort by P. O. Glass, *in litt.*) was erroneously reported by Heaney et al. (1998) under both *K. hardwickii* and this species. Additionally, two specimens taken "under banana fronds" by C. A. Ross on 8 April 1987 at Barangay Binwang, Quezon Municipality, are housed in the USNM. We captured a single individual of this species in a harp-trap near ground level in a cogon grassland (*Imperata cylindrica*) at Site 6. Cranial measurements of these four individuals (Table 2) are similar to those in Ingle & Heaney (1992) of a specimen from Mindanao, though some variation in size is present; more specimens are needed to assess geographic variation. Specimens examined: 4, Site 6 (1), Irawan, Puerto Princesa Municipality, 60 m (1), and Binwang, Quezon (2).

Miniopterus australis.—This common species is found from India to Australia; it is widespread in the Philippines, but this is the first record from Palawan (Heaney et al. 1998). It is known to roost in caves in lowland areas of agriculture or second growth

(Heaney et al. 1991, Rickart et al. 1993, Sanborn 1952). We captured this species in varying numbers at several caves. In primary and disturbed lowland forest at Sites 4 and 5 it was scarce, represented by less than 1% and less than 3% of captures, respectively. At Site 8 it was abundant (45% of 2775 captures). Cranial measurements of 4 individuals (Table 2) are similar to those reported by Ingle and Heaney (1992) and Rickart et al. (1993) from the Philippines, and by Corbet & Hill (1992) from throughout the species range. Specimens examined: 4, Site 4 (2), Site 5 (2).

Miniopterus schreibersi.—This common species is found from Europe to the Solomon Islands and is widespread in the Philippines, but this is the first record from Palawan (Heaney et al. 1998). It is common in caves throughout the lowlands in agricultural areas and forest and known from both lowland and montane forest (Heaney et al. 1991, 1999; Rickart et al. 1993; Sanborn 1952). We captured this species in and around caves in disturbed and primary lowland forest at Sites 4, 5, and 8. At Sites 4 and 8 the species was abundant, represented by 47% and 26% of captures respectively. At Site 5 it was common at 10% of 575 captures. Of 214 adult females captured in December 1999 at Site 4, only one was pregnant. Of 36 captured between 15 and 20 May 2000 at Site 5, 15 were pregnant and none were lactating. Of 421 captured at Site 8 in July 2000, none were pregnant but 4 were lactating. Cranial measurements (Table 2) are similar to those reported by Ingle and Heaney (1992) and Rickart et al. (1993) from the Philippines, and by Corbet and Hill (1992) from throughout the species range. IUCN (2002) lists this species as Near-Threatened, but its abundance in heavily disturbed habitat in the Philippines (Heaney et al. 1998, Rickart et al. 1993) makes this inappropriate. Specimens examined: 6, Site 4 (4), Site 5 (1), Site 8 (1).

Miniopterus tristis.—This widespread species is found from the Philippines to the Solomon Islands; this is the first record

Table 2.—Means and ranges of cranial measurements of adult Vespertilionidae from Palawan Island, Philippines.

Species	Sex	n	Condyloly- incisive length	Zygomatic width	Mastoid width	Orbital length	Canine to last molar	Molariform toothrow	Palatal breadth	Palatal length	Forearm length
<i>Kerivoula hardwickii</i>	m	1	13.39	8.48	7.14	4.05	5.39	3.53	2.72	6.82	33.1
	f	2	13.75 (13.63-13.87)	8.70 (8.64-8.76)	7.29 (7.05-7.53)	4.07 (4.07-4.07)	5.62 (5.50-5.74)	3.74 (3.65-3.82)	2.90 (2.84-2.96)	6.98 (6.91-7.04)	33.6 (33.4-33.7)
<i>Kerivoula pellucida</i>	f	1	13.51	8.26	7.21	3.08	5.57	3.87	2.58	6.94	31.3
<i>Kerivoula whiteheadi</i>	f	4	12.00 (11.85-12.28)	7.56 (7.44-7.64)	6.66 (6.56-6.77)	—	5.17 (5.07-5.22)	3.18 (3.12-3.30)	2.41 (2.34-2.49)	5.82 (5.70-6.08)	29.7 (29.4-30.4)
<i>Mintopterus australis</i>	m	1	13.25	7.21	7.16	4.46	5.21	3.80	3.06	5.79	36.7
	f	3	13.06 (12.90-13.15)	7.39 (7.29-7.58)	7.28 (7.23-7.33)	4.29 (4.16-4.40)	5.19 (5.16-5.21)	3.76 (3.73-3.79)	3.00 (2.91-3.06)	5.66 (5.56-5.79)	37.1 (36.2-37.8)
<i>Mintopterus schreibersi</i>	m	1	15.33	8.88	8.73	5.31	6.28	4.58	3.65	6.35	47.4
	f	5	14.78 (14.67-14.94)	8.42 (8.30-8.57)	8.19 (8.12-8.33)	5.05 (4.90-5.32)	6.14 (6.0-6.25)	4.45 (4.32-4.56)	3.39 (3.26-3.54)	6.43 (6.37-6.48)	42.3 (39.2-43.9)
<i>Mintopterus tristis</i>	m	1	18.50	10.72	9.82	6.51	7.75	5.66	4.62	8.13	54.2
	f	2	18.72 (18.71-18.74)	10.76 (10.74-10.78)	9.76 (9.62-9.93)	6.73 (6.70-6.76)	7.83 (7.75-7.91)	5.73 (5.66-5.81)	4.37 (4.33-4.40)	8.31 (8.31)	53.3 (53.3-53.3)
<i>Murina cf. tubinaris</i>	m	1	14.63	9.11	7.73	5.08	5.23	3.90	3.17	6.64	33.1
<i>Myotis macrotorus</i>	m	1	17.88	11.8	9.51	6.88	7.30	5.31	4.15	8.58	48.1
<i>Myotis rufopictus</i>	f	1	19.18	12.25	9.68	6.91	8.40	5.88	3.84	9.69	58
<i>Pipistrellus javanicus</i>	m	1	13.30	9.31	7.90	5.15	4.88	3.82	3.33	—	34.0
<i>Tylonycteris pachypus</i>	f	1	13.03	9.01	7.60	4.89	4.70	3.78	3.23	—	35.5
	m	1	10.29	7.98	6.71	3.53	3.45	2.69	2.86	3.91	23.4
	f	2	10.24 (10.10-10.34)	7.75 (7.56-7.96)	6.75 (6.59-6.96)	3.74 (3.57-3.80)	3.41 (3.37-3.45)	2.68 (2.59-2.74)	2.75 (2.71-2.81)	3.86 (3.67-4.05)	23.6 (22.8-24.6)

from Palawan (Heaney et al. 1998). The species is known to roost in caves and forage in disturbed forest (Rickart et al. 1993, Sanborn 1952). We captured one specimen in a cave surrounded by old-growth forest at Site 4 and two in a cave surrounded by disturbed areas and secondary forest at Site 10. *Miniopterus tristis* appeared to be consistently less common than the other species of *Miniopterus*. Cranial measurements of 3 individuals (Table 2) are similar to those reported by Ingle and Heaney (1992) and Rickart et al. (1993) from the Philippines, and by Corbet and Hill (1992) from throughout the species range. Specimens examined: 3, Site 4 (1), Site 10 (2).

Murina cf. tubinaris.—A single specimen of a small tube-nosed bat (genus *Murina*) was taken in a lowland grassland-forest mosaic at Site 12 on 24 March 1997, and is housed in the Staatliches Museum für Naturkunde in Stuttgart, Germany (#49238). The specimen (Table 2) is very similar to a series from Tonkin, Vietnam (FMNH 32203–32204, 46626–46627), though slightly larger. In our specimen, as in the Vietnamese series, the upper tooth-rows converge slightly, the anterior premolars are reduced, and the canines are short but longer than the premolars, as noted by Koopman and Danforth (1989) and Corbet and Hill (1992). The length of forearm (33 mm) falls at the center of the range given by Koopman and Danforth for *M. tubinaris* (28–35 mm), and at the high end given for *M. suilla* (26–33 mm). Koopman and Danforth (1989) considered *M. florium*, *M. suilla*, and *M. tubinaris* to be members of a species group, and perhaps to be conspecific, noting that few specimens are available. Corbet and Hill (1992) re-emphasized the uncertainty in current taxonomy, but took a somewhat different view, referring specimens from Borneo to *M. suilla*, rather than to *M. tubinaris*. While we agree entirely on the need for more specimens and further study, we follow Koopman & Danforth (1989) on referring Bornean specimens to *M. tubinaris*, and provisionally re-

fer the specimen from Palawan to this same species. Specimen examined: 1, Site 12 (1).

Myotis horsfieldii.—This common species is distributed from southeastern China to the Malay Peninsula, Sulawesi, and the Philippines (Heaney et al. 1998). On Borneo, the species “roosts in crevices or bell-holes in caves, usually not far from large streams or rivers” (Payne et al. 1985). In the Philippines, it has been recorded in lowland forest and agricultural areas, up to 800 m (Heaney et al. 1998). We never encountered this species; two specimens in the UMMZ taken by A. C. Alcalá in Sitio Malabusog, Tinitian, Roxas Municipality in 1984 were reported by Heaney et al. (1998).

Myotis macrotrarsus.—This species is known from Borneo and the Philippines (Heaney et al. 1998); it roosts in caves near sea level and forages in agricultural areas (Heaney and Uzzurum, unpubl. data). Md. Nor (1995) caught the species over a dry river bed and in the understory of primary lowland forest on Balambangan Island. In a cave in disturbed lowland forest at Site 8, this species was represented by <0.5% of 2775 captures. We also observed small numbers in the cave at PPSRNP. Cranial measurements (Table 2) of one individual show it to be slightly larger than those reported by Ingle & Heaney (1992). IUCN (2002) lists this species as Near-Threatened. Specimens examined: 1, Site 8 (1).

Myotis rufopictus.—This poorly known Philippine endemic has been recorded from primary lowland and montane forest (Heaney et al. 1999, Mudar & Allen 1986). We never encountered this species; on Palawan, it is known from a single specimen in UMMZ reported by Allen (1922). We follow Ingle & Heaney (1992) in regarding this as one of several distinct species within the subgenus *Chrysopteron*, rather than recognizing only a single species, *Myotis formosus*, within the subgenus (e.g., Corbet & Hill 1992). This species is not listed by IUCN (2002); we recommend listing as Data Deficient. Measurements in Table 2 of the specimen reported by Allen (1922) were

taken by Heaney. Specimen examined: 1, Puerto Princesa (1).

Pipistrellus javanicus.—This species is distributed from Korea to Java and the Philippines (Heaney et al. 1998). Taxonomic status is uncertain; *P. imbricatus* has been reported from Palawan (e.g., Allen 1922, Corbet & Hill 1992, Sanborn 1952), but Ingle and Heaney (1992) were unable to distinguish more than one species of *Pipistrellus* of this size in the Philippines; detailed study is needed. It is common in primary montane forest and uncommon in lowland and mossy forest (Heaney et al. 1999, Ingle 1992, Sanborn 1952). We captured two individuals from a roost in a hollow tree in montane forest (ca. 1300 m) at Site 3. The opening in the tree appeared to have formed where a branch had been broken off the tree and was quite small (ca. 1.5 × 5 cm). Cranial measurements (Table 2) fall within the range of specimens reported by Ingle and Heaney (1992), and are slightly smaller than a series from southern Luzon (Heaney et al. 1999). Specimens examined: 2, Site 3 (2).

Scotophilus kuhlii.—This common species is widespread from Pakistan to Taiwan and the Philippines (Heaney et al. 1998); it is abundant in urban and agricultural areas, and roosts in buildings and "tents" made from modified palm leaves (Heaney et al. 1998; Rickart et al. 1989, 1993). Hollister (1913) and Taylor (1934) reported it from Puerto Princesa, Sanborn (1952) reported it from Brooke's Point, and we found it to be abundant in buildings at the Provincial Agriculture Center, Irawan, Puerto Princesa, and in staff houses of the State Polytechnic College in Puerto Princesa, and in mixed urban/agricultural areas (Site 12).

Tylonycteris pachypus.—This tiny bat is widespread from India to the Philippines (Heaney et al. 1998). In the Philippines, it is known from bamboo stands in agricultural areas (Heaney & Alcalá 1986); Hollister (1913) reported a specimen from Puerto Princesa. We captured several individuals of this species in a bamboo thicket

at Site 11. Very near the capture site we observed what appeared to be more than a dozen individuals of this species foraging over a few remnant trees in a cleared area with houses that is immediately surrounded by logged-over and secondary forest. Specimens examined: 5, Site 11 (5).

Tylonycteris robustula.—This species is also widespread from southern China to the Lesser Sunda Islands and the Philippines (including records from Calauit, Luzon, and Palawan); its habitat is apparently similar to that of *T. pachypus* (Heaney & Alcalá 1986, Heaney et al. 1998). We never encountered this species.

Family Molossidae—Free-Tailed Bats

This family is generally poorly known in Southeast Asia, partly because they typically fly high above the canopy and are therefore rarely netted. At least one species (*Chaerophon plicata*) is widespread in the region and should be sought on Palawan.

Cheiromeles torquatus.—This poorly known species is found from Sumatra to Java, Borneo, and Palawan, but not the rest of the Philippines (Heaney et al. 1998). It roosts in large caves and hollow trees and forages in open areas, over streams, and above forest canopy on Borneo (Payne et al. 1985). We never encountered this species, which was documented on Palawan by Sanborn (1952) based on a single specimen. IUCN (2002) lists this species as Near-Threatened.

Mops sarasinorum.—This very poorly known species occurs in Sulawesi and the Philippines; the Palawan record is based on a single specimen in the Senckenberg Museum, Frankfurt (Heaney et al. 1998). It probably occurs in lowland forest (Heaney et al. 1998). We never encountered this species. It is listed by IUCN (2002) as Near-Threatened, but we recommend Data Deficient.

Order Primates

Family Cercopithecidae—Monkeys

Macaca fascicularis.—This common monkey occurs from Myanmar to Timor

and the Philippines (Fooden 1995, Heaney et al. 1998). It is known from agricultural areas near forest, second growth, secondary forest, and primary lowland and montane forest (Heaney et al. 1998, 1999; Rickart et al. 1993); Sanborn (1952) reported specimens from Iwahig, Puerto Princesa, and Brooke's Point. Reis & Garong (2001) reported a specimen from sediments in a rock-shelter near Tabon Cave, Quezon Municipality dated to 11,130 BP. We commonly observed this species at all of our sites (except Site 13), in secondary and primary forest (including mangrove, swamp forest, beach forest, and lowland forest) from sea level to 1000 m; at forest edge near agricultural areas and houses they seem to be less common and more shy. On Palawan, the species is under moderate hunting pressure for meat and the local pet trade, but appeared to have stable populations. In most areas, it was quite wary of humans, but in areas such as the PPSRNP (Site 15), the species did not associate humans with danger, and had become a regular thief of picnic baskets. It is listed by IUCN (2002) as Near-Threatened.

Order Pholidota

Family Manidae—Pangolins

Manis culionensis.—This endemic species of the Palawan faunal region, with records from Palawan and Culion Islands (Heaney et al. 1998), was formerly included within *Manis javanica* (Feiler 1998). It is known from primary and secondary lowland forest, possibly localized in distribution (Allen 1910, Hoogstraal 1951, Sanborn 1952, Taylor 1934). We sighted several in lowland grassland/forest mosaic at Site 12. It is hunted for its skin, which is used to treat asthma. We have seen it for sale in Puerto Princesa and our guide at Site 11 said that it is hunted in logged-over lowland forest in that area. The species was described by local informants as fairly common, but hunting pressure is moderately heavy. *Manis javanica* is listed by IUCN

(2002) as Near-Threatened; *M. culionensis* probably deserves the same status.

Order Rodentia

Family Sciuridae—Squirrels

Hylopetes nigripes.—This large gliding squirrel is endemic to the Palawan faunal region; the number of museum specimens (Allen 1910, Sanborn 1952) suggests that it is common. Reis & Garong (2001) reported two specimens from sediments in a rock-shelter near Tabon Cave, Quezon Municipality dated to 11,130 BP. Taylor (1934) found the species in primary and secondary lowland forest where they nest in cavities in large trees. We observed an individual running up the side of a large hollow tree in primary forest at Site 1, and we frequently heard and twice spotlighted them in mature lowland forest at Site 15. We also heard the distinctive calls several times in selectively logged but largely intact forest near Barake, Aborlan Municipality, in the Victoria Range. According to local residents, the species is common in mature forest and is occasionally hunted as a source of food. IUCN (2002) lists this species as Near-Threatened; by current criteria, it should be listed as Data Deficient.

Sundasciurus juvencus.—This tree squirrel is endemic to central and northern Palawan Island (Heaney et al. 1998). Hoogstraal (1951) and Sanborn (1952) reported this species from primary and secondary lowland forest. We commonly observed this species in primary and secondary lowland forest at Sites 1, 2, 7, 11, 12, and in both secondary forest and grassland/degraded forest mosaic at Site 15. We also found it in a very small (<1 ha.) patch of secondary lowland forest surrounded by grassland and agricultural areas at Site 6. We observed the species on Dumaran Island, but not on Malinau or Rasa. The species is reportedly a common pest in coconut plantations. It is occasionally hunted as a source of food and for the local pet trade. It is listed by IUCN (2002) as Endangered, but this is strongly

contradicted by the available data, and we recommend de-listing.

Sundasciurus rabori.—This poorly-known species, described from 5 specimens taken at 3600–4350 ft (ca. 1100–1300 m) on Mt. Mantalingajan, is endemic to Palawan Island (Heaney 1979). P. C. Gonzales deposited 2 specimens at the UMMZ that he collected on Mt. Gorangbato in Brooke's Point Municipality in 1984; these are the only reported specimens aside from the original type series from Mt. Mantalingajan (Heaney 1979). Although we worked in some seemingly suitable habitats on Cleopatra's Needle (Site 3), we did not specifically seek this species, and we never encountered it. The IUCN (2002) lists *S. rabori* as Vulnerable, but based on current IUCN criteria, it should be considered Data Deficient.

Sundasciunis steerii.—This species is endemic to Balabac and southern Palawan Island (Heaney et al. 1998); Sanborn (1952) reported a large series from Brooke's Point. Heaney et al. (1998) listed it as common in lowland forest and coconut and banana plantations. Because all of our study sites were in central and northern Palawan, we never encountered this species. It is listed by IUCN (2002) as Near-Threatened; since its habitat use is similar to the closely-related *S. juvencus*, it is probably not threatened.

Family Muridae—Mice

Chiropodomys calamianensis.—This poorly known arboreal mouse is endemic to the Palawan faunal region; it is closely related to species on the Sunda Shelf (Musser 1979). Reis & Garong (2001) reported a specimen from sediments in a rock-shelter near Tabon Cave, Quezon Municipality dated to 11,130 BP. It is known from forest near sea level (Taylor 1934), coconut plantations, bamboo thickets, and buildings (Sanborn 1952); there are 12 specimens from Palawan in FMNH and NMP from the Hoogstraal expedition (Sanborn 1952). The

genus is apparently difficult to capture (Musser 1979); we never encountered this species. We recommend IUCN listing as Data Deficient.

Haeromys pusillus.—This species is known only from Borneo, Palawan, and Calauit Islands (Musser & Carleton 1993, Musser & Newcomb 1983). It is cited in Heaney et al. (1998) as "*Haeromys* sp. A" as potentially endemic to Palawan, but we follow Musser (pers. comm.) in treating it as conspecific with *H. pusillus*. We never encountered this species, but Musser & Carleton (1993) cited a specimen from Palawan. A specimen of *H. pusillus* was taken in Sabah, Borneo, in a pit-fall trap near the edge of tall dipterocarp forest (Payne et al. 1985), and A. C. Alcalá stated that he captured the specimen from Calauit (in FMNH) by hand in a bamboo thicket (pers. comm.). IUCN (2002) listed this species as Vulnerable, but based on current criteria, it should be considered Data Deficient.

Maxomys panglima.—This common rat is endemic to the Palawan faunal region; the genus is common on the Sunda Shelf, but is absent from oceanic portions of the Philippines (Musser et al. 1979). Sanborn (1952) reported large series from several localities. We found it to be the most commonly captured small mammal in agricultural/forest mosaic at Site 12 (62% of 169 captures), and was common to abundant in secondary forest (Site 11), primary lowland (Sites 1 and 2), and montane forest (Site 3) from near sea level to at least 1550 m. We captured a single juvenile in mossy forest at 1580 m at Site 3. Because we found this species to be common, although sometimes patchy, in all lowland and montane forested sites where we trapped extensively, and in mixed agricultural/second growth areas at Sites 11 and 12, we consider the IUCN (2002) listing as Near-Threatened to be unjustified. Specimens examined: 5, Site 1 (3), Site 3 (2).

Mus musculus.—This introduced commensal has a nearly world-wide distribution, although Southeast Asian populations

are sometimes treated as a separate species, *M. castaneus* (Musser & Carleton 1993). It is common in human habitations in urban and rural areas (Heaney et al. 1998). We captured several in a residential area at Site 12, and it is most likely common in such places throughout Palawan.

Palawanomys furvus.—This poorly known monotypic genus is endemic to Palawan Island. It has been taken from a single locality on Mt. Mantalingajan and probably occurs in high mountain forest (Musser & Newcomb 1983). Our survey efforts on Cleopatra's Needle (Site 3) failed to find this species; perhaps it is restricted to the more extensive mountain ranges of southern Palawan. The IUCN (2002) lists this species as Endangered; the lack of data and lack of damage to its presumed habitat (montane and mossy forest) suggest that it should be listed as Data Deficient.

Rattus exulans.—This introduced commensal species is widespread from Bangladesh to Easter Island (Heaney et al. 1998). The first records from Palawan were named as a distinct species (*luteiventris*) by Allen (1910), but it is currently treated as a junior synonym of *R. exulans* (Musser & Carleton 1993). It is common in agricultural areas (Barbehenn et al. 1973, Rabor 1986) and sometimes present in disturbed forest and rare in primary forest (Barbehenn et al. 1973; Heaney et al. 1991, 1998). We found this species in grassland (Site 6), agricultural areas (Sites 6, 11, 12, and 14), and in secondary lowland forest (Site 7). The species appears to be absent from primary (e.g., Sites 1, 2, and 3) and logged-over forest (e.g., Site 11) on Palawan. Specimens examined: 4, Site 6 (3), Site 11 (1).

Rattus tanezumii.—This introduced commensal, formerly included within *Rattus rattus* (Musser & Carleton 1993), is widespread from Afghanistan to New Guinea and Micronesia (Heaney et al. 1998). It is often abundant in urban and agricultural areas and common in disturbed forest up to 1800 m (Danielsen et al. 1994; Heaney et al. 1989, 1999; Rabor 1986; Sanborn 1952).

Hoogstraal (1951) and Sanborn (1952) found them to be common on Palawan in some agricultural and residential areas. We captured three at Site 13, and three in a residential area in Puerto Princesa; vouchers were deposited in the NMP and the collection of the Palawan Council for Sustainable Development.

Rattus tiomanicus.—This indigenous rat is found on the Malay Peninsula and the islands of the Sunda Shelf, including Palawan (Heaney et al. 1998). Payne et al. (1985) reported the species from secondary forest, agricultural areas and gardens, scrub, and grassland. We captured this species in grassland/forest mosaic at Site 12 (9% of captures), two in selectively logged forest at Site 13, one in a ricefield at Site 14, and three individuals from mossy forest and the transition zone between mossy and montane forest at Site 3. At Site 3, two individuals were taken at ca. 1580 m during the night and one at ca. 1540 m during the day. Specimens examined: 3, Site 3 (3).

Sundamys muelleri.—This moderately large rat is found from southern Myanmar to the Sunda Shelf, including Palawan (Heaney et al. 1998); the genus is absent from the oceanic Philippines. Sanborn (1952) described a subspecies endemic to Palawan, *S. m. balabagensis*, from a single specimen taken at 3000 ft (ca. 900 m) "in thick forest near the top of Mt. Balabag"; two additional specimens in the USNM are from Pinigisan, on the lower slopes of Mt. Mantalingajan at 2100–2500 ft (ca. 640–760 m). Additional specimens from the Palawan region are from Culion Island (Sanborn 1952), Balabac, and Busuanga (USNM; Heaney et al. 1998). On Borneo, the species occurs in forest, often near streams (Payne et al. 1985) at elevations usually below 3500 ft (ca. 1070 m; Medway 1977). Md. Nor (1995) caught the species on Banggi, Balambangan, and Mollangan Islands "mostly in primary forest on low ground and near streams". We captured one individual from a riparian zone in primary forest at ca. 700 m at Site 2, and

two in lowland grassland/forest mosaic at Site 12. Specimen examined: 1, Site 2 (1).

Family Hystricidae—Porcupines

Hystrix pumila.—The only porcupine found in the Philippines is endemic to the Palawan faunal region; other species occur widely on the Sunda Shelf and continental Asia. Reis & Garong (2001) reported 3 specimens from sediments in a rock-shelter near Tabon Cave, Quezon Municipality dated to 11,130 BP. It is known to occur in secondary and primary lowland forest and to den in abandoned mine shafts (Hoogstraal 1951, Sanborn 1952). We observed this species at dusk along the edge of secondary forest at Site 11, once at night at Site 15 (where it was feeding on fruit of *Terminalia catappa*), and several times at night in grassland/forest mosaic at Site 12. Local guides reported them at Site 14, at the Iwahig Penal Colony in Puerto Princesa, in Rizal Municipality, and in Dumaran Municipality (on the mainland). This was reported as the most important game species for the Tagbanua ethnic community in Barake, Aborlan Municipality (Lacema & Widmann 1999); they are often dug out of their subterranean dens. Not listed by IUCN (2002) but listing as Data Deficient or Near-Threatened seems justified.

Order Carnivora

Family Felidae—Cats

Prionailurus bengalensis.—This small cat is widespread from Siberia to Pakistan and Bali, with reports from the Philippines on Busuanga, Cebu, Negros, Palawan, and Panay Islands only (Heaney et al. 1998, Taylor 1934). The population from the Palawan faunal region was described recently as a distinct subspecies, *P. b. heaneyi*, by Groves (1997); it is well represented by museum specimens (Allen 1910, Sanborn 1952). Rabor (1986) reported the species from agricultural areas and forest from sea level to ca. 1500 m. We spotlighted one

along a river trail in Barake, Aborlan Municipality.

Family Mustelidae—Weasels, Otters, and Badgers

Amblonyx cinereus.—This otter occurs from India to Taiwan and the Sunda Shelf (Heaney et al. 1998). On Palawan, it is found in coastal rivers and bays (Hoogstraal 1951, Rabor 1986, Sanborn 1952). Payne et al. (1985) and Sanborn (1952) reported the species feeds on crustaceans, mollusks, and fish where there is permanent water and some tree cover. Rangers at PPSRNP reported to Heaney and Widmann that otters frequently visit along the beach and small streams, and local people reported them from the Iwahig River (Puerto Princesa), Aborlan River (Aborlan Municipality), Malatgao and Taritien Rivers (Narra Municipality), and adjacent mangrove and freshwater swamp forest. We received one report of an otter raiding a prawn pond. IUCN (2002) lists this species as Near-Threatened.

Mydaus marchei.—This badger is endemic to the Palawan faunal region; it is related to a species that occurs on the Sunda Shelf. It has been documented in mixed grassland and secondary forest (Hoogstraal 1951, Kruuk 2000, Rabor 1986, Taylor 1934), and Sanborn (1952) reported series from several localities. We occasionally smelled its strong odor in areas of mixed agriculture and secondary forest throughout Palawan; we sighted it often in residential and cultivated areas, grassland, and grassland/forest mosaic at Site 12, and rarely in ricefields and freshwater swamp forest at Site 14. One individual living in a den on campus at the State Polytechnic College was easily followed and observed. Because it is widespread and moderately common on Palawan, and is rarely hunted (Grimwood 1976, Kruuk 2000), we agree with Kruuk (2000) that the IUCN listing of this species as Vulnerable is not justified.

Family Herpestidae—Mongoose

Herpestes brachyurus.—The only mongoose found in the Philippines is distributed from the Malaysian Peninsula to Borneo and Palawan (Heaney et al. 1998). The Palawan population was named as a distinct species (*H. palawanus* Allen 1910), but currently is treated as a subspecies (Corbet & Hill 1992). Allen (1910) described them based on one specimen from Iwahig; Sanborn (1952) reported one specimen from Puerto Princesa and one from Brooke's Point, and Rabor (1986) found the species most often near rivers. On Borneo, Payne et al. (1985) found the species to occur in primary and secondary lowland forest, plantations, and gardens. We never encountered this species; but we received reports of them at Site 14.

Family Viverridae—Civets

Arctictis binturong.—The binturong is known from northern Myanmar to the Sunda Shelf (Heaney et al. 1998). On Borneo, the species is arboreal and terrestrial, mostly nocturnal, and occurs in old-growth and secondary forests, sometimes entering agricultural areas near forest (Payne et al. 1985). The Palawan population, which initially was named as a distinct species (*A. whitei* Allen 1910) from four specimens, is still represented by few specimens (Heaney et al. 1998). Rabor (1986) reported observations from primary and secondary lowland forest up to 200 m. Our guide at Site 11 reported that a juvenile repeatedly entered remnant trees that were fruiting in a clearing surrounded by secondary forest. At Site 2, we observed *A. binturong* drinking water from a stream at ca. 400 m during mid-day. We spotlighted one in a fruiting *Ficus* tree at Site 15, and twice saw one in grassland/forest mosaic at Site 12 feeding on fruits of *Guioa pleuropteris*. Local people reported hunting them for food, and also catching them and selling them as pets. The IUCN (2002) listing of *A. binturong whitei* as Vulnerable seems justified.

Paradoxurus hermaphroditus.—This common species is found from Sri Lanka to the Lesser Sunda Islands and the Philippines (Heaney et al. 1998). Recorded in agricultural areas and forest over a wide elevational range (Allen 1910; Heaney et al. 1991, 1999; Hoogstraal 1951; Rabor 1986); Sanborn (1952) reported large series from several localities. We often saw them feeding in fruiting trees and shrubs in grassland/forest mosaic at Site 12, and we saw road-kills along the coastal highway. They are hunted, but the large number of museum specimens and sightings indicate that they traditionally have been and probably remain the most common carnivore on Palawan (e.g., Allen 1910, Sanborn 1952).

Viverra zangalla.—This civet is found from the Malay Peninsula to Sulawesi and the Philippines (Heaney et al. 1998). Known from primary and secondary lowland, montane, and mossy forest (Allen 1910, Heaney et al. 1999, Rickart et al. 1993). We captured and released a juvenile of this species in a cage trap in lowland primary forest at Site 1, and we observed two in forest-grassland mosaic at Site 12.

Order Artiodactyla

Tragulus napu and *Axis calamianensis* both occur in the Palawan faunal region, but we found no evidence of either species on Palawan Island.

Family Suidae—Pigs

Sus barbatus.—The bearded pig is found from the Malay Peninsula to Borneo and Palawan (Heaney et al. 1998). Rabor (1986) and Payne et al. (1985) reported the species from primary and secondary forest from sea level to the highest peaks; Sanborn (1952) reported a series from Iwahig. Groves (2001) has tentatively suggested that the population of this species from the Palawan faunal region, which has been recognized as a distinct subspecies, may warrant recognition as a distinct species, *Sus ahoenobarbus*. We regularly observed this species

or evidence of its occurrence in forest habitats (including fragmented forest) from sea level to montane forest at ca. 1500 m (Sites 1, 2, 3, 4, 7, and 11). We also observed evidence of the species entering cultivated areas near forest and damaging crops. Wild pigs are heavily hunted on Palawan with snares, low caliber rifles, and small, baited explosive devices known as "pig bombs". The species appears to be locally common, but is in decline due to heavy hunting pressure (Caldecott et al. 1993, Oliver 1992). The IUCN (2002) lists *S. barbatus ahoenobarbus* as Vulnerable.

Discussion

Adequacy of sampling.—Small fruit bats on Palawan (*Cynopterus*, *Eonycteris*, *Macroglossus*, and *Rousettus*) appear to have been fairly completely sampled; no species have been added in over 50 years (excluding the apparently erroneous reports of *Haplonycteris fischeri* and *Ptenochirus minor*), despite extensive netting. It is interesting that our mist netting in primary forest produced very few captures; for example, in primary lowland forest at 150 m elevation (Site 1), we captured 1 fruit bat in 42 net-nights; in primary lowland forest at ca. 500 m (Site 2), we captured 1 fruit bat in 56 net-nights, and in primary montane forest at ca. 1400 m (Site 3), we captured no fruit bats in 48 net-nights. Although our sample size is limited, all of these values fall well below what would be typical on islands in the oceanic portion of the Philippines (Heaney et al. 1989, 1999), suggesting that small fruit bats are not as abundant in primary forest on Palawan (e.g., Heideman & Heaney 1989, Heaney et al. 1989). Indeed, all of the small fruit bats currently known from Palawan predominantly occur in disturbed habitats, in contrast to the oceanic Philippines, where several endemic genera (*Alionycteris*, *Haplonycteris*, *Otopteropus*, and *Ptenochirus*) are most common in old-growth forest.

The ecology of large fruit bats (*Acerodon*

and *Pteropus*) has been very poorly studied on Palawan and elsewhere in the Philippines. This is the direct result of the difficulty in capturing these species by any means other than shooting. Despite the paucity of ecological information on these species, their distribution among major island groups appears to be moderately well understood because their activities and roosts are highly conspicuous, and no additional species have been found on Palawan in over 50 years. It seems unlikely that additional species will be found on Palawan, with the possible exception of *P. hypomelanus*.

Insectivorous bats are clearly the least known of all Palawan mammals. Distributions remain poorly documented, ecological information is scanty for most species, and the taxonomy is often uncertain. Our survey efforts and examination of previously collected insectivorous bats documented eight species (*Rhinolophus arcuatus*, *R. cf. borneensis*, *R. creaghi*, *R. macrotis*, *Miniopterus australis*, *M. schreibersi*, *M. tristis*, and *Murina cf. tubinaris*) on Palawan for the first time, and several more are noted in the text as very likely to be present.

Our knowledge of small non-volant mammals (including Soricidae, Tupaiidae, Sciuridae, and Muridae) on Palawan is uneven. Some lowland species (e.g., *Tupaia palawanensis*, *Sundasciurus juvenicus*, *Maxomys panglima*, *Rattus tiomanicus*, *Sundamys muelleri*, and the non-native murines) are common and well known. Very little is known of several other species (e.g., *Crocidura palawanensis*, *Crocidura* sp., *Sundasciurus rabori*, *Chiropodomys calamianensis*, *Haeromys pusillus*, and *Palawanomys furvus*). Perhaps we failed to locate these poorly known species because we did little trapping in trees or other places above the ground surface (*C. calamianensis* and *H. pusillus*), sampled only one site above 1000 m (*S. rabori* and *P. furvus*), and our trapping techniques were limited, i.e., we did not use pitfall traps (*Crocidura* spp.). The presence of so many poorly known species suggests that other species

may await discovery, especially in high mountain habitats and high in the canopy. Musser & Newcomb (1983) suggested that unknown species are yet to be discovered on Palawan, citing the report of Hoogstraal (1951), which narrated their attempt to capture a "very large rat with a white tail" described to them by native Palaw'an. Other large islands in the Philippines have been shown to support diverse communities of endemic small mammals which are restricted to montane areas (e.g., Heaney 2001, Heaney & Rickart 1990, Rickart 1993), and perhaps the same awaits discovery on Palawan.

Medium to large mammals (Cercopithecidae, Manidae, Hystricidae, the carnivores, and Suidae) are possibly the most thoroughly inventoried subset of Palawan's mammalian fauna. Because of their large size, they are easily observed compared to other mammals. Many of these species are also commonly hunted, so obtaining specimens is often easier than for non-game species. It is unlikely that other medium to large mammals await discovery on Palawan, though the ecology of all requires much additional study.

Biogeography.—As noted above, the Palawan faunal region is part of the Sunda Shelf and may have been connected to mainland Asia via Borneo (Everett 1889) during a Pleistocene episode of glacially-induced sea-level lowering (Heaney 1985, 1986, 1991a), though current data leave this uncertain. All other islands in the Philippines are oceanic and have probably never had a dry-land connection to any mainland area (Heaney 1985, 1986, 2001). Of the 58 native species currently known from Palawan Island (tentatively including the small *Crociodura* sp.), 13 species are endemic to Palawan (and usually to some of the smaller islands that were included in Pleistocene Greater Palawan; Heaney 1986); 12 of these are non-volant, all of which have their closest relatives on the Sunda Shelf. Eight of Palawan's 11 native rodents (73%) are endemic; all three non-endemics are mu-

rids. Only one endemic species is a bat (*Acerodon leucotis*), and only it has its closest relatives in the oceanic Philippines. This pattern of endemism is clearly consistent with the geological history of the Philippines and also highlights the importance of the greater vagility of bats over non-flying mammals. Of the 28 insectivorous bats, 18 species are somewhat to highly widespread in Indo-Australia (and some beyond), 2 are shared only with the Sunda Shelf and Indochina (*Rhinolophus acuminatus* and *Rhinolophus* cf. *borneensis*), 1 with the Sunda Shelf only (*Cheiromeles torquatus*), 3 occur on the Sunda Shelf and the oceanic Philippines (*Kerivoula pellucida*, *K. whiteheadi*, *Myotis macrotarsus*), 1 occurs on Palawan, Sulawesi and the oceanic Philippines (*Mops sarasinorum*), 2 occur only on Palawan and in the oceanic Philippines (*Rhinolophus virgo* and *Myotis rufopictus*), and one occurs on Borneo, Sulawesi, and throughout the Philippines (*Emballonura alecto*). These data again demonstrate that the bats are more widely distributed and do not clearly reflect the geological history, as do the non-flying mammal species, which in the Philippines are usually restricted to a single area that was united by dry land during the late Pleistocene. From the highly diverse fruit bat fauna of Borneo (17 species; Payne et al. 1985), only five species extend to the northern continental land-bridge islands of Sabah (Md. Nor 1995). These are the same five non-endemic species that can be found just to the north on Palawan Island.

We note that the combined totals of native non-volant mammal species on Palawan that either are shared with Borneo and other portions of the Sunda Shelf or that are endemic to Palawan and have their closest relatives on Borneo or adjacent areas is 22 out of 24 (92%). The apparent exceptions are *Hylopetes nigripes* (related to *H. albingeri* of Indochina) and *Palawanomys furvus* (an enigmatic genus of unclear phylogenetic position). If this analysis were extended to the entire Palawan faunal region, *Axis*

calamianensis (related to *A. porcinus* in Indochina) would also be included here. Four species are widespread in Southeast Asia (including parts of Wallacea), and no species is shared with the oceanic Philippines except for those 4 species (*Macaca fascicularis*, *Prionailurus bengalensis*, *Paradoxurus hermaphroditus*, and *Viverra zibetha*). If *Sus barbatus*, which occurs on Palawan, the Sunda Shelf, and in the marginal islands of the Sulu Archipelago is counted as a widespread Southeast Asian species, the total rises to five species. These data, in sum, strongly reinforce the conclusion of Everett (1889), based on his analysis of bathymetric features of the ocean floor and the pattern of relationships of the 18 species then known from Palawan and associated smaller islands, that the Palawan faunal region is an extension of the Sunda Shelf, probably due to a fairly recent dry-land connection, with only a small portion of its fauna shared with the oceanic Philippines.

Patterns of species richness relative to island area are also of interest. Insectivorous bats are so poorly known in the Philippines that it is possible only to say that the 28 species documented here compare favorably with most islands in the Philippines; that is, there is no evidence that Palawan is species-poor (Heaney et al. 2002). Fruit bats, on the other hand, are represented on Palawan by only 6 species, and this places their diversity far below that on much smaller islands in the oceanic Philippines; Maripipi, for example, has 10 species, but is only 22 km². It seems certain that Palawan has a depauperate fruit bat fauna, as well as probably having lower fruit bat density, as noted above, compared to the oceanic Philippines (Heaney 1991b). Species richness of non-flying mammals, on the other hand, at 24 is much above the species/area curve documented in the oceanic Philippines, though well below that of islands on the primary portion of the Sunda Shelf (Heaney 1984, 1986; Heaney et al. 2002). It is interesting that carnivores are notably

more diverse on Palawan than in the oceanic Philippines, and murid rodents notably less diverse, for an island the size of Palawan.

Conservation issues.—The most pressing issue facing terrestrial wildlife in Palawan is the rapid loss of forest cover, especially in the primary lowland forests that are targeted for logging. Palawan's forests are less commercially valuable than the dipterocarp-dominated forests of the other islands, and, consequently, deforestation occurred later on Palawan. However, once forests were exhausted on Luzon, Mindanao, Negros, etc., commercial logging operations began working in lowland forest on Palawan (Environmental Science for Social Change 1999) during the 1970's and 1980's at unsustainable levels (Quinnell & Balmford 1988, Kummer 1992). Since a logging ban was imposed in the early 1990s throughout the Province of Palawan, logging has declined, but the large commercial operations appear to have been replaced by small-scale, illegal commercial logging. We have seen that forest continues to disappear from the most accessible areas, and forest edges are gradually creeping higher and higher up the contours, in a manner similar to that experienced on Leyte (Rickart et al. 1993) and southern Luzon (Heaney et al. 1999). Lowland primary forest has been eliminated from many parts of Palawan and the destruction shows few signs of easing. Due to almost complete conversion of the coastal plain into ricefields, coconut, or other plantations, distinctive ecosystems such as freshwater swamp forest and beach forest have virtually disappeared (Widmann 1998). Slash and burn agricultural practices have also been very damaging to forests, and Palawan has experienced a population explosion due to high birth and immigration rates.

It should be noted that caves are crucial to maintaining the fauna, since approximately 18 (32%) of Palawan's mammals are bats that roost in caves. Caves have been the focus of much destruction in the Phil-

ippines; common activities in caves on Palawan include guano mining, general vandalism, recreational exploration, and treasure hunting. Unlike many other parts of the Philippines (e.g., Heaney et al. 1991, 1999; Rickart et al. 1993), we never encountered any evidence of cave-roosting bats being hunted on Palawan. We found guano mining to be common, usually near the mouth of caves. Recreational exploration of caves is steadily increasing; many caves are currently being developed or advertised for this purpose, while many more proposals are in the planning stages. At PPSRNP (Site 15), hundreds of visitors may enter a one kilometer stretch of the cave daily. The bats are clearly disturbed by the activity, but the ultimate result of such disturbance is unknown.

Many medium to large sized mammals are under significant hunting pressure on Palawan for their meat, the live animal trade, and medicinal use, as noted above, but few data are available on the impact. The recent and on-going shift from subsistence to market economies among members of the Tagbanua and other ethnic groups may contribute to the decline of some species (Lacerna & Widmann 1999), such as *Sus barbatus*, *Pteropus vampyrus*, and *Hystrix pumila* for meat, *Macaca fascicularis* and *Arctictis binturong* as pets, and *Manis culionensis* for traditional Chinese medicine.

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A new species of *Tropidonophis* (Serpentes: Colubridae: Natricinae) from the D'Entrecasteaux Islands, Papua New Guinea

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Abstract.—We describe a new species of natricine snake of the genus *Tropidonophis* from the D'Entrecasteaux Islands, off the southeastern peninsula of New Guinea. The new species is large, with 15 unreduced scale rows, a high ventral and low subcaudal scale count, and a distinctive color pattern of dark mid-dorsal bands and offset lateral blotches on a yellow or brown ground color. The species is known from two specimens collected at 900–1090 m in primary lowland hill forest. Close relationships with other members of the genus are not apparent.

The natricine genus *Tropidonophis* consists of 18 species of small to medium-sized snakes distributed from the Philippines (two endemic species) to the Bismarck Archipelago (two endemic species), with 12 species found on New Guinea and its offshore islands, four in the Moluccas, and one in Australia (Malnate and Underwood 1988). The genus is thought to be most closely related to the Southeast Asian *Xenochrophis* on the basis of shared scalation, hemipenial, and osteological features (Malnate and Underwood 1988). Most *Tropidonophis* species are nondescript, frequently with a uniformly dark dorsal ground color of brown or gray, sometimes with darker spots, short lines, or narrow bands. Some specimens of a few species have more conspicuous patterns of dark bands on a lighter ground color (cf. O'Shea 1996: 95). *Tropidonophis* species typically inhabit rainforest, occur from sea level to 2200 m (Malnate and Underwood 1988), and are reported to dwell frequently near permanent water sources (O'Shea 1996).

During the course of conducting biological surveys in the D'Entrecasteaux Islands in 2002 we collected a strikingly colored specimen of *Tropidonophis* that is unassignable to any currently recognized spe-

cies. A search of museum collections revealed another specimen belonging to the same taxon. We take this opportunity to provide this species with a name.

Materials and Methods

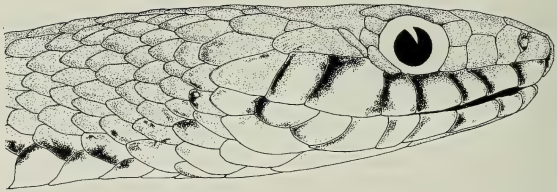
Specimens were collected under applicable national and provincial permits, fixed in 10% buffered formalin, and transferred to 70% ethanol for storage. Measurements were made to the nearest mm in the field with a fiberglass tape; mass was measured to the nearest gram in the field with a Pesola scale. Diagnostic features and comparisons to other species were based on data provided in the comprehensive study of *Tropidonophis* by Malnate and Underwood (1988) and by reference to specimens housed in the Bernice P. Bishop Museum, Honolulu (BPBM).

Specimens are deposited in the BPBM and American Museum of Natural History (AMNH).

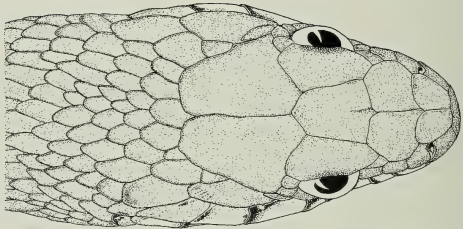
Tropidonophis dolasii, new species

Figs. 1, 2

Holotype.—BPBM 16539 (field tag FK 6118), adult female, collected by D. Salepuna on E slope of Oya Tabu (Mt. Kilker-



A



B

Fig. 1. (A) Lateral, and (B) dorsal view of head of holotype (BPBM 16539) of *Tropidonophis dolasii*. Scale bar equals one cm.

ran), 9.4555°S, 150.7857°E, 1090 m, Fergusson Island, Milne Bay Province, Papua New Guinea, on 23 August 2002.

Paratype.—AMNH 73979, adult female, collected by L. Brass on E slope of Goodenough Island, 900 m, Milne Bay Province, Papua New Guinea, on 27 October 1953.

Diagnosis.—A large species of *Tropidonophis* with 15 dorsal scale rows at mid-body and one head length anterior to the vent, 161–162 ventrals, 63 subcaudals, 2 preoculars, 3 or 4 postoculars, 8 supralabials, 8 or 9 infralabials, no postocular dark stripe, and yellow or brown ground color

with vaguely defined mid-dorsal black bands offset by lateral black blotches on scale rows 1–4. These dark bands and blotches are not solid, rather they are formed by a network of darkened scale margins.

Description of holotype.—Adult female. Dorsal scale rows 15 (reduction to 15 rows occurs at the level of the 15th ventral); all rows except first keeled; first row weakly keeled on those scales posterior to approximately 15 ventrals anterior to vent; keels on dorsal scales more weakly developed anteriorly and laterally and more strongly de-

veloped posteriorly and dorsally; paired apical pits obvious on those dorsal scales retaining the horny epidermal layer; all dorsal scales, except on first row, notched at the posterior tip. Rostral twice as wide as high; internasals longer than wide; prefrontals wider than long, as are frontal, supraculars, and parietals; lateral extension of parietal contacts middle postocular, excluding upper postocular from contact with anterior temporals on each side. Nasals divided by large nares; loreal higher than long; preoculars 2; postoculars 3 (right) and 4 (left); anterior temporals 2, upper a narrow sliver approximately 20% the size of lower, lower excluded from contact with postoculars on right side, with point contact to second and third postoculars on left; posterior temporals 3, the most anterior lying on posterior slope of lower anterior temporal and in contact posteriorly with only the middle posterior temporal (Fig. 1). Supralabials 8, 4th and 5th contact eye; infralabials 9 (right) and 8 (left), four contact anterior chin shields. Posterior chinshields separated along their entire length by 1 + 1 + 2 intergenials; lateral gulars separated from posterior chinshields. Pits present in the loreal, preoculars, postoculars, anterior temporals, posterior temporals, parietals, and supralabials; absent from the rostral, nasals, internasals, prefrontals, frontal, supraoculars, infralabials, and chin shields; many small tubercles present on all head shields.

Ventrals 161; anal divided; subcaudals 63, excluding tip; subcaudal pits unobservable because horny epidermal layer missing for all subcaudals; subcaudals/(ventrals + subcaudals) = 0.28. Dorsal scales on tail reduced to six rows at level of subcaudal 18, reduced to four rows at level of subcaudal 41, and reduced to two rows at level of subcaudal 61.

Total length 1145 mm; snout-vent length 905 mm; tail length 240 mm (21% of total length); mass 285 g.

Maxillary teeth on left side 29, the last three enlarged.

Dorsal ground color in preservative yellow, varying from deep orange-yellow anteriorly to pale straw-yellow posteriorly. Interstitial skin bright orange anteriorly, becoming gray posteriorly. Head mustard yellow, darker than neck and anterior body, without dark postocular stripe; supralabials and infralabials with black posterior margins (Fig. 1A). Dorsum bears pattern of ~48 bands; each band spans middle 7-9 scale rows and is 1-2 scales long; mid-dorsal bands staggered against equal number of lateral blotches, each 3-4 scales high and 1-2 scales long. All bands and blotches formed by black outlining of affected scales; scale centers (and usually the posterior margins) retain ground color, imparting vague and indefinite appearance to bands and blotches (Fig. 2). First (reduced) dorsal band appears at level of ventral 15, first nearly complete dorsal band at level of ventral 28, and first trace of lateral blotch at level of ventral 30. Series of black dashes on first dorsal scale row up to level of ventral 25, each dash extending for 1-5 scales (Figs. 1A, 2). Tail with ~20 dark bands; bands increasingly reduced and poorly defined posteriorly. Venter yellow, fading from deep orange-yellow on chin to light straw yellow on tail, with gray flecks laterally at origin of dorsal banding and gradually filling in mid-ventrally; the last third of venter evenly, though not heavily, freckled with gray.

Color in life (from field notes).—“Dorsum mustard yellow with vague mid-dorsal and lateral blotches created by black outlining along the margins of affected scales. Dorsum becoming more orange anteriorly and top of head orange-brown. Sides turning to yellow. Venter bright yellow with a tendency to orange-yellow on chin and throat. Black flecks scattered on venter beginning ca. ¼-way down body and increasing in frequency posteriorly.”

Variation.—The paratype is smaller (total length ~810 mm, snout-vent length ~756 mm, tail length 54+ mm) than the holotype, has a broken tail, and is eviscer-



Fig. 2. Holotype (BPBM 16539) of *Tropidonophis dolasii* in life.

ated anteriorly. It differs from the holotype in having prefrontals longer than wide; postoculars 4 on right side, 3 on left; anterior temporals two on each side, the upper (anteriormost) $\frac{2}{3}$ as large as the lower; posterior temporals two on each side; four infralabials in contact with anterior chin shields on left side, five on right; posterior chinshields meeting anteriorly and separated posteriorly by 1 + 2 intergenials; pits on head scales not observable because of loss of horny epidermal layers; ventrals 162; subcaudals 15 before tail broken; maxillary teeth on left side 32, the last 4 enlarged.

Dorsal ground color brown, no darker posteriorly than anteriorly; dorsum with ~51 bands, all bands and lateral blotches formed by dark brown, not black, margining and more solidly filled in than for holotype. Venter pale yellow anteriorly, changing to brown posteriorly. Barring on

lips dark brown, less distinct than in holotype due to general suffusion of brown pigment on the head.

Comparisons to other species.—*Tropidonophis dolasii* is distinguished from *T. negrosensis* in lacking a posterior reduction in dorsal scale rows; from *T. dahlii*, *T. dendrophlops*, *T. doriae*, and *T. hypomelas* in having 15 (vs. 17) dorsal scale rows; from *T. mairii* in having 2 (vs. 1) preocular; from *T. truncatus* in having 3 or 4 (vs. 2, rarely 3) postoculars; from *T. halmahericus*, *T. mcdowellii*, and *T. punctiventris* in having 8 (vs. 9) supralabials; from *T. aenigmaticus*, *T. novaeguineae*, and *T. picturatus* in having a larger number of ventral scales (161–162 vs. 140–152, 128–143, and 117–140, respectively); from *T. elongatus*, *T. montanus*, *T. multiscutellatus*, and *T. parkeri* in having fewer subcaudal scales (63 vs. 85–108, 71–89, 74–103, and 80–100, respec-

tively); and from *T. statisticus* in its larger size (~810–1145 mm vs. maximum of 870 mm), dorsal pattern of dark bands, offset with lateral blotches, on a yellow or brown ground (vs. uniform gray or brown with series of dorsal spots), and strongly barred labials (vs. unbarred).

Only five other species of *Tropidonophis* attain a size greater than one meter: *T. dahlii*, *T. doriae*, *T. elongatus*, *T. halmahericus*, and *T. montanus*. The first is restricted to New Britain and the last three to the western half of New Guinea or the Moluccas. Only *T. doriae* approaches the geographic range of *T. dolasii*, being found on the adjacent mainland of Milne Bay Province (Malnate and Underwood, 1988; O'Shea, 1996), but this species has 17 dorsal scale rows, no more than 153 ventrals in females, and no fewer than 71 subcaudals in females.

The conspicuous yellow dorsal and ventral coloring of *T. dolasii* (brown dorsally in the long-preserved paratype) and its pattern of lateral blotches combined with mid-dorsal bands are apparently unique among *Tropidonophis*. In other dorsally banded Papuan species (e.g., *T. doriae*, *T. hypomelas*), the bands are typically solid, instead of being formed by a network of darkened scale margins, and extend across the entire dorsum, instead of lying just on the mid-dorsal scale rows.

Ecological notes.—The holotype was collected in small-crowned lowland hill forest (Paijmans, 1975, 1976) on steep terrain at 1090 m. The collection site faces east but receives little direct sunlight because surrounding ridges and frequent clouds block the sun throughout much of the day. Nearest water source was a small (~30-cm wide) trickle among rocks in a narrow ravine approximately 50–100 m elevation below the collecting site. At the time of collection, the region had been in a month-long drought, although moisture was still present under logs and some rocks. Temperature varied from 15.8–21.0°C during the two weeks of our stay. The specimen

was active in mid-morning and attempted to escape. Other snakes occurring in the same area were *Aspidomorphus lineaticollis*, *Boiga irregularis*, and *Tropidonophis aenigmaticus*.

The paratype was noted to come from "transition oak-rain forest" and had an unidentified *Rana* in its stomach.

Etymology.—The name is a patronym honoring Dolasi Salepuna of Uluva, Ferguson Island, who was an invaluable field assistant and captured the holotype.

Distribution.—The species is known only from the uplands of eastern Ferguson Island and eastern Goodenough Island (Fig. 3). It likely occurs throughout the higher elevations of the D'Entrecasteaux Islands.

Remarks

In their revision of *Tropidonophis*, Malnate and Underwood (1988) placed considerable importance in their key on the numbers of anterior and posterior temporal scales, even while documenting that these characters show considerable intraspecific variation. We have not emphasized these scales for diagnosing *T. dolasii* because we are uncertain of their modal distribution, given our few specimens and the considerable variation these characters exhibit in the genus. In considering the holotype, it is especially uncertain 1) whether the third, small scale in the anterior-posterior series should properly be considered an anterior or posterior temporal, and 2) whether the first and the third small scales in the series are normally present or are aberrant divisions unique to that specimen. We have referred to the third, small scale as a posterior temporal based on the definition provided by Malnate and Underwood (1988: 75) that those scales meeting either the posterior slope of the supralabial apex or the anterior temporals constitute the posterior temporals. However, comparison with the paratype, whose temporals appear more normal in size and placement than those of the holotype, shows the region occupied by this



Fig. 3. Map of southeastern New Guinea showing type locality for *Tropidonophis dolasii* (star) on Oya Tabu (Mt. Kilkerran), Fergusson Island, and approximate locality for paratype (dot) on Goodenough Island, D'Entrecasteaux Islands.

small scale in the holotype to be part of the parietal in the paratype, suggesting this scale is not homologous with the other temporal scales. Further comparison of the two specimens shows the small anterior temporal of the holotype to be of similar placement but much smaller size than the corresponding scale in the paratype (~20% the size of the larger anterior temporal in the holotype vs. ~66% in the paratype). Given these observations, it seems likely that the temporal scalation seen in the holotype is aberrant.

If one assumes that the temporal scalation seen in the paratype is normal for the

species, then, among New Guinean *Tropidonophis*, having two anterior temporals would serve as a further character helping to distinguish *T. dolasii* from *T. statisticus*, *T. m. mairii*, *T. mcdowellii*, and *T. truncatus*. Similarly, two posterior temporals would be a further character diagnosing our species from *T. dahlii*, *T. hypomelas*, and *T. picturatus*.

The nearest relatives of *Tropidonophis dolasii* are not immediately evident. It shares with eight other species (*T. aenigmaticus*, *T. elongatus*, *T. montanus*, *T. multiscutellatus*, *T. novaeguineae*, *T. parkeri*, *T. picturatus*, and *T. statisticus*) the com-

mon scale conditions of 15 unreduced dorsal scale rows, two preoculars, three or more postoculars, and eight supralabials. Of these eight, only *T. elongatus* and *T. montanus* attain an equivalent size (the remainder never exceed 950 mm and individuals usually are much smaller). Only *T. elongatus*, *T. multiscutellatus*, and *T. novaeguineae* sometimes have dorsal bands, although the bands are solid and unlike the margined construction seen in *T. dolasii* and are superimposed on a brown or gray, instead of yellow, ground color. Of the eight species, all except *T. novaeguineae* typically bear a postocular dark stripe, not seen in *T. dolasii*. Ventral scale counts of *Tropidonophis dolasii* overlap only with those in *T. elongatus*, *T. montanus*, *T. parkeri*, and *T. statisticus*; subcaudal counts overlap only with *T. aenigmaticus* and *T. picturatus*; and ventrals + subcaudals overlap only with *T. aenigmaticus*, *T. multiscutellatus*, and *T. statisticus*. Given this chaotic pattern of character-state similarities and our small sample size, attempts to identify the sister taxon of *T. dolasii* would be premature.

Acknowledgments

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Appendix Specimens examined

Tropidonophis aenigmaticus: BPBM 16534, E slope Oya Tabu, Fergusson Island, 9.4556°S, 150.7896°E, 1050 m, Milne Bay Prov., Papua New Guinea; BPBM 16535, Uluu, Fergusson Island, 9.4520°S, 150.8251°E, 0–10 m, Milne Bay Prov., Papua New Guinea; BPBM 16536, S slope Oya Waka, Fergusson Island, 9.4562°S, 150.5596°E, 980 m, Milne Bay Prov., Papua New Guinea; BPBM 16537, 17241, Saidowai, Normanby Island, 9.9637°S, 150.9546°E, 0–10 m, Milne Bay Prov., Papua New Guinea; BPBM 16538, 1.4 km NE Saidowai, Normanby Island, 9.9530°S, 150.9607°E, 40–80 m, Milne Bay Prov., Papua New Guinea; BPBM 17243, Sibonai, Normanby Island, 10.13578°S, 150.9708°E, 0–40 m, Milne Bay Prov., Papua New Guinea; BPBM 17242, 17244, S end Sewa Bay, Normanby Island, 10.0340°S, 150.9822°E, 60 m, Milne Bay Prov., Papua New Guinea.

Tropidonophis doriae: BPBM 13135, E branch Avi Avi River, 5.5 km S, 5.6 km W of Tekadu Airstrip, 7.735°S, 146.496°E, 120 m, Gulf Prov., Papua New Guinea.

Tropidonophis hypomelas: BPBM 12022, Weitin River Valley, 10 km N, 8.5 km W of river mouth, New Ireland, 4.533°S, 152.95°E, 250 m, New Ireland Prov., Papua New Guinea; BPBM 12163, Weitin River Valley, 8 km N, 7 km W of river mouth, New Ireland, 4.554°S, 152.964°E, 150 m, New Ireland Prov., Papua New Guinea.

Tropidonophis mairii: BPBM 3104, 3299–3300, Balimo, 8.00°S, 142.55°E, 10 m, Western Prov., Papua New Guinea.

Tropidonophis multiscutellatus: BPBM 5030, Biak Island, 1.02°S, 136.27°E, Papua, Indonesia; BPBM 3783, May River, 400 m, East Sepik Prov., Papua New Guinea; BPBM 17232–33, W Alotau, 10.3092°S, 150.3471°E, 5–10 m, Milne Bay Prov., Papua New Guinea; BPBM 5506, Wau, 7.343°S, 146.713°E, Morobe Prov., Papua New Guinea.

Tropidonophis picturatus: BPBM 4133, Garaina, 7.883°S, 147.142°E, 750 m, Morobe Prov., Papua New Guinea.

Tropidonophis statisticus: BPBM 17293–95, 17299–300, vic. Bunisi Village, 10.0171°S, 149.6002°E, 1420–1490 m, Milne Bay Prov., Papua New Guinea; BPBM 17296–98, Siyomu Village, 10.0145°S, 149.5970°E, 1300 m, Milne Bay Prov., Papua New Guinea; BPBM 4146, 5125, vic. Wau, 7.343°S, 146.713°E, 1600–1650 m, Morobe Prov., Papua New Guinea; BPBM 4128, 5459, 6239–40, Mt. Kaindi, 7.348°S, 146.667°E, 1800–2250 m, Morobe Prov., Papua New Guinea; BPBM 5458, 6337, Edie Creek, 7.358°S, 146.658°E, 2000–2200 m, Morobe Prov., Papua New Guinea; BPBM 6484, Bulldog Rd., 9 km SE Wau, 2200 m, Morobe Prov., Papua New Guinea; BPBM 3734, Sarawaget Range, 1920 m, Morobe Prov., Papua New Guinea; BPBM 5497, Kililo, Sarawaget Range, 2100 m, Morobe Prov., Papua New Guinea; BPBM 5498, SW Kabwum, Sarawaget Range, 2300 m, Morobe Prov., Papua New Guinea; BPBM 2272, Banz, 5.50°S, 144.35°E, 1680 m, Western Highlands Prov., Papua New Guinea; BPBM 2895, 16 km NW Banz, Western Highlands Prov., Papua New Guinea.

**A new species of snake of the genus *Omoadiphas*
(Reptilia: Squamata: Colubridae) from the Cordillera
Nombre de Dios in northern Honduras**

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Abstract.—A new species of *Omoadiphas* is described from the Cerro Texíguat Wildlife Refuge in the Cordillera Nombre de Dios of northern Honduras. The new species differs from the congeneric *O. aurula* in number of subcaudal, supralabial, infralabial, and postocular scales, in color and pattern, and in having the posterior nasal scale in contact with the prefrontal scale. Even though the type-locality is declared a wildlife refuge by the Honduran government, rapid deforestation of the area does not bode well for the continued existence of the species at its type (and only known) locality.

Resumen.—Se describe una nueva especie de *Omoadiphas* del Refugio de Vida Silvestre Texíguat, ubicado en la Cordillera Nombre de Dios en el norte de Honduras. La nueva especie difiere de su congenerico *O. aurula* en el número de escamas subcaudales, supralabiales, infralabiales y postoculares, en color y patrón y en que tiene la escama nasal posterior en contacto con la escama prefrontal. Aunque la localidad tipo ha sido declarada como un Refugio de Vida Silvestre por el gobierno de Honduras, la rápida deforestación que se observa en el área es una amenaza para la nueva especie.

The Cordillera Nombre de Dios of northern Honduras is an area of extremely high endemism among amphibians and reptiles. The Cerro Texíguat Wildlife Refuge, in the western portion of this mountain range, is known to harbor 18 Honduran endemic species of amphibians and reptiles, eight of which have their type-locality within the reserve (McCranie, pers. observ.). In September 2003, we collected a specimen of snake in this reserve that represents an undescribed species of the recently described genus *Omoadiphas* Köhler, Wilson, & McCranie and another endemic for the refuge. Herein we describe this species.

Methods

We follow the format of the description of the holotype in Köhler et al. (2001) in

describing this new taxon. The Dowling (1951) method was used in counting ventral scales. Head and scale measurements were made to the nearest 0.1 mm with dial calipers held under a dissecting microscope. Snout-vent length and tail length measurements were made to the nearest mm alongside a ruler. Measurements are abbreviated to: snout-vent length (SVL); total length (TL); head length (HL); and head width (HW). Scale dimensions were made at the longest or widest points along the longitudinal or breathwise dimensions of the body, respectively. Color (capitalized) and codes (in parentheses) in life follow those of Smith (1975–1981). The term “goo-eaters” is used in the sense given it by Cadle & Greene (1993) and Fernandes (1995). Comparative statements about other snake gen-

era are taken from Köhler et al. (2001) and references cited therein.

Systematics

Omoadiphas texiguatensis, new species

Figs. 1–3

Holotype.—USNM 559599 (National Museum of Natural History), an apparently subadult female from approximately 2.5 airline km NNE of La Fortuna, 15°25'49"N, 87°18'32"W, 1690 m elev., Cerro Texiguat Wildlife Refuge, Departamento de Yoro, Honduras, collected 3 September 2003 by Franklin E. Castañeda & James R. McCranie. Original number LDW 13565.

Diagnosis.—*Omoadiphas texiguatensis* can be distinguished from the holotype of *O. aurula* (SMF 78865; subadult female), the only known specimen of the only other known species in the genus, in having 47 subcaudal scales (24 in *O. aurula*), six supralabials (seven), seven infralabials (eight), one postocular (two), the posterior nasal contacting the prefrontal (posterior nasal separated from prefrontal by loreal), a dorsal pattern of a dark stripe on scale row three on each side (dark stripe only on vertebral row), and dark brown to nearly black ventral surfaces in preservative (pale yellow). The affinities of the two species of *Omoadiphas* appear to lie with a group of six other genera of snakes (see Köhler et al. 2001) that are part of a larger group referred to as “goo-eaters.” *Omoadiphas texiguatensis* differs from the species of these six other genera in the following ways: from *Adelphicos* in having 17 dorsal scale rows (15), 172 ventral scales (120–147), and no anterior temporal (anterior temporal present); from all *Atractus* in having a divided cloacal scute (undivided) and from select species of *Atractus* in lacking an anterior temporal (anterior temporal present in some *Atractus*); from *Chapinophis* in having 172 ventral scales (178–196), 47 subcaudal scales (29–40), no anterior temporal (anterior temporal present), no scale row reduction anteriorly on body (scale row re-

duction present), and a striped body pattern (stripes absent); from *Chersodromus* in having 172 ventral scales (124–142), 47 subcaudal scales (32–43), a divided cloacal scute (undivided), and a striped body pattern (stripes absent); from all *Geophis* in having a divided cloacal scute (undivided) and a striped dorsal pattern (stripes absent) and from select species of *Geophis* in lacking an anterior temporal (anterior temporal present in some *Geophis*); and from *Ninia* in having 172 ventral scales (122–157), no anterior temporal (anterior temporal present), smooth dorsal scales (keeled), a divided cloacal scute (undivided), and a striped body pattern (stripes absent).

Description of holotype.—An apparently subadult female; TL 169 mm; SVL 143 mm; tail length 26 mm (15.4% of TL); HL 8.0 mm from front face of rostral to posterior end of mandible; HW 3.9 mm at broadest point (level of angle of mouth); head barely distinct from neck; snout broadly rounded in dorsal view; eye length 0.8 mm; snout length 1.9 mm, about 2.4 times as long as eye length; pupil circular; rostral about 2.0 times wider than high (0.6 mm × 0.3 mm); internasals about 2.0 times wider than long (0.4 mm × 0.2 mm); prefrontals much larger than internasals, about as wide as long (0.9 mm × 0.9 mm), bordering orbit above loreal and anterior to supraocular; median prefrontal suture (1.0 mm) 0.4 times as long as frontal; frontal broadly rounded anteriorly, strongly V-shaped posteriorly, about 1.6 times longer than wide (2.3 mm × 1.4 mm), much longer than distance from its anterior edge to tip of snout (1.6 mm); parietals about 2.1 times longer than wide (3.4 mm × 1.6 mm), median suture (1.9 mm) shorter than frontal length; supraoculars longer than wide (0.6 mm × 0.4 mm), bordering orbit, contacting postocular, separated from loreal by prefrontal.

Nasal divided, anterior nasal contacting rostral, internasal, and first supralabial, posterior nasal contacting internasal, prefrontal, loreal, and first and second supra-

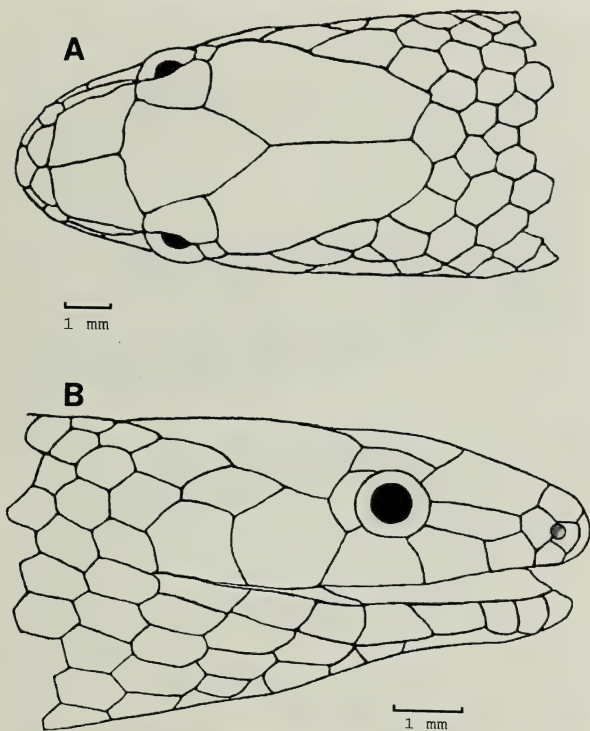


Fig. 1. Drawing of dorsal (A) and lateral (B) surfaces of the head of the holotype (USNM 559599) of *Omoadiphas texiguatensis*.

labials, nostril located in posterior portion of anterior nasal; loreal single, about 3.0 times longer than high (0.9 mm \times 0.3 mm), lower edge contacting second and third supralabials, upper edge contacting prefrontal, loreal bordering orbit (no preocular); post-

ocular single, about 2.0 times higher than long (0.6 mm \times 0.3 mm); no anterior temporal, posterior temporal single, about 1.7 times longer than high (1.0 mm \times 0.6 mm); supralabials 6-6, third and fourth bordering orbit, fifth contacting postocular, parietal,

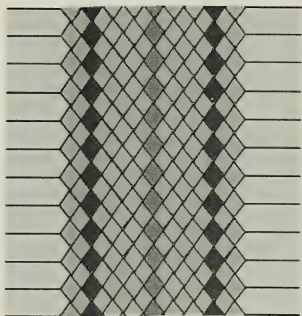


Fig. 2. Schematic drawing of the midbody dorsal pattern of the holotype (USNM 559599) of *Omoadiphas texiguatensis*.

and posterior temporal, sixth contacting posterior temporal; mental about 3.0 times wider than long (0.6 mm \times 0.2 mm), separated from chinshields by first pair of infralabials, which contact each other along ventral midline; chinshields about 1.3 times longer than wide (1.5 mm \times 1.2 mm), not extending to border of lip, separated from first ventral by two gular scales and four preventral scales; infralabials 7–7, first four contacting single pair of enlarged chinshields (their suture length 1.2 mm); a few tiny scale organs (tubercles) present dorsally and ventrally on head; dorsal scales disposed in 17–17–17 longitudinal rows, smooth throughout, lacking apical pits and supra-anal tubercles; dorsal scales in 10 rows at level of tenth subcaudal; ventrals 172; cloacal scute divided; subcaudals 47, paired; tail spine pointed.

Color in life: Dorsal surfaces of head and neck Chestnut (32) with Sepia (119) spots; dorsal surface of body Prout's Brown (121A) with Sepia (119) spots; Sepia (119) dorsolateral stripe present on scale row three on each side, lateral area below stripe Vandyke Brown (121); dorsal surface of tail

Prout's Brown (121A); ventral and subcaudal surfaces Vandyke Brown (121); iris Vandyke Brown (121).

Color in alcohol (about two weeks after preservation): Dorsal surface of head medium brown; dorsal surface of body dark brown with indistinct darker brown spots present on anterior one-third; darker brown longitudinal stripe present on scale row three on each side of body; a vague, slightly darker brown vertebral stripe present; dorsal surface of tail darker brown than that of body; ventral surface of head pale brown, that of body dark brown anteriorly, becoming even darker brown posteriorly; subcaudal surface very dark brown, almost black.

Distribution and natural history notes.—*Omoadiphas texiguatensis* is known only from within the limits of the Cerro Texiguat Wildlife Refuge (Refugio de Vida Silvestre Texiguat). The holotype was crawling in leaf litter next to a rotten log. Only the snake's tail was exposed when first sighted; its body was under the leaves. It was found at 1000 h in moderately disturbed cloud forest (Lower Montane Wet Forest formation of Holdridge 1967) at 1690 m elev. A hard rain occurred from about 1850 to 1875 h the previous day, but the weather was clear and sunny when the snake was captured.

Etymology.—The specific name *texiguatensis* is formed from Texiguat and the Latin suffix *-ensis* (denoting place, locality, or country). The name refers to the Cerro Texiguat Wildlife Refuge where the holotype was collected. We use this specific name in an effort to stress the importance of this wildlife refuge to the conservation status of many Honduran endemic species of amphibians and reptiles (but see Discussion).

Discussion

The genus *Omoadiphas* is now known from two apparently subadult females placed in two species, making it one of the most poorly known snake genera in the Neotropics. Köhler et al. (2001) concluded

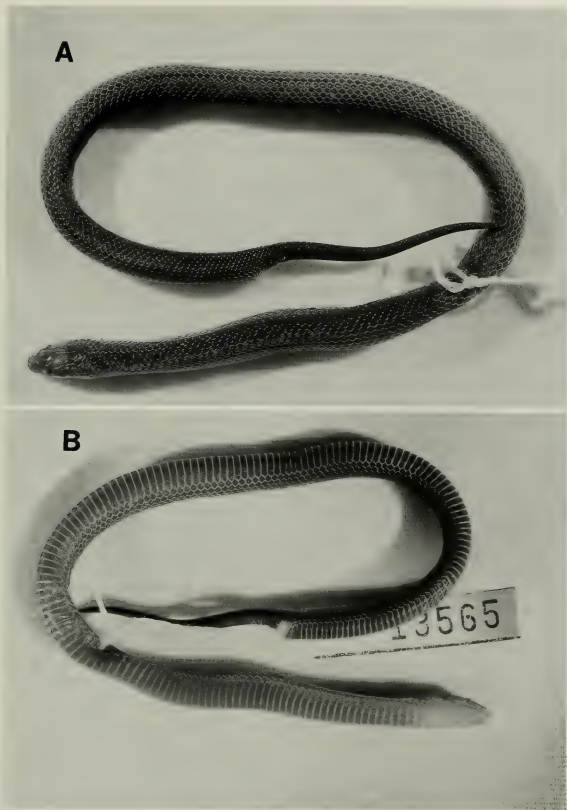


Fig. 3. Dorsal (A) and ventral (B) views of the holotype (USNM 559599) of *Ooadiphas texiguatensis*, total length 169 mm.

that its relationships appear to lie with six other Neotropical genera that are part of a larger group called "goo-eaters" by Cadle and Greene (1993) and Fernandes (1995). The discovery of *O. texiguatensis* appears to support this relationship as well as supporting the distinctiveness of the genus.

Omoadiphas texiguatensis is truly a difficult snake to find. After collecting the holotype, we spent much of the following three days in the area raking through leaves, overturning and ripping apart rotten logs, and overturning rocks in an unsuccessful attempt to find more specimens. We also walked through the area for several hours on two nights searching for active snakes. In addition, this was McCranie's fourth collecting trip to the area.

As noted by Wilson et al. (2001) and McCranie & Wilson (2002), most of the protected areas in Honduras exist on paper only. Such is the case for the Cerro Texiguat Wildlife Refuge. There are no facilities or personnel of any sort or even signage to denote the presence of a protected area. Indeed, people living in San Francisco (the closest village to the type-locality of *O. texiguatensis*) and in the area between that village and the type-locality that we queried are unaware that the area is a wildlife refuge. In addition, crop fields and cleared areas now dominate the area around the type-locality. We did not encounter any pristine forest in September 2003 within an hour or two walk in any direction from where the holotype of *O. texiguatensis* was collected. This is in sharp contrast to the condition of the area during McCranie's first visit in 1991 when pristine cloud forest dominated the region. Clearly, the rapid rate of deforestation in the area does not bode well for the continued existence of *O. texiguatensis* or any of the other species of amphibians and reptiles found in this region of unusually high endemism.

Acknowledgments

We thank C. González, M. Moreno, and H. Portillo of COHDEFOR, Tegucigalpa, for issuing collecting and exportation permits. Señor G. Enamorado, his son Bairon, and daughters Marina and Norma of San Francisco, Yoro, provided us with a ride and good company up the tortuous "road" to the type-locality and then back to San Francisco. We also thank F. D. Castañeda for loaning us the vehicle in which we reached San Francisco. An earlier draft of the manuscript was improved upon by L. D. Wilson. Figs. 1 and 2 were drawn by S. Mohammadi.

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A new species of *Kolpotocheiroidon* (Teleostei: Characidae: Cheirodontinae: Compsurini) from Bahia, northeastern Brazil, with a new diagnosis of the genus

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Abstract.—*Kolpotocheiroidon figueiredoi*, a new species of the characid subfamily Cheirodontinae, tribe Compsurini, is described from the upper rio Paraguaçu basin, Bahia, Brazil. A new diagnosis for the genus is proposed, based mostly on scanning electron microscope (SEM) analyses of the caudal organ of the new species and that of the single previously known species, *Kolpotocheiroidon theloura*. The genus is diagnosed now in part by the presence of a previously undescribed, sexually dimorphic and apparently glandular, structure found in the lower caudal-fin lobe of males. The basal relative position of *Kolpotocheiroidon* within the Compsurini, in which all species are inseminating, is further supported by the presence of aquasperm in both species rather than the apomorphic elongate sperm nuclei present in the remaining members of the tribe.

Resumo.—*Kolpotocheiroidon figueiredoi* é descrito para a porção superior da bacia do rio Paraguaçu, Bahia, Brasil. Propõem-se uma nova diagnose para o gênero, baseada principalmente na análise de Microscopia Eletrônica de Varredura do órgão caudal da nova espécie e de *Kolpotocheiroidon theloura*, a única espécie conhecida anteriormente. O gênero é diagnosticado pela presença de uma estrutura aparentemente glandular e previamente não descrita do lobo ventral da nadadeira caudal dos machos. A posição relativamente basal de *Kolpotocheiroidon* em Compsurini, uma tribo de peixes com inseminação de Cheirodontinae, é corroborada pela presença de espermatozoides aproximadamente esféricos (aquasperm) nas duas espécies, ao invés da presença de espermatozoides de núcleo alongado, como observado nos demais membros da tribo.

The genus *Kolpotocheiroidon* was recently described by Malabarba & Weitzman (2000), from a single species, *K. theloura*, from the uppermost tributaries of the rio São Francisco and rio Paraná central Brazil. The genus is a member of the tribe Compsurini, subfamily Cheirodontinae (see Mal-

abarba et al., 1998) and was diagnosed primarily by the presence of a unique specialized caudal organ at the proximal region of the ventral caudal-fin lobe of males. This organ consists of hypertrophied elongate dermal flaps attached along the fin rays and a series of relatively flat tabs and papillae

attached along the exposed border of those flaps. These structures were unknown in other inseminating or externally fertilizing species of characids.

At the time the research of Malabarba & Weitzman (2000) was conducted, F. C. T. Lima and colleagues were collecting in the rio Pratinha, a tributary of the rio Paraguaçu, Iraquara, Bahia, Brazil and there they discovered a new cheirodontine species that has a caudal organ similar to that present in *K. theloura*. This new compsurin species is herein described and ecological data and field observations from the type locality are presented.

Data from the description of the new species, examination of a new collection of better-preserved specimens of *K. theloura* than originally available, and scanning electron microscopy (SEM) observations of the caudal-fin structures of these two species allow a reanalysis of the characters diagnosing *Kolpotocheirodon* and redescription of the autapomorphies that distinguish its type species.

Methods and Materials

The systematic methods for making counts and measurements for all specimens studied here are the same as those described and used by Malabarba & Weitzman (1999) and are not re-described here. However, unlike the convention for fin rays wherein the count for the rays for the holotype is given first followed by the range and mean separately for the unbranched and the branched rays, the counts of jaw teeth do not report a single value followed by an indication of variation. Instead, only the range of the counts, for example, maxilla with 2 or 3 teeth, is provided. This is because we are confident only in counts taken from cleared and stained specimens. SEM photographs were taken from specimens fixed in formalin and preserved in 70% ethanol. Before metalization with gold, the fins were passed through 99% ethanol, then acetone, and treated with a critical point dryer.

Institutional abbreviations are as listed in Leviton et al. (1985). Character polarity for the diagnoses of the two *Kolpotocheirodon* species and a revised analysis of *Kolpotocheirodon* monophyly is here established by use of parsimony through a re-analysis of the cheirodontine clade Compsurini that was first diagnosed by Malabarba et al. (1998). This new analysis also includes species of the genera *Saccoderma*, *Compsura*, *Macropsobrycon*, and the species *Acinchocheirodon melanogramma* ("identified" as "New Genus and Species B" in Malabarba et al., 1998), and *Kolpotocheirodon theloura* (then "identified" as "New Genus and Species A").

Kolpotocheirodon Malabarba & Weitzman

Kolpotocheirodon Malabarba & Weitzman, 2000:270 (type species: *Kolpotocheirodon theloura* Malabarba & Weitzman, 2000:271 by monotypy and original designation).

Comments preliminary to the diagnosis.—The genus *Kolpotocheirodon* was diagnosed in Malabarba et al. (1998) (as New Genus and Species A) and in Malabarba & Weitzman (2000) by the presence of three apomorphic features that occur in its type species. These characters, as described by Malabarba and Weitzman (2000), are a specialized part of a caudal organ located at the proximal region of the ventral caudal-fin lobe of mature males and consist of hypertrophied elongate dermal flaps attached along the fin rays together with a series of relatively flat tabs and papillae attached along the exposed border of these flaps (= character 36 in Malabarba 1998); hooks on the anal-fin rays of mature males distributed along the most posterior unbranched and five anterior branched anal-fin rays (= character 30 in Malabarba, 1998); and the twelfth and thirteenth caudal-fin rays are dorsally concave along their basal halves and have ventrally expanded segments (= character 34, state 2 in Malabarba 1998).

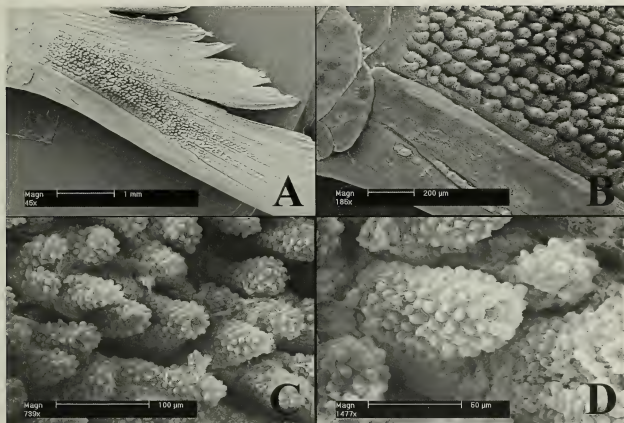


Fig. 1. SEM of caudal organ in *Kolpotocheiroidon figueiredoi*, male (MZUSP 55219, 25.5 mm SL), from rio Pratinha, Iraquara, Bahia, Brazil. (A) lower caudal-fin lobe; (B) detailed image showing the smooth border of the flap attached along the basal portion of the nineteenth caudal-fin; (C) and (D) detailed images of the pineapple organs of the ventral lobe of the caudal fin.

Diagnosis.—By using SEM the specialized caudal-fin organ described in the previous diagnosis of *Kolpotocheiroidon* is now found to be more complex than formerly known. A new caudal organ, previously undescribed, corresponds to a secondary sexually dimorphic organ found exclusively in the ventral lobe of the caudal fin of males of both *Kolpotocheiroidon* species. This “pineapple-like” organ is easily recognized by its peculiar shape, somewhat cone shaped or papilla-like, but completely covered by smaller papillae-like bodies or knobs (see Figs. 1, 2). These are distributed among the large papillae of the caudal fin of males of *K. theloura* (see Fig. 3), but form the entire caudal-fin organ in *K. figueiredoi* (see Fig. 1). This organ is found only in adult males of both species, suggesting that it may have a reproductive

function, possibly pheromone in nature. This pineapple organ has not been found in other cheiroidontines or other characids, and its presence supports a hypothesis of close relationship between the two *Kolpotocheiroidon* species.

Both *Kolpotocheiroidon* species have a conspicuous small black spot at the mid-length of the first branched anal-fin ray of males (Figs. 5, 7 and 8), absent in females (Fig. 6). Such a spot is absent in all other known cheiroidontines. It is here considered derived and a synapomorphy for the genus.

Males of *Kolpotocheiroidon figueiredoi* and *K. theloura* have the ventral body surface in the area covering the pelvic bone with a dark brown mark, nearly in the shape of an isosceles triangle. This pigment appears to externally delineate an area corresponding to the muscles inserted on the pel-

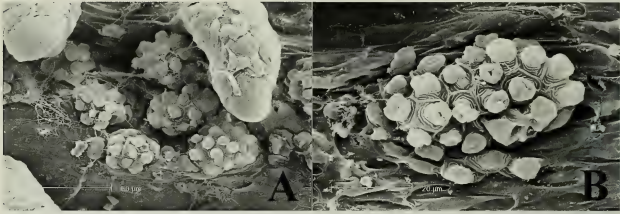


Fig. 2. Detailed SEM images of the pineapple organs found between the papillae of the ventral lobe of the caudal-fin ray of males in *Kolpotocheirodon theloura*. MNRJ 18081, SL 26.2 mm, from lagoa Perta Pé, rio São Francisco drainage, Palmital, Minas Gerais, Brazil. (A) bar = 50 µm; (B) bar = 20 µm.

vic bone (Fig. 8). Such a spot is absent in all other cheirodontines, and constitutes a synapomorphy for the two species.

Malabarba & Weitzman (2000) described the presence of well-developed hooks along the last unbranched and five anterior branched anal-fin rays of males as derived, and diagnostic for *Kolpotocheirodon* (= character 30 in Malabarba 1998). The new specimens available of *K. theloura*, MNRJ 18081, have the last unbranched and five to seven anterior branched anal-fin rays of males bearing hooks (5 branched rays in 7 specimens, 6 in 23 specimens, and 7 in 3 specimens). Males of *K. figueiredoi* have the last unbranched and five to six anterior branched anal-fin rays of males bearing hooks (5 branched rays in 6 specimens, 6 in 6 specimens; 8 in one specimen). The anal-fin region bearing hooks also contains modified soft tissues, absent in the remaining portion of the fin. Although showing more variability than previously described, the condition found in both *Kolpotocheirodon* species is different from that found in other compsurins, which have hooks along a larger number of anal-fin rays. We found that only in *Saccoderma* species among compsurins are anal-fin hooks restricted to the anterior anal-fin rays, in the last unbranched and four anterior branched rays. By parsimony both conditions are considered derived and autapomorphic for

each genus. Note: Menezes et al. (in press) and Weitzman et al. (in press) have described and discussed glandular soft tissue in the anal fins of sexually active male characids of many kinds including glandulocaudines, and some non-glandulocaudines. This tissue is most often associated with anal-fin hooks, but in one species a glandular organ was found.

Kolpotocheirodon theloura

Malabarba & Weitzman

Fig. 7

Kolpotocheirodon theloura Malabarba & Weitzman, 2000:271–281 (description; relationships); 272, fig. 1 (holotype); 273–4, fig. 2–3 (paratypes); 275, fig. 4 (caudal-fin hooks); 276, fig. 5 (ventral caudal-fin lobe); 277, fig. 6 (anal-fin hooks); 278, fig. 7 (premaxillary and maxillary teeth), fig. 8 (pelvic-fin hooks). Material examined: All specimens listed in Malabarba & Weitzman (1999), plus MNRJ 18081, 135 spms. (10 examined, SL 24.3–27.4 mm), Brazil, Minas Gerais, Palmital, lagoa Perta Pé, rio São Francisco drainage.

Diagnosis.—*Kolpotocheirodon theloura* is diagnosed from the new *Kolpotocheirodon* species and other characid fishes by the following autapomorphies: As described in Malabarba & Weitzman (2000), *K. theloura*

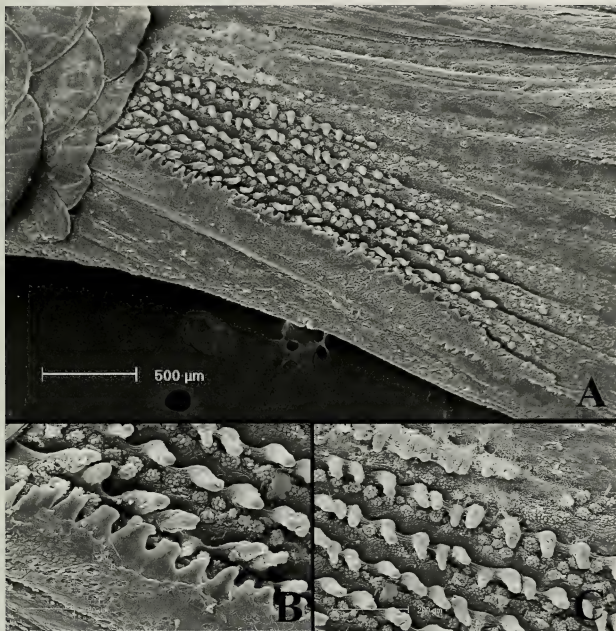


Fig. 3. SEM images of caudal organ in *Kolpotocheirodon theloura*, male, MNRJ 18081, SL 26.2 mm, from lagoa Perta Pé, rio São Francisco drainage, Palmital, Minas Gerais, Brazil. (A) lower caudal-fin lobe, bar = 600 μm ; (B) detailed image of the flap attached along the basal portion of the nineteenth caudal-fin ray with a series of relatively flat tabs along its exposed border, bar = 100 μm ; (C) detailed image of the flaps attached to the eighteenth through thirteenth or fourteenth fin-rays with a single series of papillae along its exposed border, bar = 200 μm .

has hypertrophied elongate dermal flaps attached along the fin rays of the ventral caudal-fin lobe of males (= character 36 in Malabarba 1998). The flap attached along the basal portion of the nineteenth caudal-fin ray has a series of relatively flat tabs along its exposed border (Fig. 3). The flaps attached to the eighteenth through thirteenth

or fourteenth fin-rays are relatively short, narrow and bear papillae in a single series along its exposed border (Fig. 3A, C). These modified flaps of the caudal organ are not exclusive to males in *K. theloura*, being also found in females, although less developed (Fig. 4). Modified flaps are also observed in the dorsal fin of males of *K.*

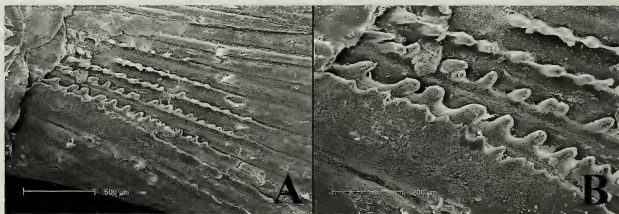


Fig. 4. Detailed SEM images of the flaps bearing papillae along the basal portion of the ventral lobe of the caudal-fin ray in *Kolpotocheiroidon theloura*, female, MNRJ 18081, SL 26.5 mm, from lagoa Perta Pé, rio São Francisco drainage, Palmital, Minas Gerais, Brazil. (A) bar = 500 µm; (B) bar = 200 µm.

theloura (Fig. 9). These modified flaps are independent of the sexually dimorphic pineapple-like organs described as a synapomorphy for *Kolpotocheiroidon* and are absent in *K. figueiredoi*. The modified flaps constitute an autapomorphy of *K. theloura*.

As described in Malabarba & Weitzman (2000), the twelfth and thirteenth caudal-fin rays of *K. theloura* are curved, dorsally concave along their basal halves, and with ventrally expanded segments (= character 34, state 2 in Malabarba, 1998). This feature was not observed in *K. figueiredoi* and is considered autapomorphic for the type species, *K. theloura*.

Kolpotocheiroidon theloura has 3–5 very small vertical bars crossing lateral body

stripe between pseudotympanum and area ventral to dorsal fin (Fig. 7). Such bars are absent in the new *Kolpotocheiroidon* species and in other compsursins and represent an autapomorphy for *K. theloura*.

Kolpotocheiroidon figueiredoi

new species

Figs. 5, 6

Holotype.—MZUSP 70037, 1 male, 30.5 mm SL, Brazil, Bahia, Iraquara, rio Pratinha, Fazenda Pratinha (12°21'13"S; 41°32'57"W), 17–21 Dec 1998; P. Gerhard, F. C. T. Lima, F. Di Dário and L. S. Rocha.

Paratypes.—All specimens collected with the holotype: MCP 22345, 3 males,



Fig. 5. *Kolpotocheiroidon figueiredoi*, new species, holotype, male, MZUSP 70037, SL 30.5 mm; rio Pratinha, Iraquara, Bahia, Brazil.



Fig. 6. *Kolpotocheirodon figueiredoi*, new species, paratype, female, MZUSP 55219, SL 30.0 mm; rio Pratinha, Iraquara, Bahia, Brazil.

25.1–30.5 mm SL, 2 females, 24.0–24.8 mm SL. MZUSP' 55219, (26) 14 males, 24.2–28.2 mm SL, 8 females, 24.0–31.0 mm SL; (1 male 28.2 mm SL and 1 female 26.9 mm SL Alizarin red s and Alcian blue stained specimens cleared with trypsin; 1 male 26.2 mm SL and 1 female 26.4 mm SL sectioned for histology; 1 male 25.5 mm SL sectioned for TEM study).

Diagnosis.—*Kolpotocheirodon figueiredoi* lacks all autapomorphies described above for *K. theloura*, but has no unambiguous autapomorphies for its diagnosis. The

following characters have alternative states between *K. figueiredoi* and *K. theloura*, but these also occur alternatively among other compsurin species. Nevertheless they are most parsimoniously accepted either as autapomorphic for *K. figueiredoi* or apomorphic for *K. theloura*.

Whereas males of *K. figueiredoi* have no hooks on the caudal-fin rays, while males of *K. theloura* have the twelfth to the fourteenth or fifteenth principal caudal-fin rays bearing 4–6 retrorse hooks on each side in a row along their dorsal divisions (Mala-

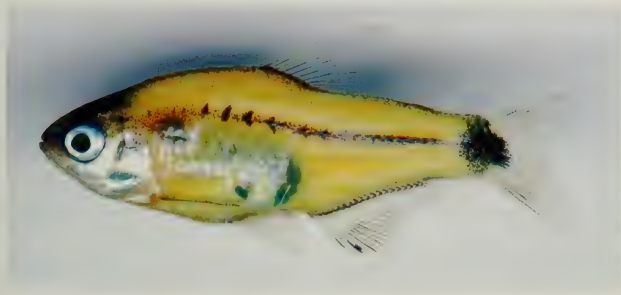


Fig. 7. *Kolpotocheirodon theloura*, male, MNRJ 18081, SL 25.0 mm; lagoa Perta Pé, rio Palmital, Minas Gerais, Brazil.

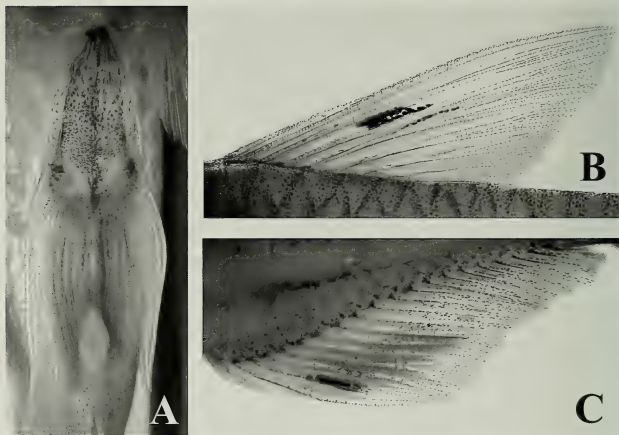


Fig. 8. *Kolpotocheirodon figueiredoi* male, MCP23455, SL 30.5 mm. (A) Ventral body surface in the area covering the pelvic bone showing a dark brown mark, nearly isosceles triangle shape, apparently externally delineating the area corresponding to the muscles inserted in the pelvic bone. (B) and (C) Left lateral view of the dorsal (B) and anal fins (C), showing the dark spots of those fins.

barba & Weitzman, 2000: fig. 4). The presence of hooks on the caudal fin is known for several compsurrins, including *Acinchocheirodon melanogramma* (hooks on caudal-fin rays 13–14, rarely on ray 15), *Saccoderma hastata* (hooks on caudal-fin rays 13–18), “*Odontostilbe*” *dialeptura* (hooks on caudal-fin rays 12–16), and *Macropsobrycon uruguayanae* (hooks on caudal-fin rays 12–14, plus several spinelets along the proximal half of caudal-fin rays 14 to 18). However, hooks are absent in *Compsura heterura*, *Compsura gorgonae*, and “*Odontostilbe*” *mitoptera*. Malabarba & Weitzman (1999, 2000) pointed out that although these hooks are present on the ventral lobe of the caudal fin in all these species, they do not all occur on the same caudal-fin rays in all species and are of different shapes. A previous analysis of character distribution

(Malabarba et al., 1998) indicated the presence of caudal-fin hooks as a synapomorphy for the compsurrin cheirodontines, and its absence a secondary reversal in some of its species. The inclusion of a new species bearing no hooks in the most basal genus of the tribe allows either the recognition of the presence of hooks as a synapomorphy for the tribe Compsurrini with a reversal in *K. figueiredoi*, or the recognition of independent acquisitions of hooks in *K. theloura* and in the clade including the remaining compsurrins. The first hypothesis is preferred, since it better conforms with the putative homology of caudal-fin hooks among compsurrins (de Pinna 1991).

Males of *K. figueiredoi* have a conspicuous small black spot in the soft tissue between midlength of first and second, and second and third branched dorsal-fin rays

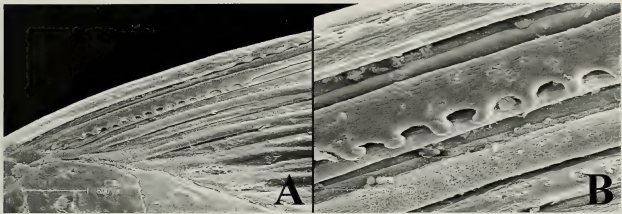


Fig. 9. Detailed SEM images of the flaps bearing papillae along the anterior dorsal-fin ray in *Kolpotocheirodon theloura*, male, MNRJ 18081, SL 26.2 mm, from lagoa Perta Pé, rio São Francisco drainage, Palmital, Minas Gerais, Brazil. (A) bar = 500 µm; and (B) bar = 100 µm.

(Figs. 5, 8). This is absent (Fig. 7) in *K. theloura* (= character 65 in Malabarba 1998). Among compsaurins, a similar spot is observed in species of *Compsura*, *Macropsobrycon* and *Acinocheirodon*, but is absent in species of *Saccoderma*. This spot was previously proposed as a synapomorphy for a clade including the last four genera cited above. Again, the inclusion of a new species in the most basal genus of the tribe allows both the recognition of the presence

of the dorsal black spot as a synapomorphy for the tribe Compsaurini with a reversal in *K. theloura*, or the recognition of independent acquisitions of the dorsal black spot in *K. figueiredoi* and in the clade including remaining compsaurins. The first hypothesis is preferred because it better conforms to the putative homology of the dorsal black spot among compsaurins.

A further character distinguishing *K. figueiredoi* is its caudal-peduncle/caudal-fin

Table 1.—Morphometrics of *Kolpotocheirodon figueiredoi*, new species. Standard length is expressed in mm; measurements through head length are percentages of standard length; the last four entries are percentages of head length. Range includes the holotype, MZUSP 70037, and paratypes MCP 22345, MZUSP 55219.

	Holotype male	n	Males				n	Females			
			Low	High	\bar{x}	SD		Low	High	\bar{x}	SD
Standard length (mm)	30.5	13	25.5	30.5	27.0	10	23.8	31.0	26.4		
Snout to anal-fin origin	59.7	13	57.3	63.0	60.0	1.30	10	61.6	65.8	63.7	1.35
Snout to dorsal-fin origin	50.5	13	45.7	52.9	49.5	1.80	10	48.1	52.4	49.7	1.35
Snout to pelvic-fin origin	42.0	13	42.0	46.7	44.5	1.51	10	45.3	48.3	47.3	1.17
Dorsal-fin base length	13.1	13	12.1	15.6	13.6	1.20	10	11.9	14.3	13.2	0.72
Anal-fin base length	25.9	13	24.5	29.0	26.8	1.27	10	23.5	26.8	25.4	1.08
Caudal peduncle length	15.1	13	12.5	15.5	14.1	0.90	10	11.1	15.4	13.6	1.25
Caudal peduncle depth	13.8	13	13.6	16.1	14.8	0.76	10	11.3	13.8	12.5	0.83
Depth at dorsal-fin origin	31.1	13	31.1	35.7	33.5	1.13	10	33.6	39.4	35.4	1.86
Dorsal-fin height	29.8	12	26.1	29.8	28.0	1.36	9	25.2	27.5	26.4	0.83
Pelvic-fin length	19.0	13	16.7	19.3	18.2	0.71	10	13.4	16.3	14.6	0.79
Pectoral-fin length	19.3	13	17.5	20.1	18.8	0.77	8	15.7	19.2	17.4	1.40
Bony head length	23.3	13	23.3	25.2	24.6	0.59	10	23.0	25.0	24.1	0.72
Snout length	21.1	13	20.3	23.8	22.0	1.10	10	19.4	23.3	21.8	1.35
Upper jaw length	31.0	13	25.4	31.0	27.7	1.47	10	22.7	30.2	27.9	2.13
Horizontal eye diameter	38.0	13	33.3	38.5	36.2	1.39	10	34.8	39.7	37.3	1.68
Least interorbital width	29.6	13	26.1	31.1	28.9	1.31	10	25.4	29.5	28.1	1.32

spot (Figs. 5, 6) that is more or less rectangular in shape and horizontally elongate. It never reaches the dorsal and ventral borders of the caudal peduncle. The same spot is vertically elongate, lozenge-shaped and reaches the dorsal and ventral borders of the caudal peduncle in *K. theloura* (Fig. 7).

Description.—Morphometric data summarized in Table 1. Body elongate and compressed, greatest depth at dorsal-fin origin. Predorsal profile slightly convex. Profile of body along dorsal-fin base posteroventrally inclined, nearly straight from base of posterior dorsal-fin ray to adipose fin. Ventral body profile convex from tip of lower jaw to pelvic-fin origin. Muscles covering pelvic bone strongly prominent in ventral body profile, especially in males. Area between pelvic- and anal-fin origins slightly concave in females and notably concave in males, with a pair of concavities, separated from each other by a small median keel visible only when pelvic fins moved out of way. These concavities lodge pelvic fins when later retracted. Ventral profile along anal-fin base slightly concave in females. In males same profile, slightly convex in region of anterior lobe and slightly convex along remaining posterior fin portion. Dorsal and ventral profiles of caudal peduncle nearly straight in females. Dorsal and especially ventral surfaces of caudal peduncle of males convex, with an internal translucent cavity, covered by caudal peduncle scales.

Head small. Snout shorter than eye diameter. Mouth terminal. Maxilla short, positioned at an angle of approximately 45 degrees relative to long body axis. Posterior tip of maxilla reaching vertical that passes through anterior border of eye.

Premaxilla with 4 teeth, each having 9 small evenly spaced cusps all about equal in size. Cutting edge arched. Maxilla with 2 or 3 teeth similar in form to those of premaxilla, with 7–9 cusps. Cutting edge slightly arched to almost straight. Dentary bone with 4 or 5 large teeth each with 7 cusps; followed by 2 or 3 smaller teeth with

7 or fewer cusps. Teeth posterior to second tooth asymmetrical with most lateral cusps situated towards tooth base and most medial cusp more distally located. Cusps small and regular and approximately equal in size. Cutting edge slightly arched to almost straight.

Dorsal-fin rays, ii, 9, $n = 22$ (ii, 8 in one specimen). First unbranched ray less than half-length of second. Dorsal-fin origin approximately at midlength of body. Adipose-fin origin nearly at vertical through insertion of posteriormost anal-fin ray.

Anal-fin rays, iii, 18, (iii-iv $X = 3.5$, 16–19, $X = 17.5$, $n = 22$). Anal-fin origin slightly posterior to vertical passing through base of posteriormost dorsal-fin ray in females and at a vertical passing through base of two last dorsal-fin rays in males. Distal border of anal fin concave in females, with anterior 5–6 branched rays very long, forming prominent anterior lobe. Distal border of anal fin of males convex in the anterior lobe, decreasing in length gradually and forming a posterior concave border. Anal-fin rays of males with slender, elongate retrorse hooks on longest unbranched ray, and anterior first 5 or 6 branched rays (scattered hooks present in branched rays 7 and 8 in one specimen). Hooks inserted at posterolateral border of fin rays, bent over lateral surface of fin ray and anteriorly directed. Hooks located on posterior ray branches, less numerous on anterior ray branches. One, rarely two, bilateral pair of bony hooks per ray segment.

Pectoral-fin rays, i, 9 (i, 8–9, $X = 8.6$, $n = 22$). Distal ends of longest rays not reaching pelvic-fin origin in females; reaching or not in males. Pelvic-fin rays, i, 7 (1,7 in all specimens, $n = 22$). Pelvic-fin origin anterior to vertical passing through dorsal-fin origin. Distal tip of pelvic fin passing anal-fin origin in males, but not in females. Male pelvic fins bearing elongate ventromedial retrorse hooks along branched rays 2 to 8.

Principal caudal-fin rays 10/10 (10/9, but 10/10 and 9/9, in one specimen each, $n =$

21). Lower caudal-fin lobe of males covered with series of papillae from 12th or 13th ray to 18th or 19th principal caudal-fin rays. Papillae most numerous near caudal-fin base, extending in some specimens to near tip of lower caudal-fin lobe. Hooks or hypertrophied dorsal fin-ray flaps absent. Dorsal fin-rays 9–10, and ventral procurrent caudal-fin rays 8–10, in two cleared and stained specimens.

Scales cycloid, moderately large. Lateral line pores incomplete, perforated scales 7, (5–9, $X = 7.4$, $n = 20$). Scales in lateral series 34, (32–36, $X = 33.7$, $n = 19$). Scale rows between dorsal-fin origin and lateral line 5, (5–6, $X = 5.2$, $n = 20$). Scale rows between lateral line and pelvic-fin origin 4, (4–5, $X = 4.1$, $n = 20$). Predorsal scales, when in regular series 11 (10–12, $X = 10.8$, $n = 18$).

Supraneurals, 4; precaudal vertebrae, 16; caudal vertebrae, 17–18 (in two cleared and stained specimens).

Color in alcohol.—(See Figs. 5, 6, 8). Head dark brownish dorsally with a silvery color in opercle and infraorbital area, where guanine not destroyed by fixative. Body pale brownish yellow; dorsolateral scales delineated in their borders with dark chromatophores. Black lateral body stripe evident, pale anterior to dorsal-fin origin, progressively wider and conspicuous posteriorly in larger specimens. Humeral spot absent. A conspicuous caudal spot centered at posterior termination of caudal peduncle, rectangle-shaped and extending to base of middle caudal-fin rays; caudal spot never reaching ventral and dorsal borders of caudal peduncle. Dorsal fin of males with a conspicuous small black spot in soft tissue between approximately mid length of first and second, and second and third branched dorsal-fin rays; dorsal fin of females without distinct marks. Anal fin of males with a concentration of dark chromatophores along midlength of first branched anal-fin ray, forming a small and conspicuous spot in adult male specimens; absent in females. An inconspicuous dark line present along

anal-fin base in both sexes, plus a small dark line on body nearly parallel to longitudinal lateral body stripe in males and parallel to anal-fin base in females. Pectoral and pelvic fins hyaline. Ventral body surface in area covering pelvic bone of males with a dark brown mark nearly shaped like an isosceles triangle, apparently delineating external area corresponding to muscles originating from pelvic bone. Ventral midline between pelvic-fin insertion and anal-fin origin of males with a pair of thin lateral black lines, seen only when pelvic fin extended. A dark mark present on lower internal border of orbits, visible only when eyes depressed.

Color in life.—Described from color slides of a male taken in the field by Pedro Gerhard. Head dark brownish dorsally; opercle and infraorbital area silvery. Body light brownish yellow; dorsolateral scales slightly delineated with dark chromatophores; belly silvery. Lateral body stripe evident, silvery, pale anterior to dorsal-fin origin. Humeral area unpigmented, but a dark area visible due to presence of a pseudotympanum. As described in preserved specimens, a conspicuous caudal spot centered at posterior termination of caudal peduncle, rectangle-shaped, and extending to base of middle caudal-fin rays; never reaching ventral and dorsal borders of caudal peduncle. Caudal spot in colorful specimens bordered dorsally and ventrally by two yellow spots. Small black spot on dorsal fin of males, located approximately at mid length of first and second, and second and third branched dorsal-fin rays, bordered dorsally by yellow pigmentation. Anal-fin spot of males located along mid length of first branched anal-fin ray, anteriorly bordered with yellow pigmentation. A small dark line along anal-fin base and a small dark line on body nearly parallel to longitudinal lateral body stripe visible above anterior lobe of anal fin. Pectoral and pelvic fins hyaline. Presence of marks on ventral body surface not visible in available photos.

Sexual dimorphism.—Males are easily

recognized by their color pattern, displaying two conspicuous small black spots on the dorsal and anal fins (see Fig. 5), and a triangular dark brown mark on the ventral body surface of the pelvic bones (see Fig. 8), absent in females (See Fig. 6). Sexes are also differentiated by the relative position of the pelvic and anal fins, both located more anteriorly in males than in females; by the larger caudal peduncle depth in males, having an expanded portion in its ventral and dorsal profiles; and by the larger pelvic-fin lengths of males (see Table 1 for all these measurements).

Distribution.—Known only from the type locality, the rio Pratinha, Bahia, Brazil. The rio Pratinha is a tributary of the rio Santo Antônio, itself a tributary of the rio Paraguaçu, a coastal drainage of eastern Brazil.

Habitat and natural history notes.—For a complete description of the site of collection of *K. figueiredoi*, the rio Pratinha, see Lima & Gerhard (2001: 112–113). In the rio Pratinha, *K. figueiredoi* was observed and collected only in those portions with a moderate water current. The species was most commonly collected in a riffle at a narrow stretch of rio Pratinha. Specimens were observed at midwater, swimming against the current, probably feeding on food items drifting downstream. During one occasion, one individual of this species was seen picking with its mouth on a large boulder in a cave entrance. The ecological preferences of *K. figueiredoi* may be remarkable, given the fact that at least some other species of the Cheirodontinae, for example *Cheirodon interruptus* (Jenyns) and *Cheirodon ibicuihensis* Eigenmann, prefer lentic waters such as lagoons or pools in slow-moving water courses in coastal streams of Rio Grande do Sul, Brazil, personal observation.

Etymology.—We take great pleasure in naming this species in honor of José Lima de Figueiredo, a Brazilian ichthyologist at the Museu de Zoologia da Universidade de São Paulo.

Discussion.—The two *Kolpotocheirodon* species are included in the tribe Compsurini (Malabarba et al. 1998) by sharing two unambiguous synapomorphies with the members of that tribe: they are inseminating (Character 70 in Malabarba et al. 1998), and the anal-fin hooks are positioned along the posterolateral border of the anal-fin rays and bent more or less anteriorly over the lateral surface of the anal-fin ray to which each is attached (Character 26 in Malabarba et al. 1998). The presence of hooks and their distribution in the caudal fin were also previously employed for the diagnosis of the tribe, but are absent in *K. figueiredoi*. Alternative hypotheses explaining this are discussed above under the diagnosis of this species. *Kolpotocheirodon theloura* was the only species of the Compsurini known to have aquasperm (a nearly spherical or spherical sperm nucleus), a condition also found in the new *Kolpotocheirodon figueiredoi*. All other species of the Compsurini so far investigated have elongate sperm nuclei (see Burns et al. 1997:434, fig. 1B–H & 1998:242, fig. 11).

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***Astyanax biotae*, a new species of stream fish from the Rio Paranapanema basin, upper Rio Paraná system, southeastern Brazil (Ostariophysi: Characiformes: Characidae)**

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Abstract.—*Astyanax biotae*, a new species of characid, is described from a first-order stream in the Rio Paranapanema basin, upper Rio Paraná system, in the interior of the state of Paraná, southeastern Brazil. The species differs from its congeners in that region in a combination of morphometric and pigimentary features.

Resumo.—*Astyanax biotae*, uma nova espécie de caracídeo é descrita de um riacho de primeira ordem na bacia do Rio Paranapanema, sistema do Alto Rio Paraná, interior do Estado do Paraná, sudeste do Brasil. A espécie descrita difere das demais espécies do gênero *Astyanax* ocorrentes na mesma região por uma combinação de caracteres morfológicos e pigmentares.

Astyanax Baird & Girard includes nearly 90 nominal species of neotropical characid fishes distributed from the southwestern United States to Argentina (Lima et al. 2003:106). The numerous nominal species assigned to *Astyanax*, in conjunction with the lack of a comprehensive treatment of the genus subsequent to Eigenmann (1921, 1927), often makes the identification of species problematic. Furthermore, *Astyanax* as now delimited is likely non-monophyletic, and various species encompassed in the genus as traditionally defined (i.e., characids with two rows of teeth in the upper jaw and with the inner tooth row consisting of five teeth) have been generically reassigned in recent years (e.g., Zanata 1997).

This uncertainty applies even in regions such as the upper Rio Paraná that until recently had been thought to be well known ichthyologically. Evidence from a series of fish groups (Britski & Langeani 1988; Menezes 1988; Vari 1988; Weitzman et al.

1988; Langeani 1990; Menezes 1996a, 1996b; Castro & Casatti 1997) demonstrates that the Rio Paraná system upstream from the now submerged Sete Quedas Falls is an area of endemism (see Castro et al. 2003), a phenomenon likely correlated with the formidable barrier to fish migration presented, until recently, by those falls. The numerous streams and headwaters that contribute to the large rivers of this system are inhabited primarily by fish species of small body sizes (mostly less than 12 cm in standard length). Such small-sized species constitute at least 50% of the described freshwater fish species of South America and typically demonstrate a high degree of geographic endemism (Castro 1999). Such species are highly dependent on riparian vegetation for food, shelter, and reproduction (see Böhlke et al. 1978; Lowe-McConnell 1987), but those habitats are threatened by a number of anthropogenic activities, most notably deforestation and the extensive use

of fertilizers and pesticides in intensive agricultural practices (see Lowe-McConnell 1975, 1987; Menezes et al. 1990; Sabino & Castro 1990; Araújo Lima et al. 1995; Castro & Menezes 1998).

The lacunae in our understanding of the fish diversity within the upper Rio Paraná basin and the possibility of extirpation of as-yet unrecognized species is clearly demonstrated by the species of *Astyanax* in that basin. In their comprehensive overview of the then-known species of *Astyanax* in the upper Rio Paraná basin, Garuti and Britski (2000) recognized seven species of the genus within that river system. Nonetheless, recent collecting efforts in that basin revealed at least two undescribed species of *Astyanax*, one of which is known only from a narrow first-order stream running through a narrow gallery forest that is a remnant of the originally widespread subtropical mesophytic forest of that region. This species, which may be in danger of extinction, is described herein.

Material and Methods

Measurements are given as proportions of standard length (SL) except for subunits of the head that are presented as proportions of head length. Lateral-line scale counts include all pored scales along that series, including scales posterior to the hypural joint. In fin-ray counts, lower-case Roman numerals indicate unbranched rays, and Arabic numerals indicate branched rays. The last anal-fin rays that are joined at the base were counted as one element. Counts for the holotype are indicated in square brackets in the text. Measurements were made following the methods outlined in Fink & Weitzman (1974:1–2) with the addition of head height measured at the vertical at the base of the supraoccipital spine. Cleared and stained specimens were prepared following a modification of the method outlined by Taylor & Van Dyke (1985). Vertebral counts include the four vertebrae associated with the Weberian apparatus.

Stomach contents were analyzed on eight specimens (37.5 to 52.5 mm SL) using the methods of frequency of occurrence and percent composition described by Bowen (1992) and Hynes (1950), respectively. The food items were grouped in broad taxonomic or ecological categories reflecting their origins, with aquatic insects and algae considered autochthonous and terrestrial insects, arachnids, and vascular plants allochthonous.

The following institutional abbreviations are used: LIRP—Laboratório de Ictiologia de Ribeirão Preto, Departamento de Biologia da Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, Brazil; MZUSP—Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; and USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Astyanax biotae, new species

Fig. 1, Table 1

Astyanax sp. 2. Castro et al., 2003:13, 20, 21, fig. 6.6 [Brazil, Paraná, Rio Parapanema basin; ecology].

Holotype.—LIRP 4009, 49.8 mm SL; Brazil, Paraná State, upper Rio Paraná system, Rio Parapanema basin, Município de Diamante do Norte, Fazenda Água Mole, Córrego Água Mole (22°38'31.7"S, 52°48'59.0"W); collected by Ricardo M. C. Castro, Hertz F. Santos, Ricardo C. Benine, Katiane M. Ferreira, and Flávio C. T. Lima, 7 August 2000 (station PPA029).

Paratypes.—LIRP 2734, 15 specimens, 27.5–52.3 mm SL; LIRP 4021, 2 cleared and stained specimens, 51.3–52.5 mm SL; USNM 373492, 15 specimens, 31.2–52.2 mm SL; MZUSP 79807, 10 specimens, 32.4–45.6 mm SL; LIRP 4276, 34 specimens, 33.0–47.4 mm SL; collected with holotype.

Diagnosis.—*Astyanax biotae* is readily distinguished from all congeners in the upper Rio Paraná basin in having the terminus



Fig. 1. *Astyanax biotae*, new species, holotype, LIRP 4009, 49.8 mm SL. Brazil, Paraná, upper Rio Paraná system, Rio Paranapanema basin, Município de Diamante do Norte, Fazenda Água Mole, Córrego Água Mole (22°38'31.7"S, 2°48'59.0"W).

of the base of the dorsal fin situated along the vertical through the base of the first or second branched anal-fin ray, versus through the origin of the anal fin (*A. fasciatus*, *A. trierythropterus*) or in the area of the vent (*A. altiparanae*, *A. cf. eigeman-*

niorum, *A. paranahybae*, *A. scabripinnis*, and *A. schubarti*). Furthermore, *A. biotae* has a distinct overall reticulate pattern formed by dark pigmentation on the exposed portion of the scales versus the lack of such a pigmentation pattern in all of the

Table 1.—Morphometric values for holotype and 30 paratypes of *Astyanax biota*. Standard length is expressed in millimeters; measurements 1–15 as percentages of standard length; 16–21 as percentages of head length.

	Holotype	Paratypes	Mean	SD
Standard length	49.8	27.5–52.3	44.20	6.11
1. Greatest body depth	34.7	34.7–41.8	38.68	1.83
2. Snout to dorsal-fin origin	54.5	50.4–56.9	53.86	1.32
3. Length of base of dorsal fin	13.3	12.3–15.1	13.55	0.69
4. Posterior terminus of dorsal fin to adipose fin	24.5	19.3–24.5	22.92	1.30
5. Posterior terminus of dorsal fin to caudal-fin base	38.4	35.6–41.9	37.39	1.30
6. Snout to origin of pelvic fin	49.6	45.7–49.8	48.33	0.98
7. Snout to anus	60.0	54.6–61.3	58.35	1.63
8. Snout to origin of anal fin	65.1	61.4–66.8	64.07	1.44
9. Length of base of anal fin	31.6	29.1–39.6	32.09	1.95
10. Length of caudal peduncle	10.4	9.4–12.8	11.31	1.29
11. Length of longest dorsal-fin ray	27.3	26.8–30.8	28.21	1.19
12. Length of first pectoral-fin ray	21.3	19.2–24.4	22.01	1.25
13. Length of first pelvic-fin ray	16.5	16.0–19.2	17.44	0.82
14. Least depth of caudal peduncle	12.0	10.9–13.7	12.40	0.55
15. Head length	27.7	25.4–28.7	27.23	0.86
16. Head height	94.2	94.2–113.5	102.15	4.40
17. Snout length	26.8	23.5–29.3	25.86	1.53
18. Gape width	29.0	26.3–34.8	30.59	1.88
19. Orbital diameter	31.9	31.9–40.0	34.85	2.17
20. Postorbital head length	42.8	35.1–43.6	39.72	2.13
21. Interorbital width	37.0	34.8–40.9	38.12	1.70

other species of *Astyanax* that occur in the upper Rio Paraná basin. *Astyanax biotae* and *A. paranahybae* can also be distinguished by the difference in their relative body heights (approximately 35–42% of SL versus 25%, respectively).

Description.—Morphometrics of holotype and paratypes presented in Table 1. Body relatively deep, less so in individuals of less than 30 mm SL; greatest body depth located along vertical through insertion of pelvic fin. Dorsal profile of head distinctly convex from margin of upper lip to vertical through posterior nostril, straight to very slightly convex from that point to tip of supraoccipital spine. Dorsal profile of body slightly to moderately convex from rear of head to origin of dorsal fin, straight and posteroventrally slanted along base of dorsal fin, straight to slightly convex from posterior terminus of base of dorsal fin to adipose fin, and slightly concave along caudal peduncle. Slight middorsal ridge present along predorsal region of body. Body transversely rounded overall dorsally, but somewhat flattened middorsally between posterior terminus of base of dorsal fin and adipose fin. Ventral profile of head strongly convex anteriorly and then slightly convex as far as vertical through posterior margin of eye. Ventral profile of body convex to insertion of pelvic fin, nearly straight but slightly posteroventrally aligned from that point to origin of anal fin, straight to slightly convex and posterodorsally slanted along base of anal fin, straight to slightly concave along caudal peduncle.

Head obtusely rounded anteriorly in lateral profile; mouth terminal, albeit very slightly upturned. Upper jaw with maxilla distinctly posteroventrally angled and extending under orbit as far as vertical through anterior margin of pupil. Nostrils of each side very close together; anterior opening circular, posterior crescent-shaped. Eye relatively large and without distinct adipose eyelid. Median fronto-parietal fontanel extending from mesethmoid to supraoccipital spine; width of fontanel approxi-

mately one-fourth of interorbital distance. Infraorbital series complete with third infraorbital by far the largest. All infraorbitals carrying laterosensory canal segments proximate to inner margin of orbital rim. Supraorbital absent. Branchiostegal rays four. Gill-rakers long and setiform; 6+1+11 rakers on outermost gill-arch of 52.5 mm SL cleared and stained specimen.

Description of dentition based on two cleared and stained specimens. Teeth on premaxilla in two rows, with teeth of inner row larger. Inner row with five teeth. Symphyseal tooth of inner series quadricuspid and more elongate than other teeth. Second tooth more massive and pentacuspid. Remaining teeth pentacuspid, with third and fourth teeth somewhat smaller than second tooth, and fifth tooth distinctly smaller than all other teeth in series. Outer row of teeth on premaxilla consisting of four tricuspid teeth arranged in regular series with size of teeth gradually decreasing laterally. Fourth tooth of outer tooth row separated from third tooth by distance twice that separating other teeth of series. Maxilla with single tricuspid or pentacuspid tooth. Dentary with eight to 10 teeth. Anterior five dentary teeth pentacuspid and arranged in single row. First four dentary teeth massive and followed by much smaller fifth tooth. Anterior five dentary teeth followed by gap and then three to five very small, elongate, conical teeth.

Scales cycloid, relatively large, and firmly implanted. Lateral line decurved anteriorly and then nearly straight along midlateral line, completely pored from supra-cleithrum to base of caudal fin and followed by apparently unossified tubular extension running along membrane between middle rays of caudal fin. Lateral line scales 32 to 35 [34]; scales in transverse series from origin of dorsal fin to lateral line 6 or 7 [6]; scales in transverse series from insertion of pelvic fin to lateral line 4 or 5 [4]; scales in transverse series from origin of anal fin to lateral line 4 or 5 [5]; scales along mid-dorsal line between tip of supraoccipital

process and origin of dorsal fin 10 to 14 [11]; scales along mid-dorsal line between posterior termination of base of dorsal fin and adipose fin 8 to 11 [9]; horizontal scale rows around caudal peduncle 13 to 15 [14].

Vertebrae 32(3), 33 (17), or 34 (7) [33].

Dorsal-fin rays ii,9 [ii,9]; anal-fin rays ii to iv,22 to 26 [iii,24]; total number of anal-fin rays 24 to 30 [28]; pectoral-fin rays i,10 to 12 [i,12]; pelvic-fin rays typically i,7, with i,6 in three specimens, and i,4 in both fins in one apparently anomalous individual [i,7]; some specimens with anteriorly directed hooks on dorsal surface of pelvic-fin rays in adpressed fin; principal caudal-fin rays 10/9 [10/9].

Dorsal-fin margin distally rounded to slightly truncate; first unbranched ray approximately 40% length of second unbranched ray. Dorsal-fin origin situated at vertical approximately at middle of SL. Origin of adipose fin located slightly anterior of vertical through posterior terminus of base of anal fin. Pectoral fin relatively well developed, profile distinctly acute in adpressed fin. Tip of pectoral fin extending to, or falling slightly short of, vertical through insertion of pelvic fin. Profile of expanded pelvic fin pointed, with lateral rays longest. Insertion of pelvic fin located distinctly anterior to vertical through origin of dorsal fin. Tip of adpressed pelvic fin extending to origin of anal fin. Distal margin of anal fin ranging from somewhat concave to straight, with third unbranched and first and second branched rays longest and subequal or first through third branched rays longest; subsequent branched rays gradually decreasing in length. Caudal fin forked with lobes rounded.

Color in life.—Description based on color transparencies of live holotype (see also Castro et al., 2003:fig 6.6). Overall coloration silvery-brownish with silvery highlights on scales, particularly in abdominal region. Basal region of exposed portions of scales darker, particularly along regions slightly dorsal of midlateral line. Iris, anteroventral portions of infraorbital region,

lower jaw, and ventral regions of head silvery. Iris with green highlights. Dark pigmentation as in preserved specimens.

Coloration in alcohol.—Overall ground color of specimens fixed in formalin yellowish-brown on body, with guanine still present on ventral portion of head and on abdomen. Snout and dorsal portion of head relatively dark. Middorsal and immediately adjoining portions of body dark. Distinct, ventrally attenuated humeral spot extending from approximately two scales ventral of dorsal midline to about one scale dorsal of horizontal through insertion of pectoral fin. Scales of lateral surface of body posterior of humeral mark with dark pigmentation field on exposed portion of each scale. Dark spots forming irregular, discontinuous dark stripe along midlateral surface of body. Caudal peduncle with distinct, anteriorly-attenuating, dark mark.

Dorsal, anal, and caudal fins with interradial membranes covered with small dark chromatophores. Dorsal fin with dark pigmentation on interradials more prominent on distal one-half of central rays of fins, particularly in larger individuals. Dark pigmentation on caudal fin particularly well developed along middle rays of fin. Anal fin with dark pigmentation distinctly more developed on distal half of fin in some individuals; otherwise pigmentation of uniform intensity across fin. Adipose fin often freckled with small dark spots. Pectoral and pelvic fins with small dark spots along fin-ray margins and on membranes.

Etymology.—The species name, *biotae*, is in recognition of the important pioneering role of the “BIOTA/FAPESP—The Virtual Biodiversity Institute Program” (www.biota.org.br/) in the inventory, conservation, and sustainable use of the biodiversity resources of the State of São Paulo, Brazil. This special research program of the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) supported the collecting efforts that yielded all known specimens of the species.

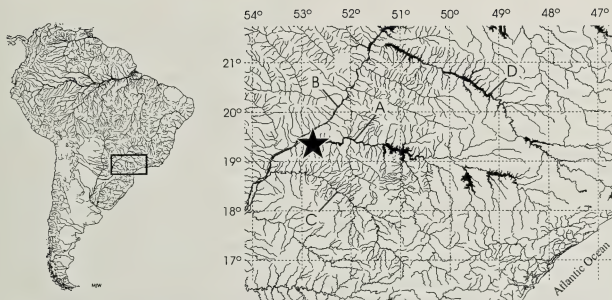


Fig. 2. Map of the upper Rio Paraná basin showing type locality for *Astyanax biotae* (star) and major river systems in the basin; A = Rio Paranapanema; B = Rio Paraná, C = Rio Uruguay, D = Rio Tietê.

Common name.—Brazil, Paraná, Diamante do Norte: “Lambari” a name also generically applied to all other species of *Astyanax* and other small characids in southeastern Brazil.

Distribution.—Known only from the type locality in the region called the Pontal do Paranapanema.

Ecology.—The sample of *Astyanax biotae* was collected during the winter dry season in the Córrego Água Mole (see Castro et al. 2003:fig. 5.6), a first-order stream running through a narrow, not very dense gallery forest within an extensive cattle grazing area, at an elevation of approximately 300 m above sea level. This location lies within what was originally an extensive subtropical mesophytic forest in southern and southeastern Brazil (Huek & Seibert 1981). The width of the stream varied between 0.7–1.0 m and the depth between 0.17–0.40 m, with a current speed of approximately 0.2 m.s⁻¹. The marginal vegetation was dominated by grasses of the family Cyperaceae (*Fimbristylis* sp.) and ferns (Pteridophyta) of the family Polypodiaceae. Water temperature was 18.6°C; pH 8.7; dissolved oxygen 10.6 mg.l⁻¹; conductivity 17

S.cm⁻¹; and horizontal water transparency 0.4 m.

Collecting efforts along an 100 m long stretch of the stream yielded seven fish species in addition to *Astyanax biotae*: *Callichthys callichthys*, *Corydoras aeneus*, *Crenicichla britskii*, *Gymnotus* cf. *inaequilabiatus*, *Gymnotus* cf. *sylvius*, *Rhamdia quelen*, and *Phalloceros caudimaculatus*. *Astyanax biotae* was the most abundant species in the sample (approximately 70% of the 110 specimens in the sample) and the second largest contributor to the fish biomass (approximately 31% of the total collected fish biomass) after *Rhamdia quelen* (approximately 53%). These values clearly indicate the ecological importance of *Astyanax biotae* at this site.

Although our food analysis results are derived from a single collecting event, the stomach content analysis of eight individuals (37.5 to 52.5 mm SL; one with an empty stomach) clearly demonstrates that *Astyanax biotae* feeds primarily on arthropods (approximately 80% of the diet composition), with debris and seeds of vascular plants (approximately 15%) and filamentous algae (approximately 6%) significantly

less important in the diet. Aquatic insects (mostly aquatic larvae of the Chironomidae followed in order by aquatic larvae of the aquatic Coleoptera, aquatic larvae of the Plecoptera and Trichoptera (equal amounts of each), nymphs of the Ephemeroptera, naiads of the Odonata, and a single adult of the aquatic Hemiptera) and terrestrial insects (primarily worker ants, Formicidae; followed by worker termites, Isoptera, and adult terrestrial Coleoptera) account for approximately 30% of the ingested arthropods, followed by distinctly lower numbers of arachnids (mostly spiders, Araneae, and a pseudoscorpion). Overall, approximately 55% of the items in the stomachs of *A. biotae* were allochthonous and 45% were autochthonous, a clear indication of the importance of the riparian vegetation as a food source for this species of *Astyanax*. One of the examined specimens, a 52.5 mm SL female (USNM 373492) with a greatly distended abdomen was found to contain approximately 350 roundish, well-developed, deep yellow oocytes 0.7–0.8 mm in diameter.

Comparative material examined.—*Astyanax altiparanae*, LIRP 35, 126 specimens, 43.0–80.1 mm SL; USNM 373491, 10 specimens, 41.1–79.9 mm SL. *Astyanax cf. eigenmanniorum*, LIRP 3401, 10 specimens, 55.0–70.8 mm SL; USNM 373495, 10 specimens, 48.5–68.3 mm SL. *Astyanax fasciatus*, LIRP 32, 28 specimens, 42.0–93.5 mm SL; USNM 373493, 10 specimens, 45.7–83.8 mm SL. *Astyanax schubarti*, MZUSP 4263, holotype, 82.9 mm SL; MZUSP 4264, 1 paratype, 90.4 mm SL. *Astyanax scabripinnis*, LIRP 124, 562 specimens, 19.1–75.0 mm SL; USNM 373494, 10 specimens, 36.5–74.8 mm SL. *Astyanax trierythropterus*, LIRP 2017, 138 specimens, 26.3–41.2 mm SL; USNM 373496, 10 specimens, 27.8–41.1 mm SL.

Acknowledgments

The specimens of *Astyanax biotae* that served as the basis for this description were collected during a collaborative LIRP-MZUSP expedition supported by FAPESP

(Fundação de Amparo à Pesquisa do Estado de São Paulo) within the “BIOTA/FAPESP—The Virtual Biodiversity Institute Program” (www.biota.org.br/) through the Thematic Project “Fish diversity of the headwaters and streams of the upper Paraná River system in the State of São Paulo, Brazil” (FAPESP grant No. 98/05072-8, Ricardo M. C. Castro (LIRP) principal investigator). Research associated with this project was supported by that grant, the Neotropical Lowland Research Program of the International Environmental Sciences Program of the Smithsonian Institution, and the PRONEX Project “Conhecimento, conservação e utilização racional da diversidade da fauna de peixes do Brasil” (FINEP/CNPq grant No. 661058/1997-2). The first author is a Conselho Nacional de Desenvolvimento Científico e Tecnológico do Brasil researcher (grant No. 301309/91-4). The success of the collecting effort was assured by the assistance of H. F. Santos, K. M. Ferreira and R. C. Benine (all of LIRP), and F. C. T. Lima (MZUSP). H. F. Santos (LIRP) assisted with the preparation of the clear and stained specimens, the stomach extractions for diet analysis and the preparation of the photograph of the holotype. A. L. A. Melo (LIRP) processed the specimens. A. C. Ribeiro (LIRP) produced the distribution map and K. M. Ferreira (LIRP) helped with the identification of the stomach contents. This paper was greatly improved by the suggestions and criticisms of S. H. Weitzman and C. J. Ferraris, Jr.

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Tetragonopterus lemniscatus (Characiformes: Characidae), a new species from the Corantijn River basin in Suriname

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Abstract.—*Tetragonopterus lemniscatus*, a new species of characid characiform, is described from the Corantijn River basin in western Suriname. The species is readily distinguished from its congeners (*T. argenteus*, *T. chalconus*) by the presence of dark, longitudinal stripes positioned between adjacent scale rows of the lateral surface of the body.

Resumo.—*Tetragonopterus lemniscatus*, uma nova espécie de caraciforme caracídeo, é descrita de bacia do Rio Corantijn, oeste de Suriname. Esta espécie é prontamente distinguida de seus congêneres pela presença de um padrão estriado de coloração ao longo do corpo, formado por faixas escuras presentes entre as fileiras de escamas adjacentes.

The Neotropical characid characiform genus *Tetragonopterus* is characterized externally by a relatively deep body with a transversely-flattened prepelvic region that is bordered laterally, particularly proximate to the pelvic-fin insertion, by distinctly-angled scales, a pronounced ventral curvature of the anterior portion of the lateral line, an anal fin with a long base, and a complete outer row of teeth on the premaxilla. Recent authors (e.g., Géry 1977:450; Reis 2003: 212) have recognized only two species of *Tetragonopterus*, *T. argenteus* and *T. chalconus*, but the examination of samples of the genus that originated in the Corantijn River basin of western Suriname revealed a third species of the genus, which we describe herein.

Material and Methods

Measurements are given in terms of standard length (SL). Lateral-line scale counts

include all pored scales along that series, including scales posterior to the hypural joint. In fin-ray counts, lower-case Roman numerals indicate unbranched rays, and Arabic numerals indicate branched rays. The last anal-fin rays that are joined at the base were counted as one element. Morphometric and meristic data were taken following the procedures outlined in Fink & Weitzman (1974). Individual meristic values in the description are followed by their frequency in parentheses, with values for the holotype indicated in square brackets. Gill rakers counts were taken from specimens that were cleared and counterstained following the method of Taylor & Van Dyke (1985). Vertebral counts were taken via radiographs and include the four vertebra of the Weberian apparatus and the terminal centrum.

Institutional abbreviations follow Leviton et al. (1985) with the addition of LIRP, La-

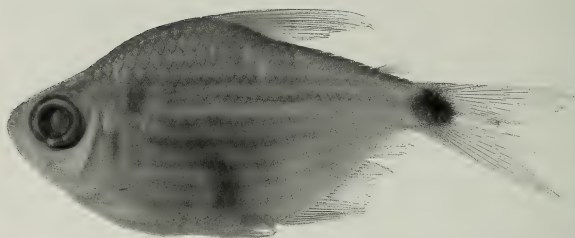


Fig. 1. *Tetragonopterus lemniscatus*, new species, holotype, USNM 225366, 47.5 mm SL; Suriname, Nickerie District, tributary to Sisa Creek.

boratório de Ictiologia de Ribeirão Preto, Departamento de Biologia da FFCLRP, Universidade de São Paulo, Ribeirão Preto, SP, Brazil; and NZCS, National Zoological Collection of Suriname, Paramaribo, Suriname.

Tetragonopterus lemniscatus,
new species
Fig. 1, Table 1

Holotype.—USNM 225366, adult male, 47.5 mm SL, Suriname, Nickerie District,

Table 1.—Morphometric data for holotype and 11 paratypes of *Tetragonopterus lemniscatus*.

	Holotype	Paratypes	
		Range	Mean
Standard length (mm)	47.5	41.8–81.4	
Percentages of standard length			
Greatest body depth	51.1	46.2–53.9	50.0
Snout to dorsal-fin origin	52.1	51.3–53.6	52.4
Snout to pectoral-fin origin	28.9	27.6–29.9	29.1
Snout to pelvic-fin insertion	50.9	47.5–52.2	49.6
Snout to anal-fin insertion	67.9	64.6–69.4	67.2
Caudal peduncle depth	12.0	10.3–12.0	11.0
Caudal peduncle length	9.3	7.1–9.5	8.3
Pectoral-fin length	22.8	21.7–24.3	23.0
Pelvic-fin length	19.6	17.6–21.1	19.7
Dorsal-fin length	32.8	32.6–44.3	37.2
Orbit to dorsal-fin origin	38.5	37.1–42.1	38.8
Head length	26.0	25.6–29.4	28.1
Head depth	22.2	20.4–22.2	21.4
Percentages of head length			
Snout length	27.0	24.4–28.2	26.2
Upper jaw length	41.3	41.3–44.9	43.3
Horizontal orbital diameter	41.8	38.1–47.0	42.9
Least interorbital width	38.6	29.6–38.6	32.9

tributary to Sisa Creek, north side of stream approximately 700 m downstream of crossing of road from Amotopo to Camp Geologie, approximately 3°42'N, 57°42'W, R. P. Vari et al., 20 Sep 1980.

Paratypes.—All collected in Suriname, Nickerie District. USNM 374750, 4 specimens, 42.0–46.6 mm SL. LIRP 4928, 2 specimens, 47.5–47.9 mm SL, cleared and counterstained, collected with holotype. USNM 225523, 2 specimens, 74.0–81.4 mm SL. LIRP 4929, 1 specimen, 79.8 mm SL, stream at km 212 of Amotopo to Camp Geology road, at Machine Park-Camp 212, approximately 3°50'N, 57°34'W, R. P. Vari et al., 15 Sep 1980. NZCS F7062, 1 specimen, 62.1 mm SL, formerly USNM 225320, stream entering Corantijn River, at approximately km 385, slightly N of Tiger Falls, approximately 4°00'N, 58°02'W, R. P. Vari et al., 16 Sep 1980. USNM 224367, 2 specimens, 48.4–60.1 mm SL, Kamp Kreek, 100 m N of turnoff to Camp Geology, approximately 4°49'N, 57°28'W, R. P. Vari et al., 13 Sep 1980.

Diagnosis.—*Tetragonopterus lemniscatus* is distinguished from its two recognized congeners, *T. argenteus* and *T. chalceus*, by the dark pigmentation on the lateral surface of the body (presence of dark, longitudinal stripes formed by pigmentation fields along the margins of the adjoining scale rows versus the absence of dark stripes, respectively). *Tetragonopterus lemniscatus* further differs from *T. argenteus* in the number of median scales between the tip of the supraoccipital spine and the base of the first dorsal-fin ray (8 versus 12–16, respectively).

Description.—Morphometric data are summarized in Table 1. Overall body size moderate (41.8–81.4 mm in SL). Body proportionally deep. Greatest depth of body at origin of dorsal fin. Dorsal profile of head slightly concave above orbit. Each nostril located closer to anterior margin of orbit than to each other. Supraoccipital spine elongate, but tip of spine not extending beyond vertical through posterior margin of opercle.

Dorsal profile of body convex from tip of supraoccipital spine to posterior terminus of base of dorsal fin; slightly convex from that point to end of base of adipose fin. Caudal peduncle profile concave both dorsally and ventrally. Ventral profile of body convex from tip of lower jaw to beginning of caudal peduncle. Prepelvic region of body transversely flattened, with flattening more pronounced proximate to pelvic-fin insertion. Scales along lateral margins of flattened region immediately anterior to insertion of pelvic fin with distinct angle. Obtuse median keel extending from immediately posterior of insertion of pelvic fin to urogenital opening.

Mouth terminal. Premaxillary teeth in two rows. Outer premaxillary tooth row with 4 (5) or 5 (7) [5] tricuspid teeth with median cusps most developed. Inner row with 5 teeth with tetracuspid symphyseal tooth followed by two pentacuspid, and then two, rarely one, tricuspid teeth. Maxilla with 3 tricuspid teeth along anterodorsal portion of free anterior margin. Dentary with 4 (4) or 5(8) [5] pentacuspid teeth followed by series of small tricuspid teeth (Fig. 2).

Dorsal-fin rays ii,9 (12) [ii,9]. Distal margin of dorsal fin straight. Adipose fin well-developed. Anal-fin rays iv,29 (3), iv,30 (5), or iv,31 (4) [iv,30]. Posterior unbranched and anterior branched anal-fin rays longest, with distal margin of remainder of fin moderately concave. Principal caudal-fin rays i,17,i (12) [i,17,i]. Pectoral-fins rays i,11 (2), i,13 (7), or i,14 (3) [i,13]. Tip of pectoral fin extending beyond vertical through insertion of pelvic fin. Pelvic-fin rays i,7 (12) [i,7]. Tip of pelvic fin reaching to base of first or second unbranched anal-fin ray in smaller individuals, barely falling short of base of first unbranched ray in larger specimens.

Scales cycloid. Median scales anterior to origin of dorsal fin 8 (12) [8]. Lateral line distinctly ventrally curved anteriorly, with 33(3), 34(5), or 35(4) [33] pored scales. Rows of scales above lateral line to origin of dorsal fin 6 (11) or 7 (1) [6]. Rows of

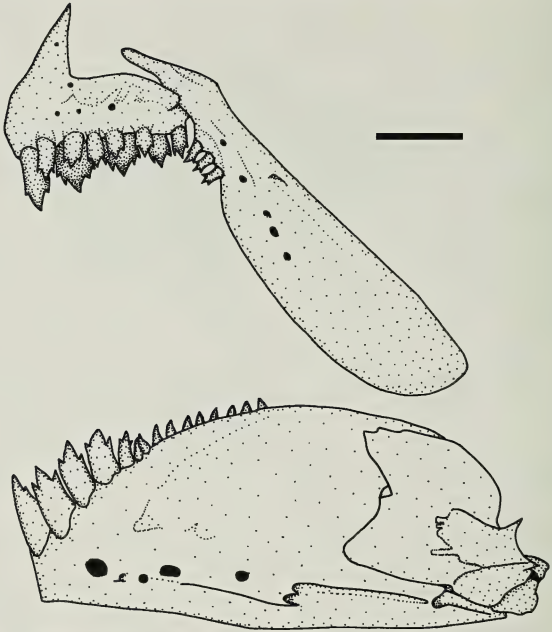


Fig. 2. *Tetragonopterus lemniscatus*, paratype, LIRP 4928, 47.5 mm SL. Premaxilla, maxilla, and lower jaw showing form of dentition; left side, lateral view. Scale bar = 1 mm.

scales below lateral line to origin of anal fin 5 (11) or 6 (1) [5]. Scales around caudal peduncle 14 (11) [14]. Scale sheath formed of one row of scales overlaps basal portions of all but three or four posterior most anal-fin rays. Field of small scales covering base of caudal fin; scale field extending further distally on fins along its dorsal and ventral margins.

Two cleared and stained specimens with 9 gill-rakers on upper limb and 13 gill-rakers on lower limb of first gill arch.

Vertebrae 30 in all specimens including holotype.

Coloration in life.—(Based on photograph of recently captured specimen from the Corantijn basin by third author). Overall coloration silvery, but somewhat purplish on portion of body dorsal to horizontal running approximately through dorsal margin of orbit. Humeral spot faintly apparent. Dark stripes on lateral surface of body apparent, but slightly masked by overlying guanine. Infraorbital series, opercle, ventral



Fig. 3. Map of Suriname showing collecting sites of *Tetragonopterus lemmiscatus*. Star = holotype locality and dots = paratype localities (some symbols represent more than one locality or lot).

portion of head, and most of body bright silver. Iris yellowish with indications of red dorsally. Fins dusky with yellowish cast.

Color in alcohol.—Overall ground coloration yellowish tan. Dorsal portion of head, jaws, nape, and portion of middorsal region of body anterior and posterior to base of dorsal fin distinctly darker. Posterior margins of scales with band of dark chromatophores. Dark pigmentation particularly well-developed on dorsal and ventral portions of exposed regions of scales and forming undulating, narrow, horizontal stripes along regions of overlap of scale rows on lateral surface of body. Stripes extending on anterior portion of body from horizontal through base of insertion of pectoral fin to region about two scales ventral of origin of dorsal fin. Stripes ventral of horizontal through dorsal margin of orbit decurved

ventrally anteriorly, with posterior portion of ventralmost stripes posterodorsally-angled in region over base of anal fin. Smaller individuals with 9 or 10 dark stripes apparent. Dorsalmost stripes becoming variably masked by overall darker pigmentation on dorsolateral region of body in larger specimens. Humeral region with indistinct, slightly posterodorsally-aligned bar in area above second and third scales of lateral line. Humeral spot becoming progressively less apparent in larger specimens. Caudal peduncle with large, rounded, dark spot continuing posteriorly onto basal portions of middle caudal-fin rays. Short, irregular, horizontal stripes extending anteriorly from anterior margin of spot in some larger individuals.

Median fins with small, dark chromatophores overlying both membranes and rays

of rayed fins and lateral surface of adipose fin. Distal margin of caudal fin somewhat darker in some large specimens. Pectoral and pelvic fins hyaline or with few, small, dark chromatophores.

Distribution.—*Tetragonopterus lemniscatus* is only known from localities in the Corantijn River basin in western Suriname (Fig. 3).

Habitat.—The holotype locality of *Tetragonopterus lemniscatus* was a black water rainforest stream with a limited amount of emergent vegetation and shadowed by overhanging trees. The stream had a moderate rate of water flow over a sand bottom with areas of detritus. Although all other population samples of the species were also collected in black water, some of the locations were in full sun and at other collecting sites the current was swift. Some locations at which the species was collected had areas of clay, rock, or mud bottom.

Etymology.—The species name, *lemniscatus*, from the Latin for beribboned, is in reference to the series of dark stripes along the lateral surface of the body in this species.

Remarks.—*Tetragonopterus* was first reported from Suriname by Kner (1859:38) who cited *T. chalceus* for that country. That citation may have been the basis for the inclusion of the species in the Surinamese ichthyofauna by Eigenmann (1912:68; 1917:58) and for the report of the occurrence of the species throughout the Guianas by Géry (1977:450). Ouboter and Mol (1993:146) reported *T. chalceus* from both the upper portion of the Corantijn River and from the Kabalebo River, the major right bank tributary to the Corantijn River. It is likely that the above citations, in particular that of Ouboter and Mol (1993), were based, at least in part, on *T. lemniscatus*. *Tetragonopterus* has not been reported from elsewhere in Suriname, although *T. chalceus* has been reported from a series of localities across French Guiana including the Fleuve Maroni along the Surinamese-

French Guiana border (Planquette et al., 1996:320).

Comparative material.—*Tetragonopterus chalceus*: MNHN A9812 (holotype); MCP 15145 (4, 1 C&S); USNM 66293 (1); MZUSP 29820 (3) (1 C&S); MCP 14015 (1, C&S); MZUSP 40819 (2, 1 C&S). *Tetragonopterus argenteus*: MNHN A-9807 (1); MZUSP 15570 (4, 2 C&S); MZUSP 5091 (2, 1 C&S); USNM 224789 (4).

Acknowledgments

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***Longipalpa saltatrix*, a new genus and species of the meiofaunal family Nerillidae (Annelida: Polychaeta) from an anchihaline cave in Bermuda**

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Abstract.—A new genus and species of the meiofaunal family Nerillidae is described from an anchihaline cave in Bermuda. The description is based on studies of live animals with dissecting and light microscopes, as well as studies of fixed material with light and scanning electron microscopy. *Longipalpa saltatrix*, new species, differs from all other nerillids by possessing a pair of extremely long latero-ventral palps on the prostomium and a pair of ciliated pygidial lobes. It is further characterized by the combination of the following characters: three very short dorsal prostomial antennae, eight chaetigerous body segments, single parapodial cirri from segment three to eight, compound chaetae, and hermaphroditism.

With 48 species in 17 genera (300 μm –2 mm in length), the Nerillidae is the largest meiofaunal family in the Polychaeta. The family has been a member of the now rejected group 'Archiannelida' (e.g., Beauchamp 1910, Goodrich 1912). The Nerillidae are now believed to be more closely related to a macrofauna family among the Aciculata and possibly have evolved by progenesis (Westheide 1990, Westheide & Purschke 1996, Rouse & Fauchald 1997, Rouse & Pleijel 2001).

Nerillids are nearly all marine and distributed worldwide, from the intertidal to abyssal depths (3660 m—see Worsaae & Kristensen 2003). While most nerillids are members of the interstitial sand fauna, some have been found in mud, fine silt, organic debris, bacterial mats, green algae and macrophytes (Jouin & Swedmark 1965, Gelder 1974, Sterrer & Iliffe 1982, Saphonov & Tzetlin 1997, Müller et al. 2001, Worsaae & Kristensen 2003). Several nerillids are known from caves: *Leptonerilla prospera* (Sterrer & Iliffe, 1982) was described from caves in Bermuda with fine silt; *Mesone-*

rilla diatomeophaga Núñez, 1997 in Núñez et al. (1997) was described from a cave in Lanzarote with diatom carpets on lapilli; *Nerilla marginalis* Tilzer, 1970 was described from a marginal cave in Istra; and *Troglochaetus beranecki* Delachaux, 1921 has been reported from various freshwater caves, groundwater reservoirs and mountain rivers in Europe and Colorado, U.S.A. [see Morselli et al. (1995) for review]. Nerillids are known from all continents, except Antarctica, and the wide geographical distribution as well as the diversity in habitats may well reflect an old evolutionary origin of the family.

The anchihaline Bermudian caves are inhabited by a rich and diverse fauna, consisting primarily of crustaceans (Sket & Iliffe 1980; Iliffe et al. 1983; Manning et al. 1986; Iliffe 1993, 1994, 2000). The most abundant stygobiont taxa are copepods and ostracods with 18 species each. Non-crustaceans include two ciliates, two gastropods, and two annelids—the nerillid *Leptonerilla prospera* and the tubificid oligochaete *Phallogriloides macmasterae* (Er-

séus, 1986). Although most of these species are endemic to Bermuda, many of them have cave-adapted congeners from the Caribbean, Mediterranean and the Pacific. Stygobiont taxa with such highly anomalous distributions are believed to be Tethyan relicts.

Materials and Methods

The geology of Bermuda is particularly unusual in that the island consists of a mid-ocean volcanic seamount, capped with marine and eolian limestone of Pleistocene age. The numerous inland caves of Bermuda are totally within this limestone and often contain tidal, anchihaline pools that extend below sea level to a maximum depth of about 25 m. Surface waters in these pools are brackish, with salinity increasing with depth to approach fully marine levels at 3–5 m depths. The island and its caves have been profoundly affected by changes in sea level associated with Pleistocene glaciation. During the Ice Ages, sea level was as much as 100 m lower and the caves of Bermuda were all dry and air filled. Large speleothems (stalactites and stalagmites) formed at this time by rainwater percolating through the ground and dripping into the caves. As glacial periods ended, sea level rose and flooded a substantial portion of the caves such that they are only accessible with the use of specialized cave diving techniques (Iliffe 1993, 1994).

The material was collected in Roadside Cave, a small anchihaline cave located in the Walsingham Tract of Bermuda (32°21'N, 64°43'W) on 15, 20 and 21 Jan 2002. A low entrance crawlway opens to a small dark chamber containing a narrow marine lake, which extends underneath a rock ledge and has a maximum depth of no more than 10 m. Surface salinity and temperature recorded on 28 Oct 1981 were 30‰ and 23°C, respectively. Tidal magnitude in the pool is 57% of that in the open ocean, with a lag of 80 minutes. A number of other anchihaline stygobionts inhabit this

small pool, including the platycopoid copepods *Antriscopia prehensilis* Fosshagen, 1985 in Fosshagen & Iliffe (1985) and *Nanocopia minuta* Fosshagen, 1988 in Fosshagen & Iliffe (1988); the calanoid copepod *Paracyclops naessi* Fosshagen, 1985 in Fosshagen & Iliffe (1985); the misophrioid copepod *Speleophria bivexilla* Boxshall & Iliffe, 1986; the bogidiellid amphipod *Bermudagidiella bermudensis* (Stock, Sket & Iliffe, 1987); the pseudoniphargid amphipod *Pseudoniphargus grandimanus* Stock, Holsinger, Sket & Iliffe, 1986; the halocyprid ostracod *Spelaeoecia bermudensis* Angel & Iliffe, 1987; the mictacean *Mictocaris halope* Bowman & Iliffe, 1985; and the gastropod *Caecum troglodyta* Moolenbeek & Faber, 1987 in Moolenbeek et al. (1987). Similar to the new species of polychaete here described, the copepods *Antriscopia prehensile*, *Nanocopia minuta* and *Speleophria bivexilla* are known only from this cave.

Samples were collected with a conical plankton net with a diameter of 30 cm and a mesh size of 40 µm. Rocks and projections below the water surface were covered with a thin layer of fine silt. Before the samples were taken, the surface layer was whirled up with hands, fins or loose stones from 0.5–6.5 meter's depth and thereafter the net was dropped and dragged through the suspended material.

More than 70 specimens were sorted out alive from the collected samples. Several of these were observed and video recorded alive with a Hitachi VK C-350 video camera mounted on a Wild M 420 Makroskop dissecting microscope. Fourteen animals were studied and photographed alive with an Olympus BX51 light microscope mounted with a digital camera (Olympus c-3030). Twelve of these were afterwards prepared as permanent whole mounts. Unless otherwise mentioned, measurements were made on live animals. Before fixation, the animals were anesthetized in an isotonic solution of MgCl₂, which was added under the cover slip for the whole mounts. The MgCl₂

of the whole mounts was replaced by a fixative (2% formaldehyde or a trialdehyde solution) and then by a glycerol series from 2–100% (diluted in distilled water). When the glycerol was fully dehydrated after two days, the cover slip was sealed with Glyceel®.

Twenty-six specimens were fixed for scanning electron microscopy (SEM) in a modified trialdehyde solution (Lake 1973) and postfixed in 1% OsO₄, or fixed directly in 1% OsO₄. The specimens were transferred to distilled water, dehydrated through an acetone series, critical point dried, mounted on stubs, sputter coated with palladium, and examined with a JEOL JSM-6335F Field Emission scanning electron microscope.

The study of live animals was carried out at the Bermuda Aquarium and Zoo (BAMZ) and the study of fixed material was carried out at the Zoological Museum, University of Copenhagen (ZMUC). Types are deposited in the Zoological Museum, University of Copenhagen (ZMUC), Denmark, and in the Smithsonian Institution, National Museum of Natural History (USNM), Washington D.C., U.S.A.

Family Nerillidae Levinsen, 1883

Longipalpa, new genus

Diagnosis.—*Longipalpa* is unique among nerillids by having two extremely long palps on the prostomium and two densely ciliated lobes on the dorsal side of the pygidium. It is further characterized by the combination of the following characters: eight chaetigerous segments between prostomium and pygidium; prostomium with three very short simple dorsal antennae; compound serrated chaetae; single parapodial cirri from segment three to eight; two pygidial lobes; one anterior and one posterior group of non-motile cilia arranged in distinct patterns and a pair of short bands of motile cilia on prostomium; transverse discontinuous rows of ciliary tufts on dorsal and ventral surface; cuticular

plates in pharyngeal apparatus; two pairs of segmented nephridia from segment II–III and III–IV; hermaphroditic reproduction with one pair of spermi ducts from segment VI–VII and one pair of oviducts from segment VII–VIII.

Type species.—*Longipalpa saltatrix*, new species, by present designation.

Gender.—Feminine.

Etymology.—From the Latin *longus* (=long) + English *palp* (=prostomial appendage), in reference to the greater length of these appendages when compared to other genera in the family.

Similarity.—*Longipalpa* differs from the seventeen described nerillid genera by the two extremely long prostomial palps and two ciliated pygidial lobes. It furthermore differs from most genera by the very short length of the prostomial antennae, lack of parapodial cirri in segment 2 and possible lack of pygidial cirri.

Four characters have been important in defining nerillid genera in recent years: number of body segments (7–9), compound or capillary chaetae, number of antennae (0–3), and number of cirri per parapodium (1–2) (Tzetlin & Larionov 1988, Tzetlin & Saphonov 1992, Westheide & Purschke 1996, Müller et al. 2001, Müller 2002). *Longipalpa* resembles eight genera (*Afronerilla*, *Akessonniella*, *Micronerilla*, *Nerillidium*, *Nerillidopsis*, *Thalassochaetus*, *Trochonerilla*, *Troglochaetus*) by having eight segments. It thereby differs from four genera with seven segments (*Aristonerilla*, *Bathychaetus*, *Paranerilla*, *Psammoriedlia*) and five genera with nine segments (*Leptonerilla*, *Meganerilla*, *Mesonerilla*, *Nerilla*, *Xenonerilla*). It resembles seven genera with compound chaetae (*Aristonerilla*, *Leptonerilla*, *Mesonerilla*, *Micronerilla*, *Nerillidopsis*, *Paranerilla*, *Thalassochaetus*) and six genera with three antennae (*Aristonerilla*, *Leptonerilla*, *Mesonerilla*, *Micronerilla*, *Nerilla*, *Trochonerilla*), although only *Trochonerilla* possesses antennae of similar short length. Two genera (*Leptonerilla*, *Micronerilla*) differ from *Longipalpa* by the

presence of two cirri per parapodium (versus one cirrus per parapodium in *Longipalpa*).

Six genera show resemblance to *Longipalpa* in three out of the four "generic" characters mentioned above: *Aristonerilla*, *Mesonerilla*, *Micronerilla*, *Nerillidopsis*, *Thalassochaetus*, and *Trochonerilla* (see Table 1). *Micronerilla* may show the greatest resemblance with *Longipalpa*, but differs by having two cirri per parapodium, pygidial cirri and two eyes. It furthermore diverges by the much longer antennae; many ciliary tufts on antennae, parapodial and pygidial cirri; parapodial cirri present on segment 2 (and sometimes on segment 1 as well) and absent on the last segment; gonochoristic reproduction and two pairs of spermi ducts (Swedmark 1959, Jouin 1970, Saphonov & Tzetlin 1997, Müller 2002). The other five genera likewise differ from *Longipalpa* in several important characters mentioned in Table 1.

Leptonerilla prospera has previously been described from the caves of Bermuda (Sterrer & Iliffe 1982). The two Bermudian cave species have not been found in the same cave or cave-systems, although Roadside Cave and Walsingham Cave (type locality for *L. prospera*) are separated by only 290 m. Their morphology is very different, and there is no reason to suspect that these two species should be closely related.

Longipalpa saltatrix, new species

Figs. 1–6, Table 2

Gen sp. A in Worsaae & Müller (2004).

Type material.—Holotype: ZMUC-POL 1675 (whole mount), 763 µm long, Roadside Cave, Bermuda (32°21'N, 64°43'W), 0.5–6.5 m depth, 20 Jan 2002. Paratypes: All paratypes with same locality as for holotype, 0.5–6.5 m depth, collected 15, 20 and 21 Jan 2002. Nine specimens as whole mounts (ZMUC-POL 1676–1684) and 26 specimens on nine SEM-stubs (ZMUC-POL 1685–1693) are deposited in the Zoological Museum, University of Copenhagen

Table 1.—Comparison with relevant genera. Abbreviations: (), exceptions from remaining species of a genus; —, not applicable; segm, segment.

Genus	Segm	Antennae	Antennae dimensions ^a	Chaetae	Eyes	Cirri segm	Cirri per parapodium	Pygidial cirri	Sex	Spermi ducts segm	Others
<i>Longipalpa</i>	8	3	short	compound	0	3–8	1	0	hermaphroditic	VI–VII	long palps, pygidial lobes ciliary tufts on antennae
<i>Aristonerilla</i>	7	3	long	compound	2	2–7	1	2	gonochoristic	VI–VII	
<i>Mesonerilla</i>	9	3 (2)	long	compound	(0)	1–9	1	2	gonochoristic, hermaphroditic	IV–V, V–VI + VI–VII	
<i>Micronerilla</i>	8	3	long	compound	2	1–7	2	2	gonochoristic	VI–VII + VII–VIII	ciliary tufts on antennae
<i>Nerillidopsis</i>	8	2	medium	capillary + compound	0	2–7	1	2	hermaphroditic	V–VI	
<i>Thalassochaetus</i>	8	0	—	compound	0	2–7	1	2	?	?	
<i>Trochonerilla</i>	8	3	short	capillary	2	2–7	1	2	gonochoristic	VI–VII + VII–VIII	palps present ^b

^a Short = antennae shorter than prostomium and palps, medium = antennae longer than prostomium but shorter than palps, long = antennae longer than prostomium and palps.

^b Unpublished observations of *Trochonerilla mobilis* with palps (Worsaae, personal observation).

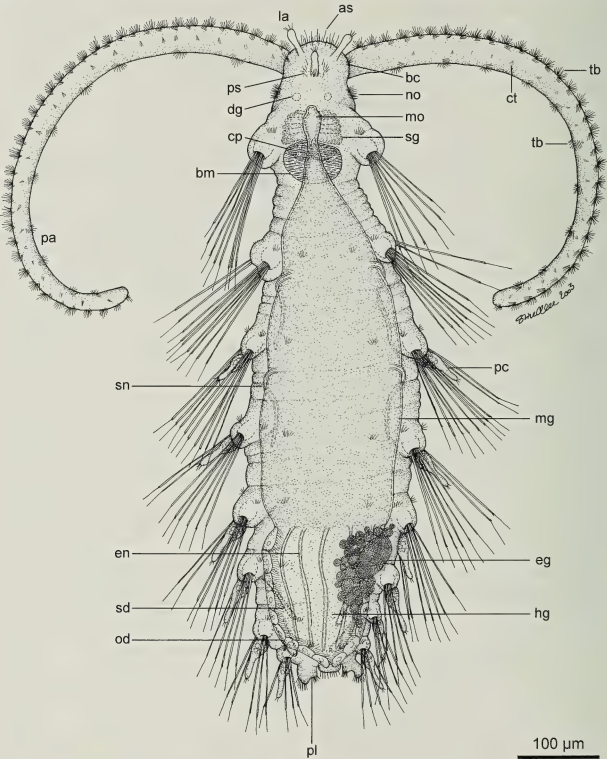


Fig. 1. Reconstruction from light micrograph of live holotype of *Longipalpa saltatrix*, new species, dorsal view. Not all chaetae are drawn. Detailed information on nephridia, gonoducts and external dorsal ciliation is included from confocal laser scanning microscopy and scanning electron microscopy. Abbreviations: as, anterior field of sensory cilia; bc, band of cilia; bm, bulbus muscle; ct, ciliary tuft; cp, cuticular plates; dg, dorsal glands; eg, eggs; en, enteronephridium; hg, hindgut; la, lateral antennae; mg, midgut; mo, mouth; no, nuchal organ; od, oviduct; pa, palp; pc, parapodial cirrus; pl, pygidial lobe; ps, posterior field of sensory cilia; sd, spermioduct; sg, salivary glands; sn, segmented nephridium; tb, transverse ciliary band.

Table 2.—Meristics and morphometric characters of holotype and total type material (measurements on juveniles in parentheses). Abbreviations: excl., exclusive; incl., inclusive; L, length; min., minimum; max., maximum; segm., segment; W, width.

	Holotype	Min.	Max.	Average	n
<i>Total</i>					
L excl. appendages, chaetae	763	624 (471)	985	788	14
max. W incl. parapodia	224	127 (116)	285	202	13
max. W excl. parapodia	192	108 (99)	268	173	13
<i>prostomium</i>					
L	72	59	77	68	12
W	81	67 (66)	90	80	12
max. L palps	696	680 (660)	718	696	6
L median antenna	43	24 (17)	43	33	7
max. L lateral antennae	56	41 (31)	65	53	10
<i>trunk</i>					
L segm. 1	80	55 (46)	97	74	12
L segm. 2	123	98 (77)	150	126	12
L segm. 3	113	76 (71)	152	108	12
L segm. 4	109	73	121	104	12
L segm. 5	103	71 (69)	103	93	12
L segm. 6	67	54	106	80	12
L segm. 7	56	54	89	68	11
L segm. 8	35	25	58	42	11
L pygidium	8	8	37	20	12
max. L parapodia segm. I	63	35	63	53	13
max. L other parapodia	48	30	50	40	12
max. L parapodial cirri	67	41	73	60	13
max. L pygidial lobes	42	30	50	41	9
<i>chaetae</i>					
max. no. chaetae segm. 1 ^a		7 (6)	13	10	8
max. no. chaetae notopodia ^a		7	10	8	6
max. no. chaetae neuropodia ^a		6	10	8	6
max. total L chaetae ^b		135	145	139	8
max. L shaft ^b		86	109	103	5
L distal extension shaft ^b		0	2	1	5
L blade ^b		33	41	37	5

^a Measured on fixed material by SEM.

^b Measured alive by LM and on fixed material by SEM.

(ZMUC), Denmark. Two paratypes as whole mounts (USNM 1022181-1022182) are deposited in the Smithsonian Institution, National Museum of Natural History, Washington, D.C., U.S.A.

Diagnosis.—Characters of the genus.

Etymology.—From the Latin *saltator* (=dancer), in reference to the swimming skills of the species, which may swim in loops while waving and twisting the long palps.

Description (see Table 2 for principle counts and measurements).—A relatively

hyaline nerillid with brown pigmentation, especially along intestinal wall. The body consists of prostomium, eight chaetigerous segments and pygidium (Figs. 1, 2A, 4). Adults with eight segments and a total length of 624–985 μm (only 454–825 μm when fixed); juveniles with six to seven segments and a total length of about 500 μm . Maximum body width generally at segment five, up to 268/285 μm (excl./incl. parapodia); narrow restriction between segment one and two, posterior to the esophagus. Prostomium up to 77 μm long, 90 μm

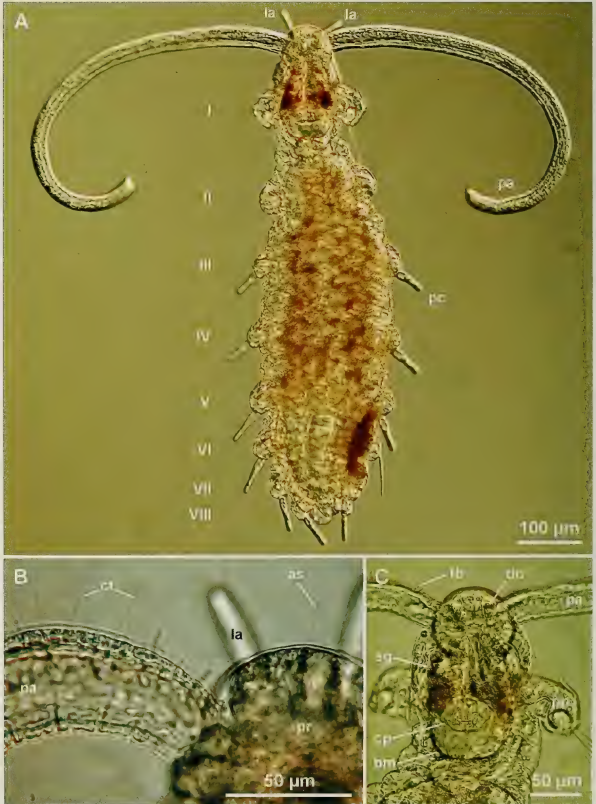


Fig. 2. Light micrographs of live holotype of *Longipalpa saltatrix*, new species. A, Whole specimen with two palps. B, Closer view of ciliation on palp and prostomium. C, Closer view of prostomium and segment one. Abbreviations: see Fig. 1; pp₁, parapodium of segment one; pr, prostomium; I-VIII, segments one to eight.

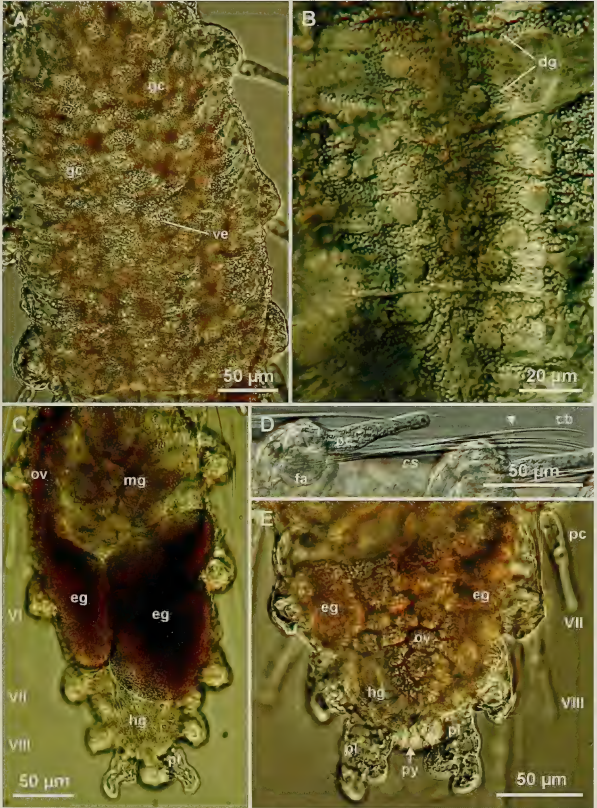


Fig. 3. Light micrographs of live specimens of *Longipalpa saltatrix*, new species. A, Dorsal view of segment three to six showing midgut lining of glandular cells with vesicles. B, Ventral view of middle segments showing diffuse glandular pattern. C, Posterior part of animal. D, Parapodium. E, Segments seven-eight and pygidium. Abbreviations: see Fig. 1; arrowhead, extension of shaft; cb, chaetal blade; cs, chaetal shaft; dg, diffuse glandular pattern; fa, fascicle; gc, glandular cells; ov, ovoids; py, pygidium; VI-VIII, segments six to eight; ve, vesicles.

wide; first four segments longest, decreasing in length posteriorly, pygidium even shorter.

Prostomium short, with two ventro-lateral palps and three dorsal antennae. Palps filiform and long, up to 718 μm (up to about 90% of body length in adults, and up to about 130% in juveniles), and with complex ciliation (see below) (Figs. 1, 2, 5A). Antennae short, filiform, with few distal cilia. Medium antenna up to 43 μm long, lateral antennae up to 65 μm long (Figs. 1, 4A, B, 5A). Nuchal organs paired, situated between palps and parapodia of segment one on a round elevated bulge on each lateral side of the prostomium (Figs. 1, 5A, C). Parapodia of segment one very large (up to 63 μm long), up to twice the length of the following parapodia (Figs. 1, 2A, 4A, C).

Parapodial cirri (with few distal cilia) between dorsal and ventral chaetal bundles of parapodia of segment three to eight; length up to 73 μm , increasing towards the posterior segments (Fig. 4A). No trace of attachment of parapodial cirri on segment one and two, neither of scars from detached cirri, or rudimentary cirri. Appendages like cirri and palps, and even chaetae, were easily lost during handling and fixing of the animals. Of the more than 70 specimens observed alive, none possessed parapodial cirri on segment one and two and scars were not found with SEM. Pygidial cirri were never observed, but it was difficult to examine the pygidium thoroughly for scars of cirri with SEM. On one specimen, a pair of scar-like structures was found at the pygidium, which could be scars from lost pygidial cirri or just an artifact (Fig. 6G). All adult (but no juvenile) animals possessed two very special structures, here named pygidial lobes due to their location on the dorsal side of the pygidium. Each lobe is up to 50 μm long, with two projections and a dense ciliation (Figs. 1, 3E, 4A, 6G, H).

All chaetae compound and relatively straight, shaft with minor pointed distal extension, less than 2 μm long (Figs. 3D, 6B).

Chaetae very slightly serrated and generally with a hairy appearance (Fig. 6A–C). Segment one uniramous, with up to thirteen chaetae in one chaetal fascicle; segments two to eight biramous, with dorsal and ventral fascicles comprising up to ten chaetae each. Similar numbers of chaetae in segments two to six, somewhat fewer chaetae in the last two segments. No noticeable differences in number or length between dorsal and ventral chaetae. Similar lengths in all segments of shaft, blade and total length of chaeta. Shaft up to 109 μm , blade up to 41 μm , total length up to 145 μm (Figs. 3D, 4, 6A).

Dorsal surface of prostomium with very specific ciliation characterized by three different groups of cilia: a pair of short bands with motile cilia (>20 cilia, up to 20 μm long), one on each dorso-lateral surface next to the lateral antennae (Figs. 1, 5A); two transverse rows of non-motile cilia in front of antennae on the anterior most part of the prostomium (Fig. 5A, B), the last of which arranged in a distinct pattern; and a posterior group of twenty non-motile cilia (Fig. 5D, E), arranged in complex pattern near the origin of median antenna on posterior part of the prostomium.

The patterns of the anterior field of cilia (probably sensory in function, see Discussion) and the posterior fields of cilia (probably sensory) are characteristic of the species and are here given in detail: anterior field of cilia (5–15 μm long) with two transverse rows of cilia (Fig. 5B). Posterior row contains about 5 cilia, spaced 2–5 μm apart (cilia no. 1–5 in Fig. 5B). Anterior row with about 20 cilia (no. 6–25 in Fig. 5B). Cilia arranged in distinct pattern mirrored halfway along the row. Moving towards the middle from the lateral sides, the first cilia are two groups of four cilia (no. 6–9 and 10–13), a single cilium next to them (no. 14 and 15), two groups of three cilia (no. 16–18 and 19–21), three cilia in the middle (no. 22–24), and one cilium (no. 25) in front of the middle cilium.

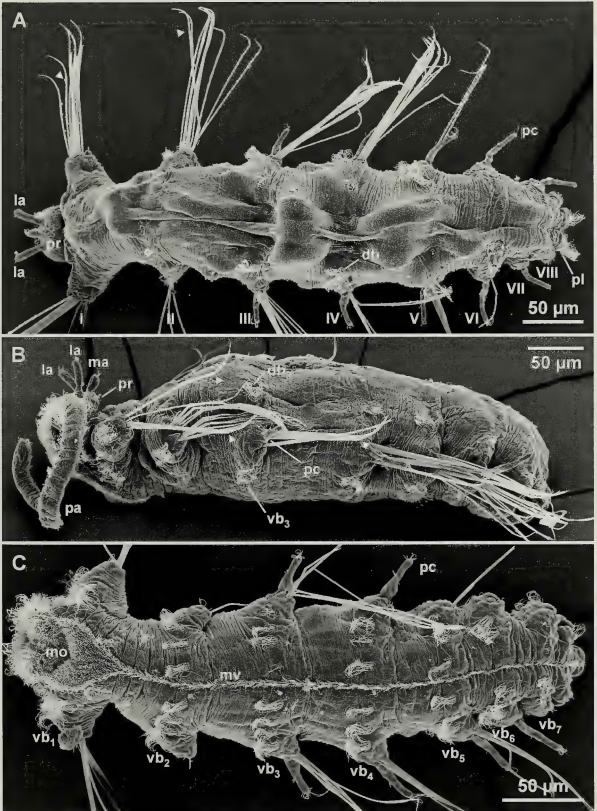


Fig. 4. Scanning electron micrographs of *Longipalpa saltatrix*, new species. A, Dorsal view of whole specimen with both palps lost. B, Lateral view of specimen with one palp lost. C, Ventral view of specimen with two palps lost. Abbreviations: see Figs. 1, 2; arrowhead, connection of chaetal shaft and blade; db₃, dorsal ciliary band of segment three; ma, median antennae; mv, midventral ciliary band; vb₁-vb₇, ventral ciliary band on segments one to seven.

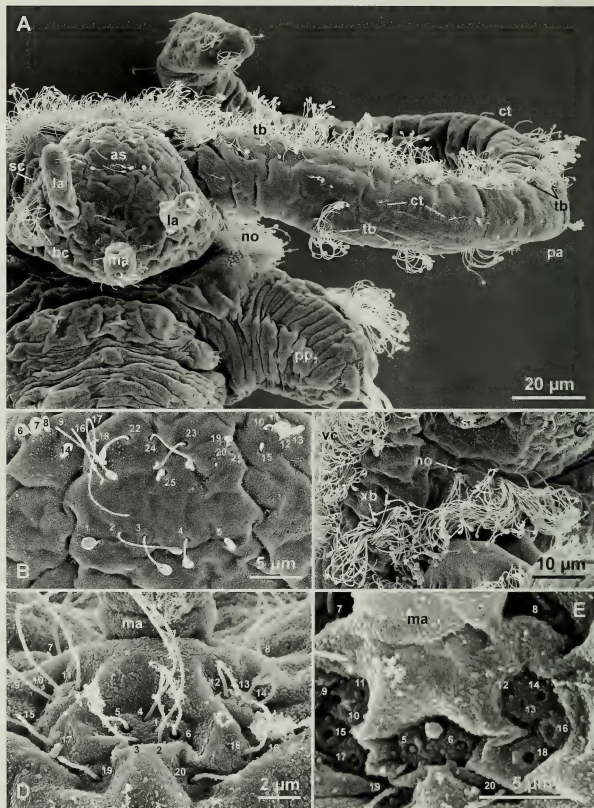


Fig. 5. Scanning electron micrographs of *Longipalpa saltatrix*, new species. A, Dorsal view of prostomium, right palp, and segment one. B, Closer view of anterior field of twenty-five cilia. C, Closer lateral view of nuchal organ and extra ventral ciliary band. D, E, Close dorsal view of posterior field of twenty cilia from two specimens. Abbreviations: see Figs. 1, 2, 4; bc, band of cilia; sc, scar from lost palp; vc, ventral ciliation around mouth; xb, extra ventral ciliary band.

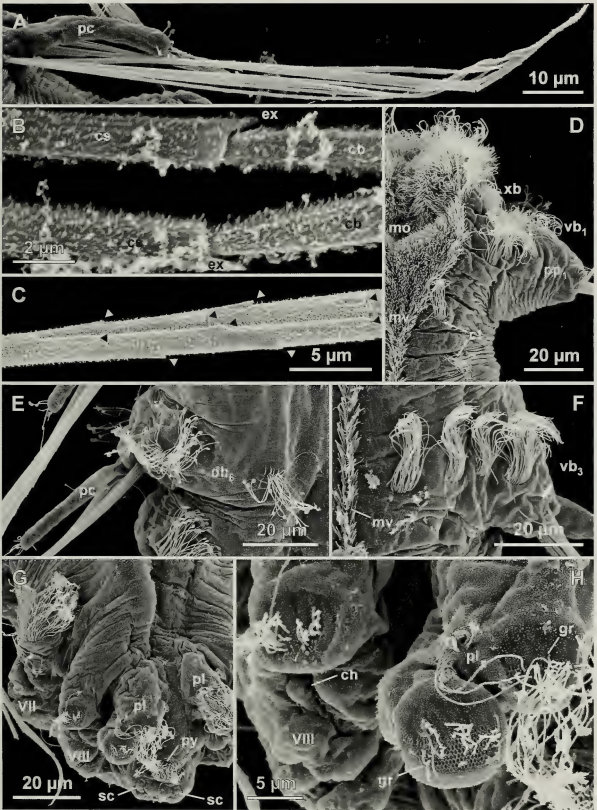


Fig. 6. Scanning electron micrographs of *Longipalpa saltatrix*, new species. A, Chaetal bundle and parapodial cirrus. B, Closer view of chaetae with microvillar hairy appearance. C, Two hairy chaetae showing serration pattern (indicated by arrowheads). D, Left ventral side of prostomium and segment one. E, Right side of segment six with half dorsal ciliary band. F, Left ventral side of segment three with half ventral ciliary band. G, Left dorsal side of posteriormost segments. H, Closer view of left pygidial lobe. Abbreviations: see Figs. 1-5; ch, holes after lost chaetae; db₆, dorsal ciliary band of segment six; ex, extension of shaft; gr, dense ciliary groups; sc, scars from lost pygidial cirri or an artifact.

Posterior field of twenty cilia (3–15 μm long) covers an area about 12 μm wide and 8 μm long (Fig. 5D, E). Four cilia in a close square (no. 1–4 in Fig. 5D) surrounded by a common elevation of the cuticle, are found in the center of the field, posterior to the basal part of the antenna. Right next to these four cilia one cilium is found on each lateral side (no. 5–6), which as all the single situated cilia in the pattern, is surrounded by a cuticular collar. On each lateral side of the antenna is one cilium (no. 7–8). About 3 μm posterior of these two clusters are found, each with three cilia in a transverse line, surrounded by a common elevation of the cuticle (no. 9–14). Next to these, on the level of the 4 central cilia, are found 2 pairs of cilia next to each other on each lateral side (no. 15–18). The last pair of cilia (no. 19–20) is located a few micrometers posteriorly with about 5 μm in between the cilia.

Palps with complex ciliation containing transverse ciliary bandlets in a longitudinal row on the inner and outer lateral surfaces of the palp, respectively. More than 20 cilia, up to 20 μm long in each ciliary bandlet, positioned 5–20 μm apart in a row extending to the tip. Farthest distance between bandlets on outer lateral surface of the palp. Longitudinal row of single ciliary tufts on both dorsal and ventral surface between the longitudinal rows of bandlets (Figs. 1, 5A). Less than 5 cilia, up to 7 μm long in each ciliary tuft, located in a row extending to the tip. Ciliary bandlets beat in metacronal waves, creating a water current leading particles towards the base of the palp. Motility of ciliary tufts not clearly distinguishable due to intense beating of ciliary bandlets. However, we suspect these cilia to be non-motile due to their small number and short length.

Dorsal surface of body segments not ciliated, except for few ciliary tufts. Two to four tufts of motile cilia are situated in a transverse line across each segment between the parapodia on each side (Figs. 4A, B, 6E). Each tuft contains 20–200 motile cilia, up to ca. 25 μm long. Each pygidial lobe possess-

es two large groups of cilia, one on each of the two projections of the lobe (Figs. 1, 4A, 6G, H). Each group contains more than 100 cilia, up to ca. 25 μm long.

Ventral surface with dense ciliation around mouth on ventral side of prostomium, continuous with relatively narrow mid-ventral ciliary band extending to the anus on the dorsal side of the pygidium. Transverse rows of ventral ciliary tufts on each segments at the level of the parapodia: four pairs on segments one to three, three pairs on segments four to seven, two pairs on segment 8. Three additional pairs of ciliary tufts: one pair between prostomium and segment one, almost connecting ciliation around mouth with that of the nuchal organs; and two pairs between segment one and two (Figs. 4C, 6D).

Pharynx with ventral opening between prostomium and segment one, and muscular bulb in segment one (Figs. 1, 2A, C). About six pairs of ventral brown glands (may have salivary function) open into buccal cavity on ventral side of pharynx (Figs. 1, 2A, C). Two additional dark brown, round cell-groups (probably glandular in function) dorsally of pharynx in prostomium. All groups contain several cells with relatively large round vesicles. A pair of triangular cuticular plates on ventral side of pharyngeal bulb in anterior part of pharyngeal organ (Figs. 1, 2C). Large round glandular cells with many small vesicles and brown pigmentation line stomach wall (Figs. 1, 3A); large ciliated cells line hindgut (Figs. 1, 3C). Diffuse superficial glands create a unique pattern in the ventro-caudal epithelium (Fig. 3B).

Studies by confocal scanning microscopy showed the distribution of nephridia and gonoducts in this and other species (Worsaae & Müller 2004). *Longipalpa saltatrix* is hermaphroditic with one pair of spermi ducts in segments six to seven and one pair of oviducts in segments seven to eight (see Fig. 1 and Worsaae & Müller 2004, fig. 2J). Two pairs of segmented nephridia are present, from segments two to three, and

from segments three to four, respectively (see Fig. 1, and Worsaae & Müller 2004, fig. 2G–I). Several enteronephridia line the hindgut (see Fig. 1, and Worsaae & Müller 2004, fig. 2G, J). Fertile animals contain a maximum of two large eggs with diameters up to 170 μm , and an additional large number (up to ca. 40 has been counted) of smaller ovoids with a diameter about 10–20 μm .

Distribution.—Presently known only from a certain anchihaline cave pool in Bermuda.

Motility.—The animals swim beautifully in the water column, describing loops and turns. Less frequently, they glide over the surface and if provoked make an escape reaction or quick turn by undulation of the body and fast curling up of the palps in a narrow spiral. When swimming, they are capable of bending the prostomium and body as well as waving, bending and curling the long palps. The pygidial lobes are flapped between positions flat along the body to an almost right angle to the dorsal surface, thereby using the densely ciliated lobes as helms. The forward drift seems to be created mainly by the ventral ciliation, possibly with additional force from the cilia on palps and pygidial lobes.

Remarks.—The description of *Longipalpa saltatrix* not only adds a new genus to the family Nerillidae, but also expands the definition of the family. The extremely long palps of this species are not only unusual in their length but probably also in their function. The longitudinal rows of ciliary bandlets create a water current propelling particles towards the mouth opening, which has never been observed in other nerillids. It seems possible that the animals collect food particles by help of the palps, thereby increasing their feeding radius extensively. Foraging could happen when gliding over or through the substrate as well as when swimming through and above the sediment collecting particles in suspension. In several species of nerillids, the ciliation of the much shorter palps creates a water current

transporting particles away from the mouth (Worsaae, personal observations). This transport may indicate that other nerillid palps may also be functional in feeding behavior, however, by transporting rejected particles away from the mouth and not by gathering them. The previous understanding of the nerillid palps as being mainly sensory in function should probably be expanded to include a function in feeding behavior. This view stands in contrast to the general comprehension of the ventral palps of the major taxon group Aciculata (see Rouse & Fauchald 1997) with which the family has the most apparent resemblance (see e.g., Schmidt 1848, Quatrefages 1866, Westheide 1990, Westheide & Purschke 1996, Rouse & Fauchald 1997, Rouse & Pleijel 2001). Aciculates are generally characterized by short sensory palps with no direct function in food collecting. If the nerillids truly belong to the Aciculata, then the long palps of *Longipalpa saltatrix* may also influence the conception of the conservativeness of the palps in this taxon group.

The extremely long palps would probably be disadvantageous in the interstitial habitat from which many nerillids are described. This disadvantage may be one of the reasons why these long palps have not been found in other nerillids. In the Bermudian caves with only a sparse layer of very fine silt on top of bare rocks, it may even be an advantage to be able to actively swim and perhaps also feed on suspended particles with the aid of the palps. However, *Leptonerilla prospera* which lives under rather similar conditions, except from more light in the Walsingham Caves in Bermuda, does not possess long feeding palps. Differences in habitat characteristics between cave and interstitial habitats include more space in caves, thus allowing for swimming as opposed to crawling, and different types of food, hence different feeding mechanisms. Many other anchihaline species are most commonly found within the water column rather than on the sediments, implying that this is where food is primarily located.

The motile ciliary bands and the anterior field of cilia on the prostomium could easily be detected on live animals with light microscopy (LM), whereas the posterior field of cilia could only be detected with SEM. The motile ciliary bands (bc in Figs. 1, 5A) are most likely not mechanoreceptors because of their long length, motility, and dense grouping. However, the anterior and posterior fields of cilia are probably sensory in function because of their non-motility, shorter length, and single appearance of cilia—each with a cuticular collar. Two fields of cilia (suggested to be sensory in function) have also been described for the nerillid *Paranerilla limicola* Jouin & Swedmark, 1965 (Worsaae & Kristensen 2003). The anterior field of cilia in *P. limicola* consists of a little group of cilia and, except for the anterior position; it is very different from the two transverse rows of cilia arranged in a pattern found in *L. saltatrix*. The posterior field in *P. limicola* is more similar with 14 cilia arranged in a distinct pattern. However, this pattern differs some from the pattern of 20 cilia found in *L. saltatrix*. It seems very possible that the two systematically significant prostomial fields of cilia (probably sensory in function) are a common feature of nerillids, which just demands SEM techniques to be described.

A few of the unusual characteristics of *L. saltatrix* have previously been found in single occasions in otherwise very different nerillid species. Structures remarkably similar to the special triangular cuticular plates on the ventral part of the pharynx have been described for *Thalassochaetus palpifoliaceus* Ax, 1954. A different, although also distinct pattern of diffuse superficial ventral glands are described for *Nerillidium renaudae* Jouin, 1970. Pygidial lobes have been described for the aberrant *Nerillidium simplex* Levi, 1953 (see also Jouin 1966, Swedmark 1959). These lobes are apparently not double-lobed or ciliated as in *L. saltatrix*; however, their position and square, non-cirrifiform appearance is very similar to *L. saltatrix*. The pygidial lobes

found in *N. simplex* have been interpreted as modified pygidial cirri (Levi 1953, Swedmark 1959), which may also count for the lobes of *L. saltatrix*. The superficial resemblance with the lobes of *N. simplex* is probably a matter of convergence; however, the lobes may be functionally comparable. The two groups of cilia on each pygidial lobe of *L. saltatrix* show great resemblance in number and length with the two ciliary tufts found on each side of the body segment dorsal to the parapodia. Furthermore, examined juveniles did not possess pygidial lobes, which would be expected if the lobes were modified pygidial cirri. These observations could mean that the pygidial lobes are modified rudiments of a strongly reduced ninth body segment. However, studies with LM and SEM of *L. saltatrix* show that there are no remains of chaetae or parapodial muscles and cLSM studies show that there are no segmental nerves posterior to the eighth body segment. Further examination of the development of *L. saltatrix* is needed to clarify the origin of the pygidial lobes.

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Neostrengeria lemaitrei, a new species of freshwater crab from
Colombia (Crustacea: Decapoda: Pseudothelphusidae), and the
vertical distribution of the genus

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Abstract.—A new species of the genus *Neostrengeria* Pretzmann, 1965, *N. lemaitrei* from Magdalena Valley, Cundinamarca Department, is described. The genus is endemic to the Eastern Andes of Colombia, at altitudes ranging from 300 to 3000 m above sea level. With the addition of *N. lemaitrei* the total number of species rises to 21. This new species, like all others in *Neostrengeria*, is distinguished primarily by the morphology of the first male gonopod, particularly by the form of lateral and accessory lobes, and the shape of the apex.

The genus *Neostrengeria* Pretzmann, 1965, comprises 21 species of freshwater crabs that inhabit mountain springs and streams on the slopes and high plain of the Eastern Andes in Colombia (2° to 9°40'N, 73° to 74°50'W), at altitudes ranging from 300 to 3000 m above sea level (Campos 1994).

The taxonomy of *Neostrengeria* was reviewed by Rodríguez (1982), with follow up studies by Campos (1992, 1994, 2000). Campos & Lemaitre (1998) presented a key for the identification of the species based on the morphology of the male first gonopod. The distribution of the genus has been discussed by Campos & Rodríguez (1985), and Campos (1992, 1994). The present new species was found in the Magdalena Valley, at altitude of 720 m above sea level.

The general carapace morphology of *Neostrengeria* species is very similar. The species are characterized primarily by the shape of the first male gonopod which has a distinct lateral lobe generally divided in two halves forming an accessory lobe. The form of the gonopod's apex is also variable according to the species, and can be oval, oblong, or expanded into a projection.

The terminology used for the different

processes of the gonopod is that established by Smalley (1964), Rodríguez (1982) and Campos & Lemaitre (1998). The material is deposited in Museo de Historia Natural, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN-MHN). The abbreviations cb and cl, reported as cl × cb, indicate carapace breadth and carapace length, respectively. Color nomenclature follows Smithe (1975).

Family Pseudothelphusidae Rathbun, 1893
Tribe Hypolobocerini Pretzmann, 1971
Genus *Neostrengeria* Pretzmann, 1965
Neostrengeria lemaitrei, new species

Fig. 1

Holotype.—Agua Blanca stream, Vereda Lamal, Inspección Guadualito, Municipio Yacopí, Cundinamarca Department, Colombia, 720 m alt., 4 Nov 1995, leg. M. R. Campos: 1 male, 13.9 × 23.6 mm, ICN-MHN-CR 1991.

Paratypes.—Same locality data as holotype: 5 males, size range 8.1 × 12.9 mm, to 12.5 × 20.0 mm, 4 females, size range 9.4 × 14.7 mm, to 7.4 × 11.2 mm, ICN-MHN-CR 1533.

Type locality.—Agua Blanca stream, Vereda Lamal, Inspección Guadualito, Mu-

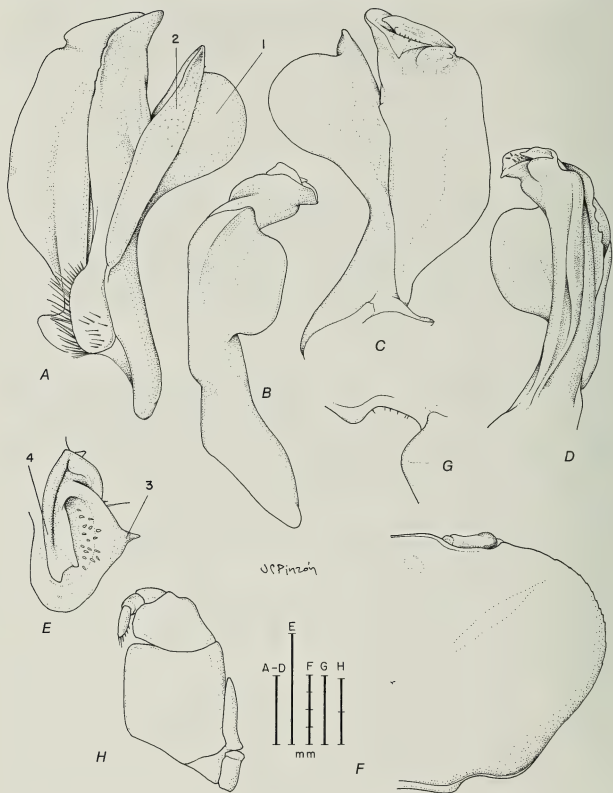


Fig. 1. *Neostrengeria lemaitrei*, new species, male holotype, ICN-MHN-CR 1991. A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, apex, distal view; F, right carapace half, dorsal view; G, left opening of efferent branchial channel, external view; H, left third maxilliped, external view. 1, lateral lobe; 2, accessory lobe; 3, cephalic expansion; 4, mesocaudal projection of spermatic channel.

nicipio Yacopí, Cundinamarca Department, Colombia, 720 m alt.

Diagnosis.—Carapace without median groove; front lacking distinct upper border. Third maxilliped with exognath 0.67 times length of ischium. First male gonopod with lateral lobe semicircular distally, proximally narrow, with external margin concave; accessory lobe elongated, semi-acute distally, forming excavated ridge on caudal surface; accessory lobe as long as lateral lobe. Apex outline oval with expansion projected cephalically into prominent, acute spine.

Description of holotype.—Carapace (Fig. 1F) with cervical groove straight, shallow, ending some distance from lateral margin. Anterolateral margin lacking depression behind external orbital angle. Lateral margin with series of approximately 15 papilliform teeth. Postfrontal lobes oval, high, indicated anteriorly by 2 transverse depressions. Median groove lacking. Front without distinct upper border, frontal area sloping downwards, slightly bilobed in dorsal view, lower margin visible in dorsal view, strongly sinuous in frontal view. Dorsal surface of carapace smooth, covered by small papillae, regions well demarcated. Third maxilliped with distal half of external margin of merus rounded, exognath 0.67 times length of ischium (Fig. 1H). Orifice of efferent branchial channel open, irregularly ovate (Fig. 1G). First pereopods heterochelous; palm of larger chela strongly swollen, fingers slight gaping when closed, smaller chela slight swollen, fingers not gaping when closed. Walking legs (pereopods 2–5) slender, but not prominently elongated (total length 1.10 times the breadth of carapace).

First male gonopod wide in caudal view; mesial side forming convex expansion with deep subdistal notch; caudal margin wide with excavated surface, festooned (Fig. 1A, D); lateral lobe wide, semicircular distally, proximally narrow with external side concave, separated from accessory lobe by deep notch (Fig. 1A–D); accessory lobe elongated, semi-acute distally, forming excavated ridge, covered with diminute papil-

lae and row of spinules on external border on caudal surface; accessory lobe as long as lateral lobe (Fig. 1A, C); apex outline oval in distal view with expansion projected cephalically into prominent, acute spine; mesial lobe subtriangular; mesocaudal projection of spermatic channel with bifid tip; spermatic channel with conspicuous rows of spinules; proximal cephalic border with two setae (Fig. 1C, D, E); conspicuous setae along outline of prominent basal rounded lobe, and a patch of setae on caudal surface (Fig. 1A).

Color.—The holotype, preserved in alcohol, is brown-olive (near 129, Dark Brownish Olive) on the dorsal side of the carapace. The dorsal and ventral surfaces of the chelae and the walking legs are brown (near 223, Raw Umber). The ventral surface of the carapace is beige (near 92, Pale Horn Color).

Habitat.—The specimens were collected in shaded, moist banks of springs and streams. They were found in soft mud, under rocks.

Etymology.—The species is named in honor of Colombian scientist Dr. Rafael Lemaitre, who has dedicated his life to studying Crustaceans. This species is not only a recognition of Rafael's contributions to science, but to the stimulus he has provided to a new generation of up and coming Colombian scientists.

Remarks.—A comparison of both descriptions and material of other species of the genus with that of this new species revealed that it is most similar to *Neostrengeria gilberti* Campos, 1992. The main distinguishing feature between both species is the form of the first gonopod. The male first gonopod of *N. gilberti* has been described and illustrated by Campos (1992: 542, fig. 2). In this new species, the mesial side of the gonopod is convex expanded with deep subdistal notch, whereas in *N. gilberti* it is rounded basally, straight tapering distally without subdistal notch. The lateral lobe in *N. gilberti* is rounded distally with the proximal external side straight, whereas in *N.*

Table 1.—Vertical distribution of the *Neostrengeria* species.

Species	Meters above sea level
<i>Neostrengeria appressa</i> Campos, 1992	1125–1900
<i>N. aspera</i> Campos, 1992	1600
<i>N. binderi</i> Campos, 2000	470
<i>N. botti</i> Rodríguez & Türkay, 1978	1350–2600
<i>N. boyacensis</i> Rodríguez, 1980	2350–3000
<i>N. charalensis</i> Campos & Rodríguez, 1985	1450–2150
<i>N. gilberti</i> Campos, 1992	950–1250
<i>N. guenteri</i> (Pretzmann, 1965)	500–1575
<i>N. lasallei</i> Rodríguez, 1980	1110–2150
<i>N. lemaitrei</i> , new species	720
<i>N. libradensis</i> Rodríguez, 1980	1200
<i>N. lindigiana</i> (Rathbun, 1897)	1800–2350
<i>N. lobulata</i> Campos, 1992	1700–2350
<i>N. macarenae</i> Campos, 1992	300–500
<i>N. macropa</i> (H. Milne Edwards 1853)	2200–2900
<i>N. monterodendoensis</i> Bott, 1967	1320–1500
<i>N. niceforoi</i> (Schmitt, 1969)	1000–1750
<i>N. perijaensis</i> Campos & Lemaitre, 1998	1270–1800
<i>N. sketi</i> Rodríguez, 1985	1800
<i>N. tencalanensis</i> Campos, 1992	1600–2400
<i>N. tonensis</i> Campos, 1992	1600–2400

lemaitrei it is distally semicircular, and proximally narrow with the external side concave. The apex outline in *N. gilberti* is oblong in distal view with a mesially directed semi-acute spine; the mesocaudal projection of spermatid channel is awl-shaped with a distal spinule on the inner side. In contrast, in *N. lemaitrei*, the apex outline is oval in distal view with the expansion projected cephalically into a prominent, acute spine, and the mesocaudal projection of spermatid channel has the tip bifid.

Distribution of *Neostrengeria* species

The distribution of the species of *Neostrengeria* comprises both slopes and the high plain of the Eastern Cordillera of Colombia that encompasses the Magdalena, Orinoco and Catatumbo basins. It is limited to the north by Serranía de Perijá, and to the south by Serranía de La Macarena (2° to 9°40'N, 73° to 74°50'W), (H. Milne Ed-

wards 1853; Rathbun 1897; Pretzmann 1965; Bott 1967; Schmitt 1969; Rodríguez & Türkay 1978; Rodríguez 1980, 1982, 1985; Campos & Rodríguez 1985; Campos 1992, 1994, 2000; Campos & Lemaitre 1998).

Based on the collected material, the vertical distribution of the species of the genus *Neostrengeria* (Table 1) ranges from 300 m to 3000 m. *Neostrengeria botti* has the greatest altitude range of between 1350 and 2600 m. The species that exhibit a range of between 300 and 1000 m are *N. binderi*, *N. macarenae* and *N. lemaitrei*, new species. Most of the species are distributed between 1000 and 2400 m. The highest altitude, 3000 m, is reached by *N. boyacensis*.

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A new species of *Agostocaris* (Caridea: Agostocarididae) from Acklins Island, Bahamas

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Abstract.—The new bresilioid shrimp *Agostocaris acklinsensis* is described from an anchialine cave in Acklins Island, Bahamas. This is the third species described in the genus. The new species is characterized by having small exopods on the third and fourth pereopods, one spine on the ischium of the fifth pereopod, and an outer ramus of the uropods with one distolateral spine. A key to the species of *Agostocaris* is provided.

The family *Agostocarididae* Hart & Manning, 1986, was created to accommodate *Agostocaris williamsi*, from Grand Bahama and Turks and Caicos, a species that appeared to be morphologically similar to some species in the *Atyidae* De Haan, 1849, and the *Bresiliidae* Calman, 1896, but had a distinct morphology of the propodus and dactylus of the first two pereopods. Kensley (1988) described a second species from Cozumel, Mexico, *Agostocaris bozanici*, which exhibits the same unique pereopodal morphology, placing it also in the *Agostocarididae*. Holthuis (1993) synonymized the *Agostocariidae* with the *Bresiliidae*. However, Martin & Davis (2001) have proposed to recognize the family *Agostocarididae* within the superfamily *Bresilioidea* Calman, 1896, where a heterogeneous assemblage of forms are included in five families.

At best, as pointed out by Kensley (1988), the relationships of *Agostocaris* are unclear. The particular articulation of the propodus of the first pair of legs, and the morphology of the chela of the second pair of legs, are unique characters not shared by any other genus in the *Bresilioidea*. With respect to the diagnosis of *Agostocaris*, with the new species described herein, the

range of variation in taxonomically important characters increases, making it necessary to provide a new diagnosis for the genus.

Materials and Methods

Specimens of the new *Agostocaris* described herein were collected during an expedition to Crooked and Acklins Islands, Bahamas, in January 1999. The new species was captured in Jumby Hole Cave (22°29.275'N, 73°53.501'W), Snug Corner, Acklins Island, Bahamas, 11 January 1999 (Fig. 1). This cave is located about 250 m inland from the west side of the island facing the shallow water Bight of Acklins. It is actually a complex of closely associated caves that were mined for guano in the past. More than 3 m of soil and guano were removed from pits within dry portions of the cave. One of these caves contains a 20 m diameter, shallow (30 to 50 cm deep) pool. Sediments in the pool consist of a thick layer of guano from a bat roost located directly above. Tidal range in the pool appeared to be about 30 cm. This pool is in total darkness but is close to 4 or more entrances on all sides. Salinity was measured at 32.5‰



Fig. 1. Map showing the location of the type locality of *Agostocaris acklinsensis*, Acklins Island in the Bahamas.

with a refractometer and water temperature was 25.5°C. Specimens of *Agostocaris* were observed walking across the surface of rocks and the guano bottom in 50 cm depth. They were collected by hand using glass vials. Other invertebrates collected from the cave pools included copepods, archiannelid and other polychaetes, mites and the shrimp *Barbouria cubensis* (von Martens, 1872) (Hippolytidae).

The specimens representing the new species are deposited in the Colección Nacional de Crustáceos (CNCR), Instituto de Biología, Universidad Nacional Autónoma de México. Other abbreviations used are: cl, postorbital carapace length, and tl, total length.

Results

Agostocaris Hart & Manning, 1986

Diagnosis.—Rostrum well developed, with or without dorsal teeth. Carapace lacking spines and grooves. Eyes reduced, fused, without pigment or weakly pigmented. Antennal scale with lateral spine. First maxilliped with lash on exopod. Second maxilliped with terminal segments serial. Pleurobranchs on all pereopods or on pereopods 2–5. First and second pereopods chelate, first pair heavier than second one. First pereopod with propodus articulating with carpus at one third of its length. Second pereopod with carpus undivided; dactylus digitiform, heavier and longer than propodus, both fingers without teeth or spines. Telson with 4–5 pairs of dorsal spines, posterior margin with variable number of spines.

Agostocaris acklinsensis, new species

Figs. 2–4

Material examined.—Holotype, female, cl 7.3 mm, tl 21.5 mm; 11 January 1999; Jumby Hole Cave, Snug Corner, Acklins Island, Bahamas; collected by T. M. Iliffe; CNCR 19601. Paratypes, 8 females, cl 4.0–8.0 mm, tl 13.6–21.7 mm; same locality,

date and collector as holotype; CNCR 19602.

Description.—Carapace globose, smooth, devoid of spines. Rostrum laterally compressed, triangular, ending in sharp tip, reaching distal end of first antennular segment; without teeth in mature individuals, with three dorsal teeth with alternating setae in juveniles (Fig. 2a, b). Carapace without grooves, inferior margin of orbit and pterygostomial angle slightly produced (Fig. 2a), pterygostomial regions produced laterally (Fig. 2b).

Abdomen smooth, somites 1–2 with rounded pleura, somites 3–5 with posterior angle of pleura subacute, sixth somite with posterior margin sinuous at insertions of telson and uropods. Telson 2.5 times as long as its basal width, tapering distally, distal width less than half of basal width; bearing four pairs of movable spines on dorsal surface, spines located on distal two thirds of dorsal surface; posterior margin rounded, bearing 9 spines, second pair from external one longest (Fig. 4g).

Eyes pigmented, fused, forming part of a single plate, peduncle and cornea not discernible, projected dorsally (Fig. 2c). Antennule with first segment as long as segments 2 and 3 combined; stylocerite acute, reaching distal margin of first segment (Fig. 4e). Antennal scale 1.8 times as long as wide, laterodistal tooth short not exceeding distal margin of blade (Fig. 4f), flagellum 1.25 times total length (Fig. 2a).

Mandible with stout 2-segmented palp, incisor process with six distal teeth, molar process conical, sharp distal end (Fig. 2d). Both mandibles approximately symmetrical. First maxilla with distal lacinia oval shaped, bearing three rows of short, thick setae on mesial surface; proximal lacinia with single row of short, thick setae on distomesial margin; palp bearing one distal, long setae and two subdistal short ones on internal margin (Fig. 2e). Second maxilla with scaphognathite approximately rectangular distally, subtriangular proximally; distal margin with long, plumose setae; lateral

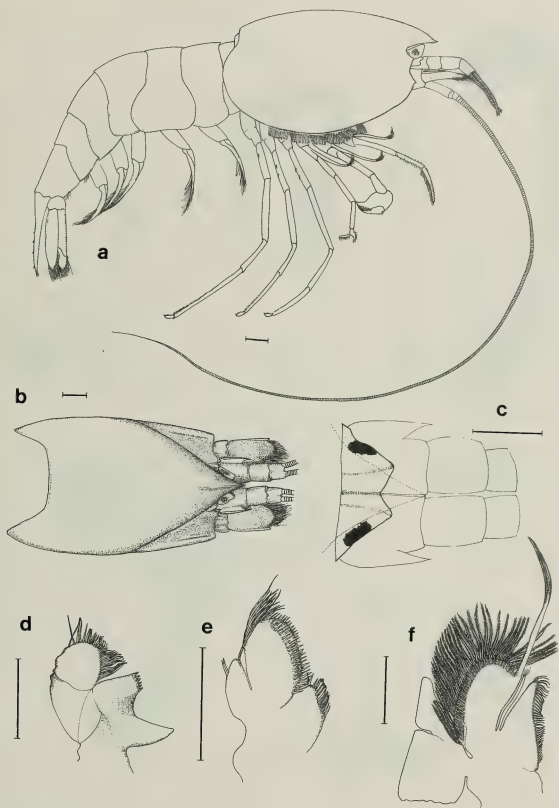


Fig. 2. *Agostocaris acklinsensis*, new species, a female holotype, b-f female paratype: a, total lateral view; b, carapace, dorsal view; c, dorsal view of eyes, carapace removed; d, mandible; e, first maxilla; f, first maxilliped. Scale bar represent: a-c, f, 1 mm; d-e, 0.5 mm.

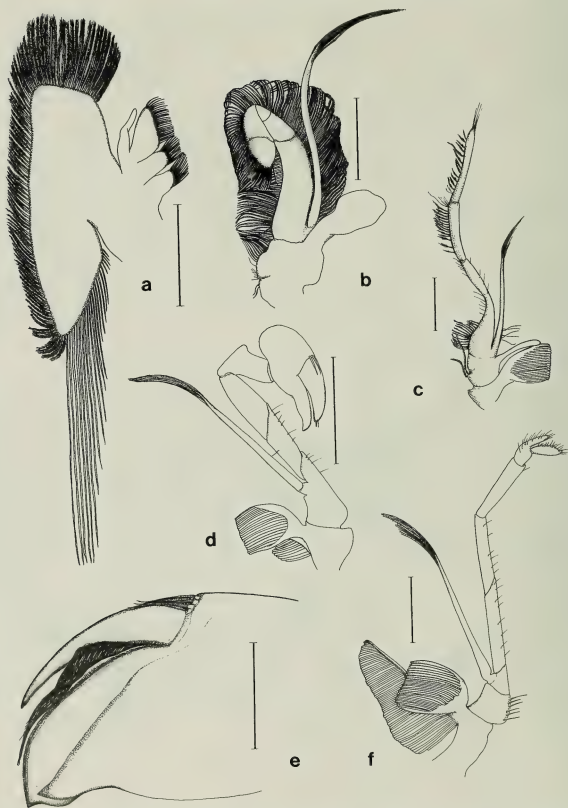


Fig. 3. *Agostocaris acklinsensis*, new species, female paratype: a, second maxilla; b, second maxilliped; c, third maxilliped; d, first pereiopod; e, detail of propodus and dactylus of first pereiopod; f, second pereiopod. Scale bars represent: a-d, f, 1 mm; e, 0.5 mm.

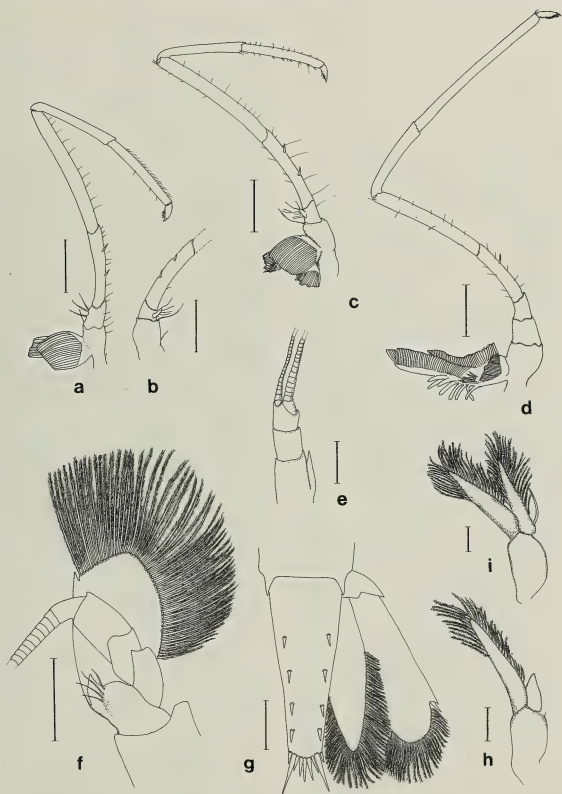


Fig. 4. *Agostocaris acklinsensis*, new species, female paratype: a, third pereiopod; b, detail of proximal segments of third pereiopod; c, fourth pereiopod; d, fifth pereiopod; e, antennule; f, antenna; g, telson and uropods, left side omitted; h, first pleopod; i, second pleopod. Scale bars represent 1 mm.

margin with short plumose setae; internal margin with long simple setae, increasing in length distally, almost as long as scaphognathite; palp digitiform, devoid of setae; distal endite trapezoidal, middle and proximal endites approximately rectangular, all three bearing simple setae on distal margins (Fig. 3a).

First maxilliped with triangular endite bearing marginal setae; palp digitiform, with apical tuft of setae; exopod elongated, bearing long, simple setae distally; caridean lobe broadly rounded, with submarginal row of short setae and long plumose setae along margin; epipod bilobed, both lobes trapezoidal, distal one smaller, devoid of setae (Fig. 2f). Second maxilliped with endopod pediform, 4-segmented, with continuous row of setae along margin; exopod slender, bearing long simple setae distally; epipod simple, flat, rounded (Fig. 3b). Third maxilliped with endopod 4-segmented, bearing setae on mesial margin; exopod as long as first segment of endopod, with distal tuft of long setae; epipod digitiform, less than half the length of exopod; arthrobranch present (Fig. 3c).

First pereopod with ischium and merus of about same length and width, carpus wider proximally, propodus articulating with carpus at one third of its length, palm as long as fingers, cutting edges of both fingers with minute sharp teeth, dactylus with long setae arising from proximal half teeth (Fig. 3d); exopod as long as ischium and merus combined, with apical tuft of long setae; arthrobranch and pleurobranch present (Fig. 3d). Second pereopod longer than first one, with merus slightly shorter than ischium, carpus becoming wider distally and as long as merus, propodus with palm shorter than fixed finger, dactylus heavier and longer than fixed finger; exopod shorter than ischium and merus combined, bearing apical tuft of long setae; arthrobranch and pleurobranch present (Fig. 3f). Third pereopod with ischium with two spines, merus the longest segment, carpus and propodus of about the same length,

dactylus with corneous sharp tip and four smaller teeth on internal surface, arthrobranch and pleurobranch present, finger-like exopod arising from basis (Fig. 4a, b). Fourth pereopod with ischium with two spines, merus the longest segment, carpus and propodus of about the same length, dactylus with corneous sharp tip and three smaller teeth on internal surface, arthrobranch and pleurobranch present, finger-like exopod arising from basis (Fig. 4c). Fifth pereopod with ischium with one spine, propodus the longest segment, dactylus with corneous sharp tip and eight smaller teeth on internal surface, arthrobranch and pleurobranch present (Fig. 4d).

First pleopod with exopod setose, endopod devoid of setae, one third the length of exopod (Fig. 4h). Second pleopod with endopod and exopod setose, appendix interna slender more than half the length of endopod (Fig. 4i).

Uropods with external ramus bearing one distolateral movable spine, distal margin broadly rounded, with long plumose setae on distal and internal margins. Internal ramus bearing marginal long plumose setae except on proximal third, distal margin subacute (Fig. 4g).

Etymology.—The specific name is derived from "Acklins", the name of the Bahamian island where the new species was captured.

Key to the species of *Agostocaris*

1. First maxilliped with palp 2-segmented, ischium of fifth pereopod devoid of spines, outer ramus of uropods devoid of distolateral spines, . . . *Agostocaris williamsi*
- First maxilliped with palp unsegmented, ischium of fifth pereopod with spines, outer ramus of uropods with spines, outer ramus of uropods with distolateral spines 2
2. Ischium of fifth pereopod with two spines, outer ramus of uropod with two distolateral spines, telson with five pairs of dorsal spines *Agostocaris bozanici*

– Ischium of fifth pereopod with one spine, outer ramus of uropod with one distolateral spine, telson with four pairs of dorsal spines . . . *Agostocaris acklinsensis*

Remarks.—*Agostocaris acklinsensis* can be easily distinguished from the other two known species in the genus by the presence of: exopods on the third and fourth pereopods, a fifth pereopod with one spine on the ischium and one distolateral movable spine on the outer ramus of the uropods. Other taxonomically important characters vary among the three species. A second maxilla with a palp devoid of setae and an unsegmented palp of the first maxilliped distinguish *A. acklinsensis* from *A. williamsi*, whereas the number of dorsal spines on the telson, unpigmented eyes and two distolateral spines on the outer ramus of the uropods separate *A. bozanici* (Table 1).

Noteworthy are the eyes of *Agostocaris*, which are composed of one single plate not differentiated into peduncle and cornea. This plate is projected outside the orbits creating the eye-like structures, which in the three species are pointed distally. Since all the species of *Agostocaris* are cave dwellers it is reasonable to suppose that the cornea was lost and later the peduncle was reduced, in such a way that the “eyes” we see now are part of the basal plate. This singular morphology merits further studies on its ontogeny and functionality.

The placement of the genus *Agostocaris* is a matter of controversy. Holthuis (1993), by synonymizing Agostocaridae with the Bresiliidae, gave more weight to characters that are shared by many taxa in the Caridea (mandible with palp, carpus of second legs undivided, first two pairs of legs chelate, first pair of legs more robust than second one, Williams, 1984) with little resolution among families, than to exceptional autapomorphic characters such as the fused eyes and the particular morphology of the first two pereopods of *Agostocaris*.

We agree with Martin & Davis’ (2001) proposal of recognizing a superfamily Bre-

Table 1.—Comparison of selected characters of the three species of *Agostocaris*.

	<i>A. williamsi</i>	<i>A. bozanici</i>	<i>A. acklinsensis</i>
Eyes	Weakly pigmented	Without pigment	Weakly pigmented
Second maxilla	Palp with setae	Palp without setae	Palp without setae
First maxilliped	Palp 2-segmented	Palp unsegmented	Palp unsegmented
Third pereopod	Basis without exopod	Basis without exopod	Basis with finger-like exopod
Fourth pereopod	Basis without exopod	Basis without exopod	Basis with finger-like exopod
Fifth pereopod	Ischium devoid of spines	Ischium with two spines	Ischium with one spine
Second pleopod	Appendix interna two thirds length of endopod	Appendix interna less than half length of endopod	Appendix interna less than half length of endopod
Telson	With four pairs of dorsal spines	With five pairs of dorsal spines	With four pairs of dorsal spines
Uropods	Outer ramus without distolateral spines	Outer ramus with two distolateral spines	Outer ramus with one distolateral spine

silioidea, which includes five families, and concur with the opinion that this taxon still represents an artificial grouping. While it is beyond the scope of this paper to discuss the relationships among bresilioids, it is clear that Agostocarididae represents a distinct family that can be easily separated from the other four bresilioid families. The Alvinocarididae Christoffersen, 1986, and Mirocarididae Vereshchaka, 1997, lack exopods on all pereopods, whereas the Agostocarididae can have exopods on all five pereopods. The Diascididae Rathbun, 1902, have well developed eyes with peduncle and cornea, a dorsoventrally flattened rostrum and a disc-like dactylus of the first pereopod, contrasting with the fused eyes, acuminate rostrum and typically shaped dactylus of pereopod I of the Agostocarididae. Finally the Bresiliidae, and the rest of the bresilioid families, can be separated from the Agostocarididae based on the carpus-propodus articulation of the first pereopod which is normal in the former, being the distal end of the carpus articulated to the proximal end of the propodus; while in the latter the carpus is articulated to an area close to the middle portion of the propodus. In addition, the chela of the second pereopod in the Agostocarididae is unique in that the digitiform dactylus is longer than the fixed finger and lacks teeth or spines.

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A new species of caridean shrimp of the family Stylodactylidae from the eastern Pacific Ocean

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Abstract.—Four specimens of shrimp of the family Stylodactylidae were collected at two stations off Baja California, Mexico, and California, U.S.A. These are the first specimens of the family reported from the eastern Pacific. The shrimp are described as a new species, *Bathystyloactylus echinus*. The species can be recognized by the following features: rostrum straight, much longer than the carapace, bearing at least 23–27 dorsal and 18–25 ventral spines; eye small and without pigment, stylocerite slender and not reaching middle of first segment of antennular peduncle, carapace without prominent posterior dorsal hump, body set with minute spinules, posterior pereopods considerably longer than anterior two pair, slender and lacking fringe of setae.

Shrimp of the family Stylodactylidae are recognized by their peculiar first and second pereopods, which end in elongate but nearly equal fingers with setae on the cutting edges. These pereopods and the maxillipeds are densely setose. Species of the family are widely distributed from tropical to temperate regions (e.g., Cleva 1990a), although most of the species described to date have come from the tropical Indo-Pacific (Chace 1983; Cleva 1990b, 1994, 1997; Okuno and Tachikawa 2000). Chace (1983) and Cleva (1994) reviewed the members of the family, described new species, and provided keys. Hanamura and Takeda (1996) described an additional genus, *Bathystyloactylus*, for a new species (*B. inflatus*) from off Taiwan (and for the former *Styloactylus bathyalis* from the Coral Sea), bringing to 5 the number of recognized genera in the family (*Styloactylus*, *Neostyloactylus*, *Parastyloactylus*, *Styloactylus*, and *Bathystyloactylus*). There have been no previous reports of the family in the eastern Pacific Ocean.

While sorting specimens in the Benthic

Invertebrate Collection of Scripps Institution of Oceanography, we found four specimens of shrimp of this family from three stations taken off California, U.S.A., and Baja California, Mexico. The specimens include both males and females. We compared these specimens with specimens of *Styloactylus rectirostris* in the collections of Texas A&M University (catalog number 2-7212, Oregon station 5916) and with published descriptions of other species in the family. The specimens represent an unknown species of *Bathystyloactylus*, described herein.

Systematic Account

Bathystyloactylus echinus, new species
Figs. 1–5

Holotype: Male, carapace length (CL) 32.7. Basin off Magdalena Bay, Baja California, Mexico (24°35'N, 113°25'W), 3563–3621 m, 6-foot Sigsbee trawl, 24 June 1965, ship *Horizon* sta. MV65-I-38, Carl Hubbs, collector; Scripps Institution of

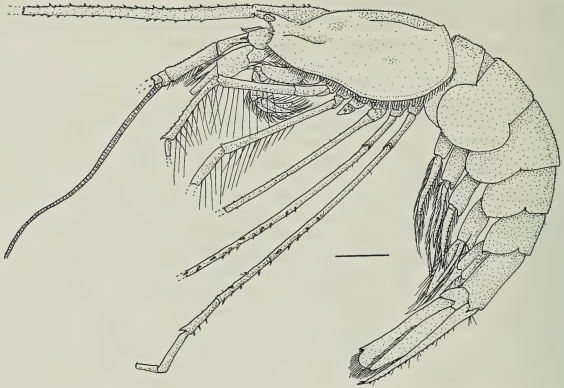


Fig. 1. *Bathystylodactylus echinus*, new species, male holotype, Scripps Institution of Oceanography C3188. Scale bar = 10.0 mm.

Oceanography (SIO) catalog number C3188.

Paratypes: Male, CL 41.4, same station as holotype, LACM CR 1965-349.1 (Natural History Museum of Los Angeles County). Female, CL 29.7. Basin off Magdalena Bay, Baja California, Mexico ($24^{\circ}23'N$, $113^{\circ}17'W$), 3427–3621 m, 45-foot otter trawl, 25 June 1965, ship *Horizon* 2 sta., MV65-I-39, C. Hubbs, SIO cat. no. 3203. Female CL 27.6 Patton Escarpment ($32^{\circ}25'N$, $120^{\circ}40'W$), 3689–3630 m, 40-foot otter trawl, 7 Feb. 1981, ship *New Horizon* sta. 133, collector S. Luke, SIO cat. no. C10324.

Description: Rostrum (Figs. 1, 2B, C) nearly straight, nearly $2\times$ length of carapace but broken in all specimens, with 23–27 movable dorsal and 18–25 ventral spines; series of 7–9 minute spinules on carapace just posterior to rostrum proper, long setae along distal ventrolateral surface. Carapace (Fig. 2A) with hepatic depression well delineated. Antennal and branchiostegal spines short but obvious, antennal spine

located ventral to suborbital angle. Lateral surface of carapace inflated over branchial region, suprbranchial carina curved. Area posterior to eye and antennal origin slightly depressed. Anterior regions of carapace set with small, simple, movable spinules, posterior regions punctate or with few spinules.

Abdomen (Fig. 1) with small spinules on dorsal and lateral surfaces, somites one and two rounded dorsally, somite three weakly carinate dorsally; somite four rounded to weakly carinate, with or without shallow depression interrupting dorsal carina; pleura of somites rounded, those of somites four and five (Fig. 5B) each with sharp posteroventral spine; one specimen with minute spine on pleuron of somite three. Telson (Fig. 5C, E) $8\times$ longer than wide, tapering to apex, with 11–13 pairs of dorsolateral spines located on weak ridges and numerous small spinules; two mesial spines flanking apex on either side. (Apex of telson preserved in only one specimen; observed asymmetry may be due to injury.)

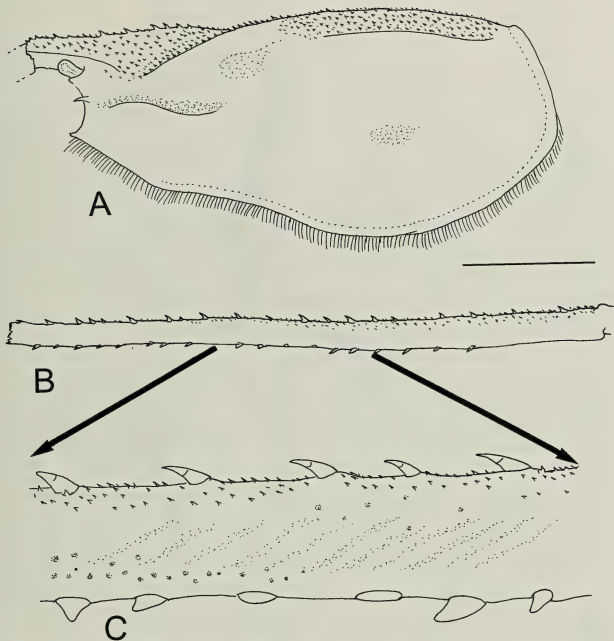


Fig. 2. *Bathystylocdactylus echinus*, new species, male holotype, carapace and rostrum. A, carapace and eye, lateral view. B, rostrum (attached at area of dashed lines in A and illustrated at same scale as A). C, higher magnification of region of rostrum shown in B and denoted by arrows. Scale bar = 10.0 mm A, B; 2.5 mm C.

Eyes (Figs. 1, 2A, 5A) reduced, cornea without trace of pigment.

Antennular peduncle (Fig. 5A) elongate. Stylocerite slender, not reaching middle of first segment. First and second segments subequal in length, third segment very short. Antennal scale (scaphocerite) more than $4\times$ long as broad, outer margin slightly concave, with microscopic spinules, not reaching end of second segment of anten-

nular peduncle, blade exceeding distolateral spine. Carpocerite covered by minute spinules, reaching second segment of antennular peduncle. Basicerite bearing strong lateral spine.

Mandible (Fig. 3A) with molar process bearing teeth in the following configuration: 2 small, one large, 4 small and large blunt process; stout, 2-jointed palp present. First maxilla (Fig. 3B) with distal endite broad

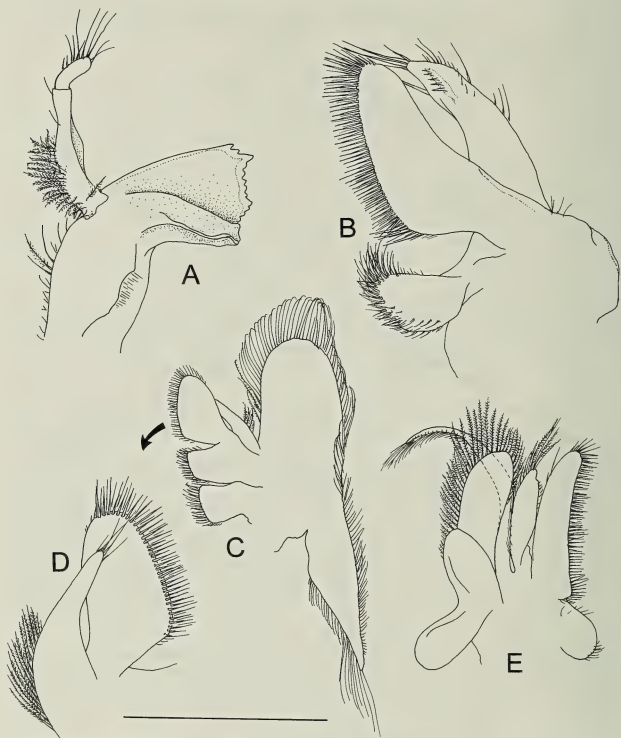


Fig. 3. *Bathystylocyclus echinus*, new species, male paratype (LACM CR 1965-349.1). A, mandible; B, first maxilla; C, second maxilla; D, inner surface of second maxilla slightly enlarged and showing palp; E, first maxilliped. Scale bar = 5.0 mm A, B, D; 10.0 mm C, E.

and with stiff mesial setae; proximal endite curved inward and ending in brush of setae; palp ending in long setae and having tufts of setae on lateral surface. Second maxilla (Fig. 3C, D) with distal endite larger than

2 more proximal endites; long palp ending in 5 setae, scaphognathite with anterior half rounded, posterior half slender and curved mesially, bearing long setae. First maxilliped (Fig. 3E) with long distal and short

proximal endites; palp reaching 3/4 length of distal endite and ending in tuft of setae; exopod with lash, well developed caridean lobe and deeply bilobed epipod.

Second maxilliped (Fig. 4A) much larger than inner mouthparts, with exopod having lash and reaching end of basal segments; podobranch and epipod present; basal segments fringed with stiff curved setae; antepenultimate segment short, with long simple setae on flexor margin at articulation with basal segments; penultimate segment with fringe of long setae on flexor margin; two terminal segments; that on flexor side longer than one on extensor side, both fringed with long setae. Third maxilliped (Fig. 4B) setose, with arthrobranch but without exopod, exceeding antennular peduncle by about length of distal segment. Ultimate segment longest, with dense setae on flexor side. Penultimate segment with long, pinnately branched setae. Antepenultimate segment with both long and short setae.

Pereopods all lacking exopods or epipods. First pereopod (Fig. 4B, C) with entire flexor surface fringed with long setae, merus longer than carpus, propodus about equal in length to carpus, ending in elongate chela (Fig. 4C); fingers simple, with long setae and shorter spine-like setae along cutting edges. Second pereopod similar to first. Third to fifth pereopods (Fig. 1) elongate, with few scattered setae; merus of third pereopod with 8–10 spines on flexor and lateral surfaces; merus of fourth pereopod with 15, merus of fifth pereopod 14; carpus shorter than merus; propodus broken and dactylus missing in all specimens.

All pleopods densely setose. First pleopod shorter than second to fifth pleopods. Male second pleopod (Fig. 4D, E) with appendix interna and appendix masculina, appendix masculina reaching nearly 1/2 length of appendix interna, with apex notched and bearing small hooks.

Lateral branch of uropod with spinules, margin nearly straight, two small teeth by

suture (Fig. 5D). Uropods shorter than telson.

Etymology.—The specific name is derived from the Greek word for spiny.

Remarks.—The new species can be assigned to the genus *Bathystyrodactylus* according to the features given by Hanamura and Takeda (1996). The new species bears a well-developed and two-jointed mandibular palp. Both sexes bear well-developed arthrobranches on the four anterior pereopodal somites. There is no supraorbital spine. The stylocerite falls far short of the mesiodistal margin of the basal segment. There are no fringes of setae on pereopods 3–5, as there are in *Styrodactylus rectirostris* and other species of *Styrodactylus*. Hanamura and Takeda (1996) mentioned that the third to fifth abdominal somites were “weakly carinate” dorsally. In our specimens, only somite three is consistently weakly carinate. The posterior three pereopods definitely are longer than the anterior two in the new species, but due to breakage, their relative lengths to each other cannot be determined.

Two species of *Bathystyrodactylus* have been described previously: *B. bathyalis* (Cleva, 1994), from the Coral Sea (as *Styrodactylus bathyalis*); and *B. inflatus* Hanamura and Takeda (1996), from off Taiwan (Hanamura and Takeda 1996). *Bathystyrodactylus echinus* can be distinguished from the former by its curved rostrum and characteristic sharp spine on the ventral margin of abdominal pleuron three. Like *Bathystyrodactylus inflatus*, *B. echinus* has a straight rostrum with numerous dorsal and ventral spines. The pleura of the fourth and fifth abdominal somites each bear a posteroventral spine. However, in *B. inflatus* the carapace has a marked wide elevation near the posterodorsal margin. This is not present in *B. echinus*. The shape of the supra-branchial carina is more sinuous in *B. inflatus* than in *B. echinus*. In *B. inflatus*, there are 11 spinules on the carapace posterior to the rostrum; in *B. echinus*, there are 8–9. In *B. inflatus*, there are 9–10 dorsal rostral

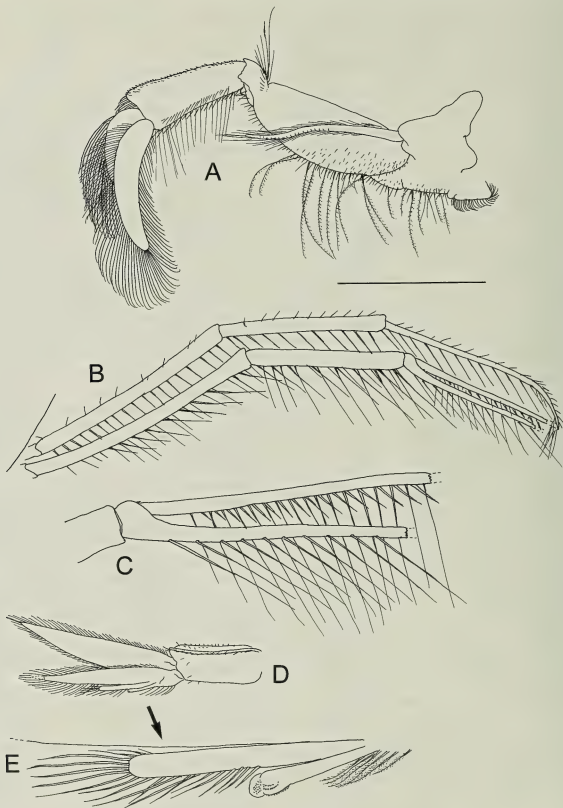


Fig. 4. *Bathylstyrodactylus echinus*, new species, male paratype (LACM CR 1965-349.1) (A) and holotype (SIO C3188) (B-E). A, second maxilliped (paratype). B, right third maxilliped (upper appendage) and first pereopod (holotype). C, higher magnification of chela of first pereopod (tips of fingers broken). D, second pleopod (holotype). E, higher magnification of appendix interna and appendix masculina (arrow from D). Scale bar = 10.0 mm A, E, E; 7.5 mm B, C.

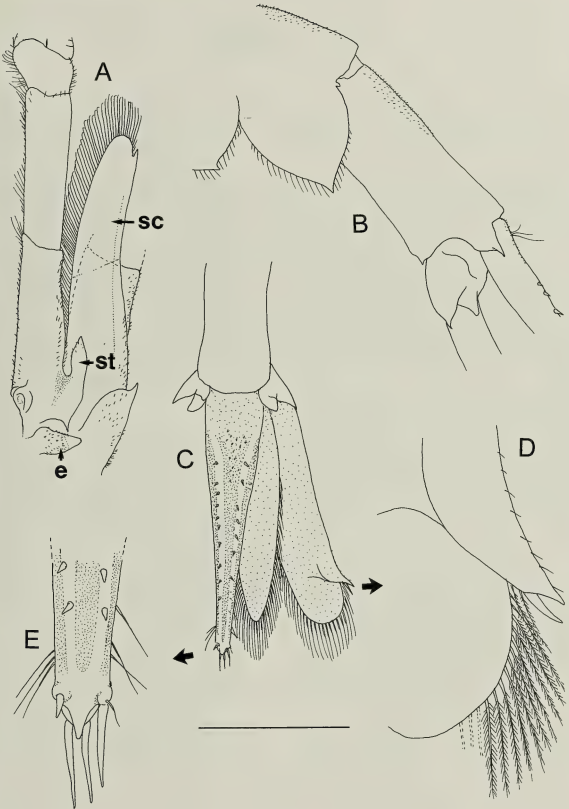


Fig. 5. *Bathystyrodactylus echinus*, new species, male paratype (A) and holotype (B-E). An, antennule, antenna, and eye (e), right side, dorsal view, male paratype (LACM CR 1965-349.1). sc = scaphocerite; st = stylocerite. B, lateral view of abdominal somite 6 plus portions of the telson, uropods, and pleurae of somites 4 and 5, holotype. C, telson and right uropods, dorsal view, holotype. D, higher magnification of distolateral area of outer uropod (arrow from C). E, higher magnification of tip of telson (arrow from C). Scale bar = 10.0 mm A, B; 7.5 mm C; 3.75 mm D, E.

spines located proximally to the origin of the first ventral rostral spine; in *B. echinus*, there are no more than 4. The integument of *B. inflatus* was described as "thin" and the body consequently "soft." In *B. echinus*, the integument appears to us to be typical of a benthic caridean, and not membranous (as seen in midwater species of the Ophlophoridae, for example).

Cleva (1994) and Hanamura and Takeda (1966) described the body of *Bathystylodactylus* species as "pubescent." Their illustrations show a very light coating of pile. In *B. echinus*, the spinules on the body are characteristic and easily seen, especially on the dorsal aspect of the carapace. These spinules conform in shape and structure to tactile or vibrational sensory structures seen in other crustaceans (Cohen and Dijkgraaf 1961).

Bathystylodactylus echinus is the largest and deepest species known in its family. It was collected with the flatback lobster *Willemoesia inornata* Faxon at stations MV65-I-38 and MV65-I-39, and with the galatheid crab *Munidopsis antonii* (A. Milne-Edwards) at station MV65-I-39.

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A new pedunculate barnacle (Cirripedia: Heteralepadidae) from the Northwest Atlantic

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Abstract.—A species of *Heteralepas* has been discovered attached to a gorgonian coral from 500 meters of depth off Nova Scotia (~42° N). A brief review of the previously described *Heteralepas* species is presented. Of the 29 previously described species (including 2 in synonymy), the new species is more similar to some from the Indo-West Pacific than to any of the 8 previously known species from the Atlantic. While the new species can be distinguished from Atlantic but not some Pacific species by some characters, it can be distinguished from all species of the genus by small but marked differences in the configuration of the apertural region of the capitulum. Therefore it is proposed as a new species, *Heteralepas cantelli*, the most northern known member of the family.

Introduction

A specimen of *Heteralepas* was discovered during a survey of the coral-associated fauna at ~42°N on the continental shelf and slope off Nova Scotia, Canada, in 2002. This is not only several degrees of latitude farther north than any previously known species of the genus along the Atlantic seaboard, but at a higher latitude than any previously known species of *Heteralepas* (Young 1999, Zevina 1982). It was collected by a benthic trawl from ~500 m of depth, attached to the gorgonian *Primnoa resedaeformis* (Gunnerus, 1763).

Thirty species of *Heteralepas* have been described, and 2 of these are presently in synonymy. Of the 28 recognized species (Table 1), 8 have been recorded from the Atlantic; 3 from the Western Atlantic, 4 from the Eastern Atlantic and 1 found in both areas; *H. cornuta* (Darwin, 1852), *H. lankesteri* (Gravel, 1901), *H. belli* (Gravel, 1901), and *H. luridas* (Zevina, 1975), and *H. microstoma* (Gravel, 1901), *H. meteo-*

rensis Carriol, 1998, *H. alboplaculus* Zevina & Kolbasov, 2000 and *H. segonzaci* Young, 2001 plus *H. cornuta* respectively (Zevina 1975, Young 2001). All these species are from relatively low latitudes and none compare favorably with the new form. The closest affinities of the new form are with species like *H. japonica* (Aurivillius, 1892) from the Indo-West Pacific. However, the new form can be distinguished from all previously described species by characteristics of the apertural regions, and therefore it is considered to represent a new species.

Systematics

Subclass Cirripedia Burmeister, 1834
Superorder Thoracica Darwin, 1854
Order Pedunculata Lamarck, 1818
Suborder Heteralepadomorpha
Newman, 1987
Family Heteralepadidae
Nilsson-Cantell, 1921

Pilsbry (1907b) revised *Alepas* and extracted two distinct but related taxa from it,

Table 1.—Species of the genus *Heteralepas* of the world ocean from locality and depth data compiled from Foster (1979), Ren (1983), Carriol (1998), Zevina & Kolbasov (2000) and Young (2001). ? = taxonomic uncertainty (see discussion). * = species that are compared with *H. camelli* sp. nov. because of similarity in external morphology and/or geography.

Heteralepas		Western Atlantic	Eastern Atlantic	Eastern Pacific	Indo-West Pacific	Depth (m)
1	<i>H. cornuta</i> (Darwin, 1852)	West Indies, North Carolina to Brazil	W. Africa & offshore islands to Madeira, Meteor Seamount	?Chile	Andaman Sea, Philippines	73–210 ?4315
2	<i>H. japonica</i> (Aurivillius, 1892)	—	—	—	Japan to New Zealand and west to Reunion Is.	48–1,020
	= <i>H. indica</i> (Gruevel, 1901)	—	—	—	Philippines, Australia, New Zealand	Shallow water
3	? <i>H. quadrata</i> (Aurivillius, 1894)	—	—	N. & S. America	Japan, New Zealand	91–1,500
	= <i>H. perconicola</i> (Hiro, 1937)	West Indies, Brazil	—	—	—	?
4*	<i>H. lankesteri</i> (Gruevel, 1900)	Cuba	—	—	—	269–623
5*	<i>H. belli</i> (Gruevel, 1901)	—	Azores, Madeira, Meteor Seamount	—	—	—
6*	<i>H. microstoma</i> (Gruevel, 1901)	—	—	—	—	—
7	<i>H. gigas</i> (Annandale, 1905)	—	—	—	Bali Straits	238–915
8	? <i>H. malaysiana</i> (Annandale, 1905)	—	—	—	Malaysia	54
9	<i>H. ovalis</i> (Hoek, 1907)	—	—	—	Malaysia	984
10	<i>H. tenuis</i> (Hoek, 1907)	—	—	—	Malaysia	204
11	<i>H. rex</i> (Pilsbry, 1907a)	—	—	—	Hawaiian Islands	415–428
12	<i>H. cygnus</i> Pilsbry, 1907b	—	—	?California	—	?
13	<i>H. nicobarica</i> Annandale, 1909	—	—	—	Nicobar Islands	?
14	<i>H. vetula</i> Pilsbry, 1911	—	—	—	Japan	277–329
15	<i>H. ?dubia</i> Broch, 1922	—	—	—	New Zealand	55–73
16	<i>H. hattai</i> Hiro, 1937	—	—	—	Japan	Intertidal
17	<i>H. utinomii</i> Newman, 1960	—	—	—	Tasmania	450
18	<i>H. mystacophora</i> Newman, 1964	—	—	S.E. Pacific	—	228
20	<i>H. luridas</i> Zevina, 1975	Caribbean	—	—	—	300–700
21	<i>H. adiposa</i> Zevina, 1982	—	—	—	Japan	400
22	<i>H. fulva</i> Zevina, 1982	—	—	S.E. Pacific	—	300
23	<i>H. similis</i> Ren, 1983	—	—	—	China Sea	217
24	<i>H. fessa</i> Zevina & Shreider, 1992	—	—	—	N. of Madagascar	480
25*	<i>H. ?meteoensis</i> Carriol, 1998	—	Meteor Seamount	—	—	300
26	<i>H. ?aloplaculus</i> Zevina & Kolbasov, 2000	—	Meteor Seamount	—	—	280–300
27	<i>H. segonzaci</i> Young, 2001	—	Meteor Seamount	—	—	2,235
28	<i>H. camelli</i> sp. nov.	Nova Scotia	—	—	—	500

Heteralepas and *Paralepas*, but he left them in the family Lepadidae. Nilsson-Cantell (1921) noted that these two genera, in addition to lacking calcareous plates, differed from the remaining Lepadidae in the nature of their trophi and cirri and therefore he proposed a new family, the Heteralepadidae, for them. Species of *Heteralepas* are generally considered to have ctenopod or lasiopod cirri used for setose feeding, while those of *Paralepas* have acanthopod cirri, generally used to feed on the food or tissues of their hosts, including the eggs of hosts such as spiny lobsters. The two genera are further distinguished by the inner ramus of the posterior two pairs of cirri (cirri V & VI) being similar to the outer rami in *Paralepas*, but conspicuously reduced in length and breadth in *Heteralepas*. However, as will be noted in the discussion, there is at least one species that is somewhat intermediate in these characters and it likely should be assigned a genus of its own.

Heteralepas Pilsbry 1907b
Heteralepas cantelli sp. nov.
 (Figs. 1–4)

Type material.—The sole specimen (holotype) is deposited in the National Museum of Washington, Washington, D.C. USNM 1019509.

Etymology.—Named in honor of the Swedish cirripedologist, Carl August Nilsson-Cantell (cf. Newman 1990) who erected the family Heteralepadidae.

Material.—Known from a single specimen collected in the Northeast Channel, south of Nova Scotia, Canada (41°55.9'N, 65°42.5'W), by a commercial bottom trawler on October 9, 2002 from 500 m depth. It was attached to the exposed skeleton of the gorgonian *Primnoa resedaeiformis*.

Diagnosis: Capitulum and peduncle relatively smooth, without tubercles, carinal ridge or indications of the insertions of the carapace adductor muscle; apertural region slightly recessed or depressed below general surface; aperture $\sim \frac{1}{2}$ height of the ca-

pitulum, with crenulate lips restricted to upper $\frac{1}{3}$.

Description

The fresh specimen was translucent yellowish pink. The capitulum is 3 cm high and 2 cm wide, globular or nearly ovoid in lateral aspect, slightly pointed apically, laterally compressed, frontal margin interrupted by a depressed apertural region with slightly protuberant lips in the upper $\frac{1}{3}$ of the aperture (Figs. 1A, B, 2A, B). The slightly recessed apertural region is outlined by a thin edge and in the region below it, where the carapace adductor muscle is found, there is a chin-like thickening. Otherwise the capitulum is smooth, without carinal crest or ridge, warts, bumps or protuberances. Aperture $\frac{1}{2}$ height of capitulum; crenate lips produced in upper $\frac{1}{3}$. Peduncle 1.2 cm in diameter, equal in length to capitulum and marked with several folds and lines in the otherwise smooth cuticle, basal portion expanded into attachment disc. Labrum too damaged to describe; mandible (Fig. 3B) with 4 teeth including inferior angle, surface covered with numerous fine setae, lower margins of teeth 1–3 with a few fine pectinations (5 under the first and second, and 3 under the third tooth; Fig. 3B, a1-a3). First maxilla (Fig. 3C) with cutting edge stepped (plane of superior cutting edge indented relative to plane of inferior cutting edge) rather than notched, with three major spines (one large flanked by two somewhat smaller ones) above and approximately 14 spines below step, with soft setae in a group along the superior margin and spread out along the inferior margin, lateral surfaces clothed with numerous setae. Second maxilla (Fig. 3A) with a proximal cluster of long spine-like setae and a similar array of setae separated into two groups along the cutting edge.

Cirrus I not separated from posterior pairs but modified as a maxilliped of relatively short, unequal, densely setose rami; cirri II–VI basically similar in structure, se-

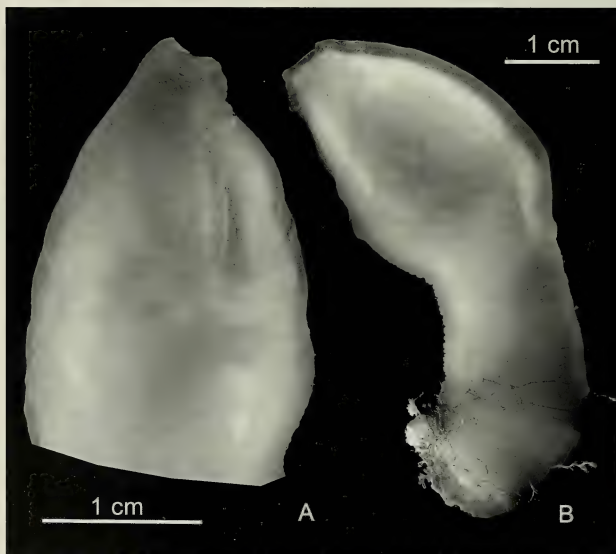


Fig. 1. *Heteralepas cantelli* sp. nov.: A, right-frontal aspect of capitulum, enlarged to show details of apertural region; B, lateral aspect of entire animal;

tation lasiopod (Fig. 4C). However, while cirri II–IV have long subequal rami nearly equal in length to the outer rami of cirri V and VI, the inner rami of V and VI are atrophied (Fig. 4D, Table 2). The number of articles comprising the cirri is as follows:

Cirrus:	I	II	III	IV	V	VI
Inner ramus:	18	42	56	56	25	22
Outer ramus:	24	51	57	58	60	60

Caudal appendage (Fig. 4D) of 13 articles, slightly longer than pedicel of cirrus VI. Penis (Fig. 4A, B) relatively long, slender, annulated, without specialized hooks or grap-

ples but clothed with numerous, long soft setae distally.

Discussion: The cirri of the new species are fully lasiopod (Fig. 4C) and the inner rami of the cirri V & VI are substantially reduced in length as well as breadth (Fig. 4D; Table 2). Therefore the new species is a *Heteralepas* in the strict sense. The number of articles comprising the rami of the cirri and the form of the mouthparts, while sometimes useful in distinguishing species, are considered somewhat variable (Nilsson-Cantell 1921), as are elaborations of the capitulum as well as its length relative to the peduncle (Young 2001). Therefore keys,

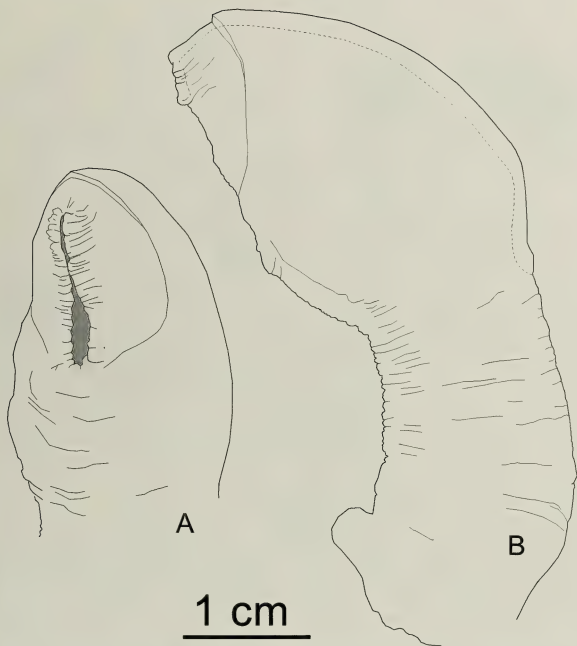


Fig. 2. *Heteralepas cantelli* sp. nov.: A, left-frontal aspect of capitulum, enlarged to show details of apertural region; B, lateral aspect;

such as that presented by Zevina (1982) for the 19 species of *Heteralepas* recognized at the time, should be used with caution.

Zevina (1982) did not include complete synonymies in her monograph, and at least two species once attributed to *Heteralepas* were assigned to *Paralepas* without amending either genus. Therefore we review all species attributed to the genus and, as can be seen from Table 1, 28 species (including the new form) are presently recognized. In

the process we encountered some problematic forms, and these are briefly discussed below before moving on to those that are strictly relevant to the new species.

Heteralepas quadrata (Aurivillius, 1892). This shallow-water species [including 1) *H. percnicola* as a junior synonym (Hiro 1937), 2) the forms attributed to the species by Rosell (1972), and 3) a little-known form from the Eastern Pacific (Zullo 1991)] sat uncomfortably in *Heteralepas* un-

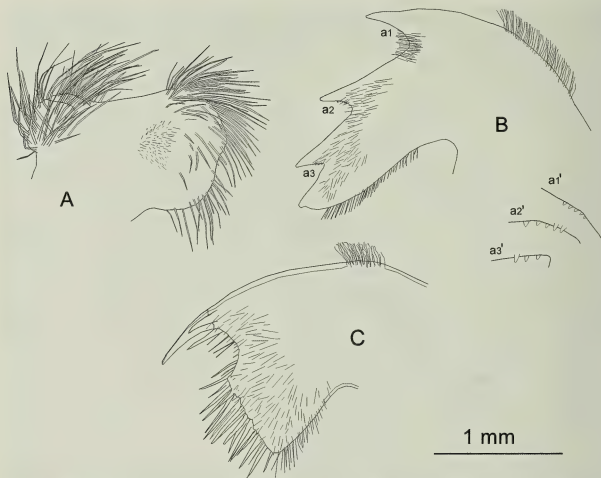


Fig. 3. *Heteralepas cantelli* sp. nov., mouth parts: A, second maxilla; B, mandible (a1'-a3', enlarged undersides of teeth a1-a3); C, first maxilla. (A-C same scale).

til Foster (1979) transferred it to *Paralepas*, a decision accepted by Zevina (1982). However, the species also sits uncomfortably in *Paralepas* because in some ways it is morphologically intermediate between the two genera. The characters largely involve the cirri, their setation being neither strictly lasiopod nor acanthopod, the relatively low number of articles of their rami, and the somewhat reduced inner rami of cirri V & VI, as well as the somewhat intermediate armature of the mandible and first maxilla. This suggests that proposal of a new genus is in order, and such a study would be of interest to evolutionary biologists as well as cirripedologists in light of the inferred relative primitiveness of the Heteralepadidae (Foster 1979), a view recently corroborated genetically and mor-

phologically (Harris et al. 2000; Pérez-Lozada et al. 2004). While there are a number of samples from the Eastern Pacific attributed to this species in the Benthic Invertebrate Collection at Scripps Institution of Oceanography, an appropriate review of the situation would also require studying materials from the Western Pacific. However, such a study is beyond the scope of the present paper.

Heteralepas malaysiana (Annandale, 1905). From a telegraph cable at approximately 54 m depth in the Gaspar Straits. Annandale (1909:84) accepted Pilsbry's (1907b) revision of *Alepas* and transferred *Alepas xenophorae* Annandale, 1906 to *Heteralepas* (*Paralepas*) and described *Heteralepas* (*Heteralepas*) *nicobarica* sp. nov. In the same paper, in a list of species

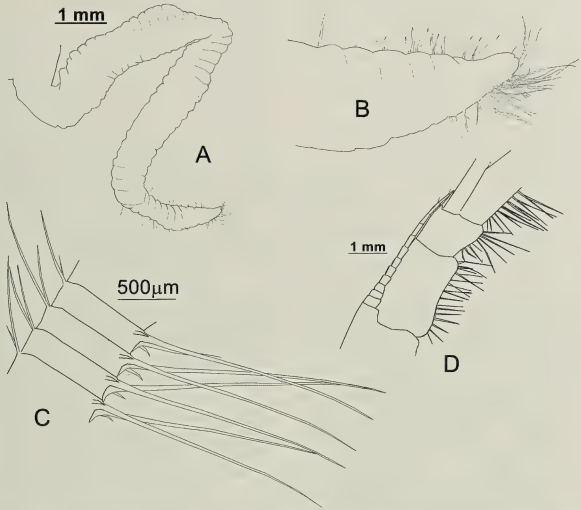


Fig. 4. *Heteralepas cantelli* sp. nov., thoracic appendages: A, penis; B, enlargement of distal portion of penis; C, intermediate segments of outer ramus of cirrus VI; D, posterior of thorax supporting right caudal appendage and pedicel of cirrus VI with proximal portions of inner and outer rami in outline (narrow and wide respectively, boundaries of articles omitted).

contained in the Indian Museum, Annandale (1909:130) included *Heteralepas malayana* (sic) under the subgenus *Heteralepas*. This was presumably because Annandale (1905:81) had clearly stated that the posterior (= inner) ramus of cirrus V was "... reduced to a mere thread, less than one-third as long as the anterior ramus", and that cirrus VI was "... in much the same condition". However, subsequently, and without a word of explanation, he (Annandale 1916:298) transferred *Heteralepas malaysiana* to the subgenus *Paralepas*. While Newman (1960) retained *malaysiana* in *Heteralepas* s.s., Zevina (1982) followed

Annandale by returning it to *Paralepas*. This is puzzling, considering the habitat as well as the characteristics of cirrus V & VI given in the original description. In light of these considerations, and the fact that the ornamentation of the capitulum appears more similar to that of *Heteralepas rex* (Pilsbry, 1907a) from Hawaii and *H. utinomii* Newman, 1960 from Tasmania than it does to any species of *Paralepas*, we have tentatively returned the species to *Heteralepas*.

?*Heteralepas ovalis* (Hoek, 1907): This species is represented by a single specimen taken along with *Paralepas morula* from an

Table 2.—Morphological comparison among *Heteralepas japonica*, *H. microstoma*, *H. metoensis*, *H. belli*, *H. lankesteri* and *H. cantelli* sp. nov., based on C/P = Ratio of length of capitulum (C) to length of peduncle (P). A/C = Ratio of height of aperture (A) to height of capitulum (C).

	<i>H. japonica</i>	<i>H. microstoma</i> *	<i>H. metoensis</i> *	<i>H. belli</i>	<i>H. lankesteri</i>	<i>H. cantelli</i> sp. nov.
Demarcation between capitulum & peduncle	Varying	Weak	Weak	Clear	Clear	Weak
Width of capitulum to capitulo-peduncular junction	Varying	Slightly wider	Slightly wider	Wider	Wider	Slightly wider
Capitulum						carinal side
Width (cm)	0.6-2.3 (1.5)	2.3	1.2-1.7	2.5	1.2-2.0	2
Length (cm)	0.9-3.6 (2.0)	1.7	1.2-1.8	1.6	1.7-2.2	3
Width (cm)	0.5-1.9 (0.9)	0.9	0.7-1.3	0.95	0.9-1.3	1.2
Length (cm)	0.5-11.6 (3.8)	2.4	3.1-7.2	3.2	1.3-3.8	3
C/P	0.2-1.8 (0.5)	0.7	0.25-0.47	0.5	0.6-1.3	1.0
Mantle	No	Yes	?	Yes	Yes	No
Carinal margin thickened	Varying	Yes	Yes	Yes	Yes	No
Aperture	½	½?	¾-½	½	½	½
Flaring from side	No	No?	No	Yes	Yes	Partly
Crenulate	?	?	Slightly	No	Conspicuously	Slightly
Lower margin demarcated	?	?	?	No	No	No
Tubular	No	Yes	?	?Yes	?Yes	No
Inner ramus	13-29	29	23	27	19-21	25
Outer ramus	36-69	?	93	?	74-92	60
Inner ramus	13-27	26	26	27	19-22	22
Outer ramus	37-68	?	92	?	89	60
Caudal appendage	4-12	15	14	5	10-12	13
Mandible pectination	***	Yes	Yes	Yes	No	Yes

* = considered synonymous by Young (2001).

** = Refers to special vase-shaped structures "de granulations chitineuses arrondies dont quelque-unes portent des crochets" (Gruvel 1902).

*** (for *H. japonica*) = see Discussion.

echinoid spine in Malaysian waters. Hiro (1936:223) noted that nothing is known of the internal parts, but from the original figures it is evident that the capitulum to aperture ratio is approximately 3:1. This is suggestive of *Paralepas*, but for lack of more conclusive evidence we have left it in *Heteralepas*.

Heteralepas cygnus Pilsbry, 1907b: The original description was based on a specimen acquired from the "Ward's Natural Science Establishment, Monterey, California", and hence the specimen was presumably from California, but it has not been recorded from this region since. Furthermore, Annandale (1909) indicated that there is a specimen in the Edinburgh Museum, questionably from the West Indies. The description may be adequate to distinguish it from similar albeit relatively undistinguished forms, but what ocean it came from remains uncertain.

Heteralepas cornuta (Darwin, 1852): A species usually having more-or-less distinctive carinal protuberances on its capitulum, first reported from the Caribbean (presumably from 90 m or so). It has since turned up in the Gulf of Mexico (Gittings et al. 1986), off Madeira and other West African islands (cf. Haroun et al. 2003), and along the coast of Northwest Africa. Furthermore it has been found in the Indian Ocean, the Philippines and the Southeast Pacific, off Chile (4315 m!) (cf. Young 2001 for review). Young (2001) commented not only on its wide geographical range and the extraordinary depth of the Chilean record compared to other populations attributed to the species, but on differences in cirral setation of the Chilean form compared to the population he has studied from the eastern Atlantic. Thus *H. cornuta* may represent a number of similar species. In any event, like the previous species, it is sufficiently distinct from the new form to no longer concern us here.

Heteralepas microstoma (Gravel, 1901): Known from off Madeira, the Azores and Meteor Seamount immediately to the south.

While known to range from between 269–623 m, it is most commonly found around 300 m (Young 2001). Zevina & Kolbasov (2000) illustrated and compared it to another recently described species, *H. meteorensis* Carriol, 1998, as well as to their new species, *H. alboplaculus* Zevina & Kolbasov, 2000, which was also from Meteor Seamount. Having such similar forms sympatric on Meteor Seamount, and then largely from the same depth, is troubling. Young (2001) synonymized *H. meteorensis* with *H. microstoma*, but he was apparently unaware of the work of Zevina & Kolbasov (2000) who claimed that all three species can be distinguished from each other by minute cuticular structures revealed by SEM. However, their photographs are not clear in this regard. As can be seen from our Table 2, there appears to be little in the way of macro-morphological differences among them, although the peduncle of *H. meteorensis* seems to be relatively longer and the aperture does not appear as tubular as in *H. microstoma*. On the other hand, *Heteralepas alboplaculus* is described as having the capitulum and to some extent the peduncle covered by well-spaced tubercles containing calcareous structures. Such calcareous structures are unprecedented in the family and could be the work of a pathogen. We hope that workers in the Atlantic will clarify this situation in the near future. In the meantime, while the specific status of *H. meteorensis* and *H. alboplaculus* is uncertain (Table 1), we have included the former as well as *H. microstoma* in Table 2 for comparative purposes.

When it comes to determining the affinities of the new species, the logical place to begin is in the Atlantic. Of the 8 previously known species of *Heteralepas* noted in the introduction, 5 occur in the eastern Atlantic. These include *H. cornuta*, *alboplaculus* and *segonzaci*, and taking their capitular features at face value, they are distinct from the new form and therefore no longer concern us here. This leaves *H. microstoma* and *meteorensis*, which are very similar if

not synonymous, but as noted above both have been characterized in Table 2 for comparative purposes.

As for the western Atlantic species, *H. cornuta*, which ranges as far north as the Carolinas, was noted above as being distinct from the new form. This leaves *H. luridas*, *belli* and *lankesteri*. The first, from 300–700 m of depth in the Caribbean, is known to range between 2 and 9.5 mm in height and the specimen illustrated in the original description is less than 6 mm high, so it is a small species. Its capitulum, with a somewhat tubular or flaring apertural region, is otherwise undistinguished, and its cirral and caudal appendage counts are lower than in the new species. So, assuming *H. luridas* is not based on juveniles, it too need no longer concern us. This leaves *H. belli* and *lankesteri*, and since in outward appearance they are similar to the new form, they have been included in Table 2. As we shall see, so far none of the species included in Table 2 agree well with the new species in numerous detail; but what about species from the Indo-Pacific?

Of the Indo-West Pacific species, *H. japonica* and similar species such as *H. fulva* from the Southeast Pacific are rather close to the new form. The former has been reported from between 18 and 1020 m depth from Japan to Singapore, Australia and New Zealand, the Nicobars in the Andaman Sea and Réunion Is. (Foster & Buckeridge 1995). Therefore, while not as wide-ranging as *H. quadrata*, it is wide-ranging compared to most species of the genus. Part of this range is due to synonymies, and that of Nilsson-Cantell's (1927, 1938) for *H. indica* (Gravel, 1901) has long been accepted. This extended the range of the species to Singapore and into the Indian Ocean where it was reported from Nicobar Is. on floating wood. Furthermore, Foster (1979), in his report on New Zealand cirripeds, synonymized *H. dubia* Broch, 1922 from 55–72 m in Disaster Bay, Australia, with *H. japonica*. However, Zevina (1982), without explanation, continued to recognize *H. du-*

bia as a distinct species, and subsequent authors have followed suit.

Considerable variability in characters might be expected in such a wide-ranging species and for present purposes we are accepting the opinion of these authors. However, considering such variation in cirripeds as geographical rather than indicative of genetically distinct populations has generally proven wrong (Newman 1993). Thus caution seems in order because the reported variations in the mandible of presumed *H. japonica* from different populations, appear to go beyond the range of variability found within a species. Although Aurivillius (1894) did not illustrate the mandible of *H. japonica*, his written description agrees with Nilsson-Cantell's (1921:247, fig. 43b) and Pilsbry's (1911:71, fig. 4A) illustrations, and also with that of Gravel (1902: 284, Pl. 24, fig. 24) for *H. indica*. Thus the teeth of the mandible appear to be without pectinations, but on close inspection of Nilsson-Cantell's illustration there might have been low pectinations of the lower margins of teeth 1–3, especially 2 and 3. However, since there is no such suggestion in the other illustrations, the evidence favors the mandible being simple.

The situation at the southern end of the range for *H. japonica* looks quite different with regard to the mandible. Foster (1979) synonymized *H. dubia* Broch from Australia, and the population he was studying in New Zealand, with *H. japonica*. While Broch (1922:288, fig. 37B) gave no indication of pectinations on the first tooth, he clearly illustrated them on the upper sides of teeth 2–4 as well as the lower sides of 2 and 3. Foster (1979:16, fig. 3J) illustrated the same for the upper sides, but limited pectinations on the underside to tooth 1. So, the populations attributed to this species from north and south of the equator appear to differ in the characteristics of the mandible, and the new species, with its inconspicuous pectinations on the lower sides of teeth 1–3 (Fig. 3, a1-a3), differs from both of them.

In view of the foregoing considerations we include *H. dubia* in Table 1 as a questionable species rather than a synonym of *H. japonica*. Nonetheless, *H. japonica* still includes sufficient variability to make it an ideal Indo-Pacific representative similar to the new form from the Atlantic, and therefore it is included in Table 2 for comparative purposes.

Summary and Conclusions

The essentially naked heteralepadids present a difficult problem to systematists since, being unarmored, they lack a number of distinct features customarily utilized in separating genera and species (Zullo & Newman 1964). Aside from the work of Nilsson-Cantell (1921, 1927), and to some extent, Young (2001), no studies have evaluated the usefulness of morphological characters in distinguishing *Heteralepas* species. Thus it is difficult to establish a new species with a high degree of certainty. But, in spite of the latitude allowed by synonymy, the present form could not be assigned to any known species.

As can be observed in Table 2, the Atlantic species most similar to the new species (*H. microstoma*, *meteorensis*, *belli* and *lankesteri*) are readily distinguished from it as well as from *H. japonica* from the Indo-West Pacific, by several characters. However, the new species, *H. cantelli*, cannot be distinguished from *H. japonica* by the characters presented in the table. This is due in part to the variability attributed to *H. japonica*, but there are notable differences between these two species, not included in the table, that distinguish them. These include 1) the lack of any indication of a carinal thickening, crest, or protuberances along the carinal margin (but sometimes also found lacking in individuals of *H. japonica*), 2) a marked crenation of the apertural margin largely restricted to the upper third rather than along its entire margin, and 3) a slightly depressed area around the entire apertural region, setting it off from the gen-

eral surface of the capitulum. The last two differences are sufficient not only to distinguish the new form from *H. japonica*, but from all known heteralepadids.

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**Two new species of seven-spined *Bathyconchoecia* from the
North Atlantic and Indian oceans
(Crustacea: Ostracoda: Halocypridae)**

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Abstract.—A new species of halocyprid ostracode *Bathyconchoecia omega* from abyssal depths of the North Atlantic Ocean, off Newfoundland, Canada, is described and illustrated, and a new species *Bathyconchoecia georgei* is proposed for a specimen from the Indian Ocean previously referred to *Bathyconchoecia deeveyae* Kornicker, 1969.

The R/V *Chain*, operated by the Woods Hole Oceanographic Institution, collected in 1972 at a depth of 4400 m in the North Atlantic Ocean, off Newfoundland, Canada, a bottom sample containing a single A-1 male of *Bathyconchoecia omega*, new species. The A-1 male from off Newfoundland is considerably larger than previously described seven-spined species of the genus, and is the northernmost occurrence of the group. Additional ostracodes in the sample are mostly bottom-living Podocopida, Cladocopida and Myodocopida, which suggests a bottom or near-bottom habitat for *B. omega*. However, a specimen of pelagic species of *Conchoecia* in the sample suggests that it contains some shallow water contaminants.

Only three species of *Bathyconchoecia* having seven spines on the carapace (four on right valve, three on left), have been described previously: *B. deeveyae* Kornicker, 1969, *B. septemspinosa* Angel, 1970, and *B. longispinata* Ellis, 1987. One of the specimens previously referred to *B. deeveyae* is proposed as a new species herein. Thus, the number of 7-spined species of *Bathyconchoecia* is now five. Their distribution is shown in Fig. 1.

Correction.—Kornicker (1981:1237) reported that the slide containing the appendages of the holotype of *B. deeveyae* (USNM 123335) had been lost. It has been recovered.

Bathyconchoecia omega, new species
Figures 2–6

Holotype.—Unique specimen, A-1 male on slide and in alcohol, MCZ Harvard University, MCZ50432.

Type locality.—R/V *Chain* 106, 30 Aug 1972, Station 334, North Atlantic Ocean, off Newfoundland, Canada, 40°42.6'N–40°44'N, 46°13.8'W–46°14.6'W, epibenthic sled, depth 4400 m.

Material.—Holotype.

Description of A-1 male (Figs. 2–6).—Carapace with linear dorsal margin except for slight bulge near middle just posterior to base of dorsal spine. Posterodorsal corner of each valve with gland on very slight bulge. Posterodorsal corner evenly rounded except for long spine on right valve; spine parallel with length of valve, but at slight upward angle (very tip of spine of specimen broken off; soft matter projects from broken tip). Base of spine projects slightly medial

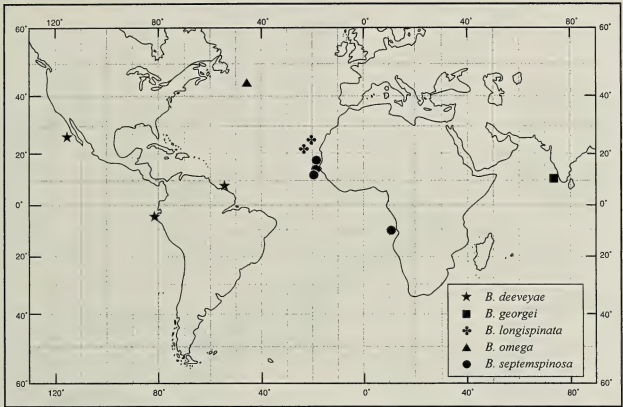


Fig. 1. Distribution of species of seven-spined *Bathytoconchoecia*.

to slightly overlap posterior edge of left valve (Fig. 2B). Rostrum of each valve with anterior spine at slight angle to each other (Fig. 2B). Spine at midlength of dorsal margin of each valve at slight outward and upward angle (Fig. 2A, B). Spine near ventral margin of each valve at about $\frac{2}{3}$ length of valve at slight downward and outward angle. Anterior spines on rostra and posterior spine on right valve with surface ridges parallel to lengths of valves; a few of the ridges of the rostral spines bear short stout spines. Other long spines with minute surface spines. Carapaces completely covered by distinct punctae and slightly curved vertical frills (not all shown in Fig. 2A). Frills generally on each side of 2 or 3 rows of punctae (Fig. 2C). Indistinct reticulations and ridges on anteroventral surface of valve ventral to incisure (Fig. 2A).

Pigmentation: No black pigment spots on either carapace or body.

Central adductor muscle attachments (Fig 2A): Indistinct, near center of valve

and consisting of 2 individual scars; striations of muscle ends indistinctly visible from outside view of valve; scars not covered by punctae.

Carapace size (mm): Length including spines 3.79, length excluding spines 2.92, height excluding spines 1.68, width without spines 1.52.

First antenna (Fig. 2E): Shaft short with indistinct segmentation. Brush-like structure with about 315 filaments in about 9 rows, each with about 35 filaments. Dorsal bristle on segment following brush-like structure stout, spinous, about $\frac{2}{3}$ length of brush filaments. Terminal segment with 4 bristles: 1 long stout bristle reaching well past brush filaments and with widely scattered marginal spines (not shown); 3 shorter than brush filaments. Limb with densely packed amber-colored cells.

Second antenna (Fig. 3A-D): Protopod bare. Endopod: 1st article with 2 spinous dorsal bristles (1 long, 1 short) and few indistinct medial spines near ventral margin;

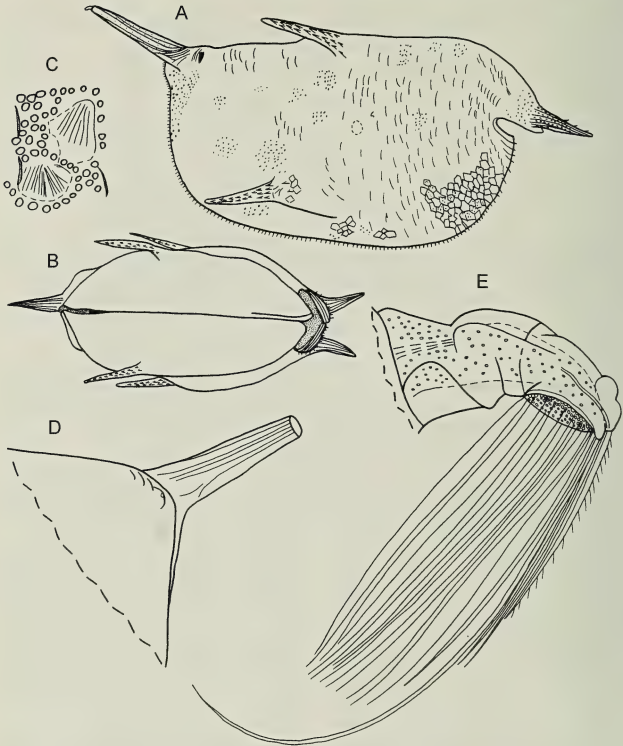


Fig. 2. *Bathyonchoecia omega* holotype, MCZ 50432, A-1 male: A, Complete carapace from right side, length without spines 2.92 mm; B, Complete carapace, ventral view; C, Left valve, detail of ornamentation on outer surface; D, Posterodorsal corner of complete specimen (spine on right valve, glandular opening on left valve); E, Right 1st antenna, lateral view.

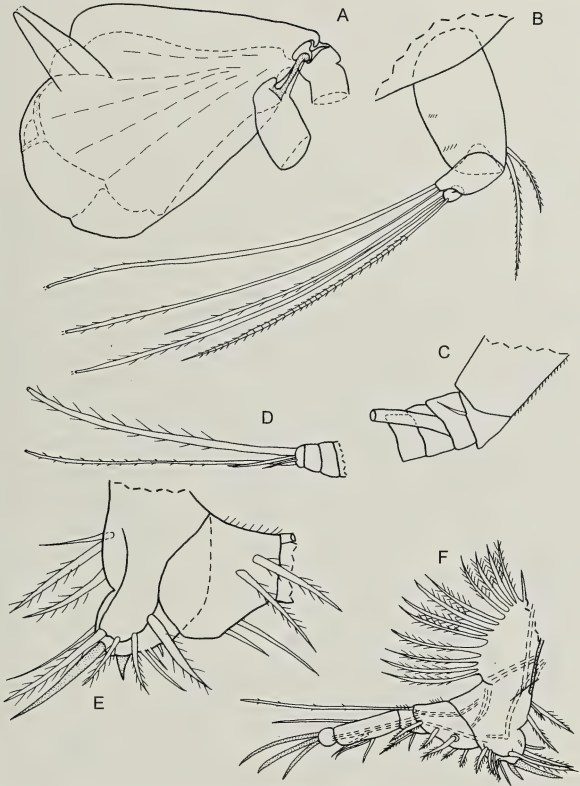


Fig. 3. *Bathyconchoecia omega* holotype, MCZ 50432, A-1 male: A, Left 2nd antenna, medial view; B, Endopod right 2nd antenna, lateral view; C, Proximal part exopod left 2nd antenna, medial view; D, Distal part exopod right 2nd antenna, lateral view; E, Proximal part left 5th limb, lateral view; F, Right 5th limb drawn on body, lateral view.

2nd article with 1 minute bristle medial to 3rd article and 2 stout terminal bristles with few indistinct marginal spines (inner bristle stouter, both about same length as exopod bristles); 3rd article with 3 bristles: middle bristle longer and stouter than others, more than 1/2 length of bristles of 2nd article, with few marginal spines; outer bristle about 1/2 length of middle bristle, with many marginal spines; inner bristle similar in length to outer bristle, with marginal spines; base of 3rd article lateral to distal end of 2nd article; endopods of left and right limbs similar. Exopod: 1st article with short ventral spines and small medial terminal bristle; articles 2 to 8 with long natatory bristle; 9th article with 4 bristles (2 short lateral; 1 ventral of medium length and with short marginal spines; 1 long dorsal, with natatory hairs).

Mandible (Fig. 4): Coxa (Fig. 4B-E): Pars incisivus with 5 ventral teeth and slender distal tooth at ventral tip of triangular posterior section; anterior edge serrate (Fig. 4C). Proximal list with 10 teeth in 2 layers (Fig. 4D); distal list with 19 teeth in 3 layers (Fig. 4E). Spined posterior part with 6 lobes with numerous spines and 7th lobe with short stout spinous bristle and minute spines along distal posterior edge of lobe near bristle (Fig. 4C). Anterior margin of coxa evenly rounded, without triangular process. Basis (Fig. 4A, F, G): 2 long plumose bristles present on or near dorsal margin and 1 long spinous medial bristle near midwidth some distance from dorsal margin (Fig. 4F); lateral surface with 3 long bare distal bristles and long spines (Fig. 4F); posterior margin spinous and with 2 short distal bristles (proximal bristle sclerotized and with ventral spines; distal bristle tube-formed) (Fig. 4G); anterior margin with long bare distal bristle (Fig. 4G); ventral margin with 5 short teeth with minute secondary teeth (Fig. 4G); 1 short tooth with minute secondary teeth on posterior margin proximal to posterior ventral tooth. Posterodorsal corner of basis with oval sclerite (Fig. 4A, B). Endopod (Fig. 4F, H): Article

1 with dorsal, ventral, lateral, and medial slender spines and 4 bristles (1 long, terminal, dorsal, spinous; 1 long, distal, ventral, bare; 2 medium length, medial with bases close to ventral bristle, bare). Article 2 with 5 bristles (2 long and 1 shorter, terminal, dorsal, spinous; 2 medium length, distal ventral, bare) and few distal spines on ventral margin and medial and lateral surfaces near ventral margin. Article 3 with long spinous terminal claw and 6 bristles (2 long, spinous, terminal (shorter of these with base on medial side), and 4 short, ventral, bare (1 of these with lateral base)) and medial spines.

Maxilla (Fig. 5A-C): Endite of precoxa with 2 tube-formed bristles, 3 claws, and 2 long spinous bristles. Coxa: dorsal margin with long stout dorsal bristle (Fig. 5B); proximal endite with 3 tube-formed bristles and total of 4 claws and claw-like bristles; distal endite with 2 tube-formed bristles and 4 claws. Basis with 2 long stout plumose bristles near dorsal margin, and short bare ventral bristle. Endopod: article 1 spinous with 4 dorsal bristles (3 proximal, 1 distal); medial surface with 4 distal bristles (3 long, 1 short); article 2 with 2 stout claws of unequal length and 4 slender bristles.

Fifth limb (Fig. 3E, F): Epipod with 3 groups of 4 stout plumose bristles; dorsal group with additional small 5th bristle (Fig. 3F). Precoxa with 3 ventral bristles (Fig. 3E). Coxa with 11 or 12 ventral bristles (not all shown). Basis with 6 bristles plus long terminal dorsal exopod bristle with minute widely separated marginal spines (not all shown). Endopod: article 1 with dorsal and medial spines and 3 bristles (not all shown). Article 2 with dorsal and medial spines and 4 bristles (3 near ventral margin and 1 longer dorsal). Article 3 with 2 long terminal slender claws and 1 long ringed, terminal, slender ventral bristle. A muscle terminates at base of exopod bristle.

Sixth limb (Fig. 6A): Epipod with 3 groups of 5, 5, and 6 (dorsal) long plumose bristles; dorsal group with additional short 7th bristle (Fig. 6A). Coxa with 1 spinous,

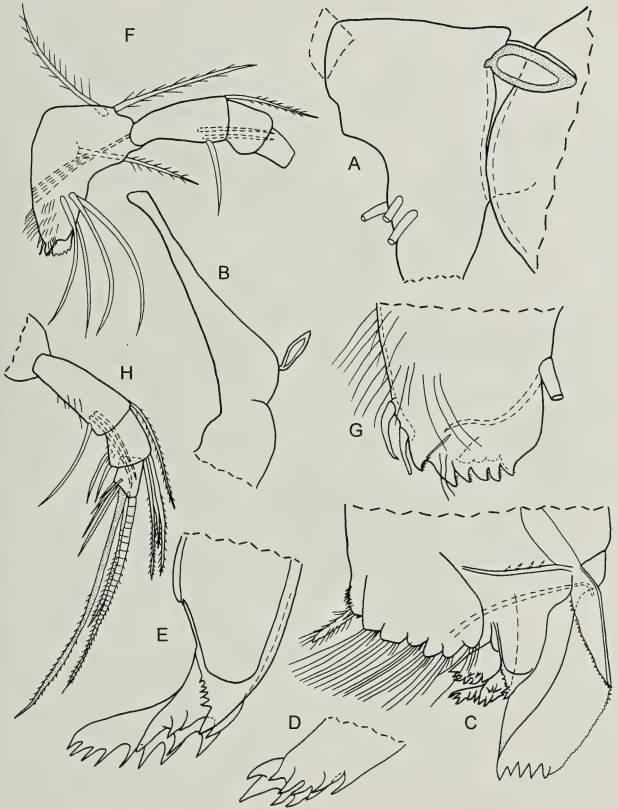


Fig. 4. *Bathyconchoecia omega* holotype, MCZ 50432, A-1 male: A, Left mandible, junction of coxa and basis, lateral view. B-H, Right mandible, lateral views: B, Proximal part of coxa; C, Distal end of coxa; D, Detail of proximal tooth of coxa (detail from C); E, Detail of distal tooth of coxa (detail from C); F, Basis and endopod; G, Distal end of basis; H, Endopod.



Fig. 5. *Bathyonchoecia omega* holotype, MCZ 50432, A-1 male: A, Right maxilla, medial view (arrow indicates tube-formed bristles); B, Left maxilla, lateral view; C, Right maxilla, oblique dorsal view (not all bristles shown); D, Anterior of body from right side showing upper and lower lips (esophagus dashed); E, F, Lower lip from left side, anterior of body to left; G, Upper lip, dorsal view.

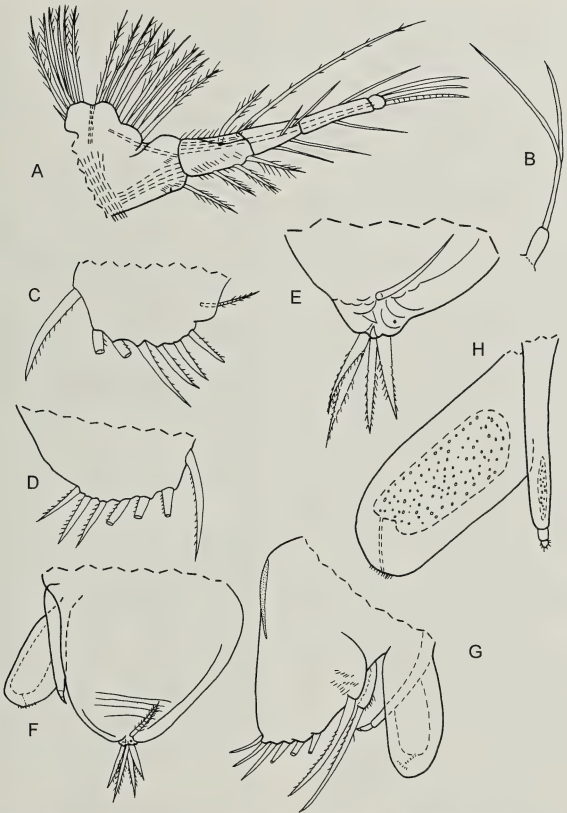


Fig. 6. *Bathyconchoecia omega* holotype, MCZ 50432, A-1 male: A, Right 6th limb, medial view; B, 7th limb; C, Left lamella of furca and unpaired bristle, lateral view; D, Right lamella of furca, lateral view; E, Posterior view of ventral end of body showing unpaired bristle and furca; F, Posterior view of body showing copulatory organ on left side; G, Posterior of body from right side showing furca and copulatory organ; H, Copulatory organ from left side, anterior to upper left.

ventral, terminal bristle. Basis with spines, 4 spinous bristles and 1 long, terminal, dorsal, exopod bristle with widely scattered minute spines (basis may consist of medial and lateral parts). Endopod: article 1 with 4 bristles; article 2 with 2 bristles; article 3 with 3 long terminal bristles (dorsal 2 claw-like). A muscle terminates at base of exopod bristle.

Seventh limb (Fig. 6B): Broad thumb-like process with 2 long unequal bare bristles.

Furca (Fig. 6C–G): Each lamella with 7 claws with teeth along posterior margins; 1 unpaired spinous bristle following claws on lamellae (Fig. 6E).

Bellonci organ: Not developed.

Lips (Fig. 5D–G): Upper lip with spinous posterior edge (Fig. 5D, G). Lower lip spinous (Fig. 5E, F).

Copulatory organ (Fig. 6F–H): Organ with 2 separate branches on left side of body. Broad anterior branch with minute terminal teeth; narrow posterior branch with small tapered tip.

Comparisons.—The length of the unique A-1 male from off Newfoundland (excluding spines) is 2.92 mm, whereas A-1 instars of *B. deeveyae* and *B. septemspinosa* are shorter than 1.8 mm (Kornicker and Angel, 1975: table 1; Kornicker, 1981:1240). A length of 0.66 mm was reported for an A-4 instar of *B. deeveyae* by Kornicker (1991: 30). The adult male of *B. longispinata* has a range of lengths of 1.95–2.11 mm (Ellis, 1987: Table II), much shorter than the 2.92 mm length of the A-1 male referred herein to *B. omega*. The 2 mid-dorsal spines on the carapace of the later specimen are shorter than those of *B. longispinata*. Also, the fossae and frills of *B. omega* are on all parts of the valve, whereas, they cover only certain areas on *B. longispinata*. The length of the adult male of *B. georgei*, new species, is 1.28 mm, much smaller than the length (2.92 mm) of the A-1 male of *B. omega*. The carapace of the former species is without the frills present on the carapace of *B. omega*.

The 2nd endopod articles of both mandibles of the A-1 instar of *B. omega* bear 5 bristles compared to 4 on the A-1 mandibles of *B. septemspinosa* and *B. deeveyae* and the adult male mandible of *B. longispinata*, and 3 on the adult male mandible of *B. georgei*. Mandibles of a total of six A-1 and A-2 instars of *B. septemspinosa* examined by Kornicker and Angel (1975: Table 1) indicate that the number of bristles on the 2nd endopod article of the mandible of those instars do not vary from 4 bristles and, therefore, may be a reliable character to use to discriminate specimens of *B. omega*, but reliability of the character in the latter species is unknown.

Bathyconchoecia georgei, new species

Bathyconchoecia deeveyae Kornicker.—George, 1971: 141, figs. 1–9.
Not *Bathyconchoecia deeveyae* Kornicker, 1969: 403, pl. 1, figs. 1–2.

Etymology.—Species named in honor of Jacob George, National Institute of Oceanography, Cochin-18, India, who described the specimen upon which the new species is based.

Holotype.—Unique specimen, adult male. Specimen is in a vial labeled 07.43, with serial number 0130, deposited in the archive room at the Indian Ocean Regional Centre, National Institute of Oceanography, Cochin – 14, India (there are no mounted slides). (Information about specimen supplied by Dr. Rosamma Stephen, Scientist, National Institute of Oceanography Regional Center, Cochin, in correspondence with the junior author. Dr. Stephen did not examine specimen in vial, but stated that she “could make out that there is a white specimen inside.”)

Type locality.—International Indian Ocean Expedition station Co. 62 (I. O. B. C.1969), in vertical haul from 200 to 0 m, off SW coast of India, 10°39'N, 75°22'E.

Material.—None examined.

Discussion of B. deeveyae Kornicker, 1969.—This species was described from an

A-1 juvenile collected at a depth of 508–523 m in a benthic trawl in the Peru-Chile Trench System, Pacific Ocean (Kornicker, 1969:403). A second specimen, an adult male, was collected in a vertical plankton haul from 200 to 0 m in the Indian Ocean off the SW coast of India (George, 1971: 141). A third specimen, an adult or A-1 female, was collected at a depth of 520 m in an epibenthic sled from off Surinam, Atlantic Ocean (Kornicker, 1981:118). Ellis (1987:83) observed, "It is possible that these three specimens are not conspecific." That observation prompted the present authors to reconsider the three specimens that had been referred to *B. deeveyae*, and led to our conclusion that the Indian Ocean specimen is not conspecific with the other two specimens of *B. deeveyae* from the Atlantic and Pacific Oceans. The Indian Ocean specimen was adequately described by George (1971: 141), so that only a brief diagnosis based on the adult male is presented here.

Diagnosis (adult male).—Carapace 1.28 mm long, excluding spines. Second endopod article of mandible with 3 bristles. Furca with 8 claws on each lamella.

Comparisons.—The carapace of the new species, *B. georgei* is much smaller than equivalent stages of *B. septemspinosa*, *B. deeveyae*, and *B. longispinata* (because only the adult male of *B. georgei* is known, the relative sizes of its instars is an extrapolation). The 2nd endopod article of the mandible of the adult male *B. georgei* bears 3 bristles compared to 5 on the adult male of *B. longispinata* and 4 on the A-1 instars of both *B. septemspinosa* and *B. deeveyae*. The adult male *B. georgei* bears 8 claws on each lamella compared to 7 on the adult male *B. longispinata*.

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**The hermaphroditic sea anemone *Anthopleura atodai* n. sp.
(Anthozoa: Actiniaria: Actiniidae) from Japan, with a redescription
of *A. hermaphroditica***

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Abstract.—A new species of internally brooding sea anemone, *Anthopleura atodai*, is described from the middle to northern Pacific coasts of Honshu, Japan. This species attaches to mussels or in rock crevices of the higher tidal zone. This is the second hermaphroditic species and fourth internally brooding species of *Anthopleura* to be reported; it is distinguished from other members of *Anthopleura* by a combination of the following features: brooding its young, synchronously hermaphroditic, S-shaped basitrichs in filaments, 40 to 68 tentacles, verrucae in the proximal part of the column larger than those in the distal part, cobalt-blue spot at the distal end of each siphonoglyph. *Anthopleura hermaphroditica*, the species that most closely resembles *A. atodai*, is re-described to clearly differentiate it from *A. atodai* and to resolve questions about its taxonomy and identity.

Anthopleura Duchassaing and Michelotti, 1861, one of the largest genera in the Actiniaria, includes about 50 species (Carlgren 1949; Dunn 1974, 1978, 1982a; Fautin 2003). In Japanese waters, six species of *Anthopleura* are known: *Anthopleura asiatica* Uchida & Muramatsu, 1958; *A. fuscoviridis* Carlgren, 1949; *A. kurogane* Uchida, 1938; *A. mcMurrichi* Wassilieff, 1908; *A. pacifica* Uchida, 1938; *A. uchidai* England, 1992. Additionally, Atoda (1954) reported the post-larval development of an unidentified species of *Anthopleura*, which broods its young in the colenteron. Although Atoda (1954) mentioned that the species could be distinguished from other species of *Anthopleura* by its coloration, it has never named; we formally describe it here as a new species, *A. atodai*.

Internal brooding is widely known in the Actiniaria: e.g. *Actinia* spp. (Chia & Rostrom 1960; Rossi 1971; Black & Johnson

1979; Ayre 1983; Manuel 1988; Russo et al. 1994; Yanagi et al. 1996, 1999), *Aulactinia* sp. (Dunn et al. 1980), *Cereus pedunculatus* (Rossi 1971), *Cnidopus japonicus* (T. Uchida 1934, T. Uchida & Iwata 1954), *Epiactis* spp. (Dunn 1975, Fautin & Chia 1986, Edmands 1995), and *Bunodactis hermaphroditica* (McMurrich 1904). Aside from *A. atodai*, three species of *Anthopleura* are reported to brood internally: *A. handi* Dunn, 1978, from the Philippines, Hong Kong, and Malaysia (Dunn 1978, England 1987); *A. aureoradiata* (Stuckey, 1909a) from New Zealand (Stuckey 1909a, 1909b; Carlgren 1949, 1954; Parry 1951); and *A. hermaphroditica* (Carlgren, 1899) from Chile (Carlgren 1899, 1927, 1949, 1959).

Anthopleura atodai most closely resembles *A. hermaphroditica*. Because the anatomy and cnidom of *A. hermaphroditica* is incompletely known, and its taxonomic status is unclear, we redescribe it to clearly



Fig. 1. Distribution of *Anthopleura atodai*, new species. Stars indicate records of *Anthopleura* sp. given by Atoda (1958); circles indicate sites visited in this study.

distinguish *A. hermaphroditica* from *A. atodai* and to evaluate the proposed synonymy between *A. hermaphroditica* and *A. handi*. We find that *A. hermaphroditica* and *A. atodai* can be distinguished based on color, number of tentacles, cnidom, and geographic range, and that *A. hermaphroditica* is distinct from *A. handi*.

Materials and Methods

Specimens of *Anthopleura atodai* were collected from high intertidal rocky shore around Asamushi (40°54'N, 140°51'E), Otsuchi (39°22'N, 141°58'E), Katsura (35°07'N, 140°16'E), and Tateyama (34°58'N, 139°46'E) (Fig. 1). Anatomical observations were made on 17 specimens of *A. atodai*; histological sections were made from 11 specimens. Anatomical observations were made on 10 preserved specimens of *A. hermaphroditica*; histological sections were made from 5 animals. For specimens of both *A. atodai* and *A. hermaphroditica*, histological sections 6–8 μ m thick were stained with hematoxylin and eosin or with Haidenhain's Azan (Presnell and Schreiber, 1997).

Cnidae data were gathered following the method of England (1987) and Williams (1996). Cnidae were measured from both live and preserved specimens of *A. atodai*, and from preserved specimens of *A. hermaphroditica*. Cnidae were measured in smash preparations at 1000 X using differential interference light microscopy. The terminology for cnidae follows Weill (1934), Mariscal (1974), and England (1991).

The material examined was deposited in the Costal Branch of Natural History Museum and Institute, Chiba (CMNH), National Science Museum, Tokyo (NSMT), Swedish Museum Natural History, Stockholm (SMNH), State Zoological Museum, Munich (ZSM), and The University of Kansas Natural History Museum and Biodiversity Research Center (KUMNH).

Systematic Account

Family Actiniidae Rafinesque, 1815
Genus *Anthopleura* Duchassaing and Michelotti, 1860

Anthopleura atodai, new species
Figs. 2–5

Anthopleura sp.—Atoda, 1954: 274, figs. 1–29, pls. 6–7.—Isomura et al., 2003: 293, fig. 1.

Holotype.—Kenashi-jima, Otsuchi, Iwate Pref., Honshu, Japan (39°21'30"N, 141°57'50"E), 14 July 1997, collected by KY, 1 specimen, with histological sections and cnidae preparations (CMNH-ZG 64).

Paratypes.—All from Honshu, Japan and collected by KY: Kenashi-jima, Otsuchi, Iwate Pref., 14 Jul 1997, 1 specimen with cnidae preparations (CMNH-ZG 65), 1 specimen with histological sections (NSMT-Co 1373), 1 specimen (NSMT-Co 1374), 1 specimen (KUMNH 1808), 1 specimen entirely sectioned longitudinally (CMNH-ZG 3692), 1 specimen entirely sectioned transversely (CMNH-ZG 3693); Banda, Tateyama, Chiba Pref., 28 Oct 1996, 1 specimen with cnidae preparations



Fig. 2. A–C, Photographs of *Anthopleura atodai*, new species (A, collected at Banda, 24 Feb 1997; B, C, collected at type locality, Kenashi-jima, 14 Jul 1997): A, 2 specimens expanded and 1 specimen contracted; B, semi-expanded specimen; C, fully contracted specimen. D, E, Photographs of *A. hermaphroditica* (collected from Chiloe Island, Chile): D, Two specimens expanded; E, Typical oral disc patterning. Photographs in D, E courtesy of V. Häussermann. Scale Bars: A, D = 10 mm; B, C = 5 mm, E = 20 mm.

(CMNH-ZG 115), 1 specimen (CMNH-ZG 200), 11 Dec 1996, 24 Feb 1997, 1 specimen with cnidae preparations (CMNH-ZG 44), 1 specimen (NSMT-Co 1372), 5 Dec 1997, 1 specimen entirely sectioned longitudinally (CMNH-ZG 3695), 1 specimen entirely sectioned transversely (CMNH-ZG 3696); Hadaka-jima, Asamushi, Aomori Pref., 22 Jun 1998, 1 specimen with histological sections and cnidae preparations (CMNH-ZG 209), 1 specimen with cnidae preparations (CMNH-ZG 210), 1 specimen (KUMNH 1809), 1 specimen entirely sectioned transversely (CMNH-ZG 3697).

Non-type material examined.—All specimens collected from Honshu, Japan by KY: Kedo-ura, Katsuura, Chiba Pref., 1 May 1999, 4 specimens (CMNH-ZG 253); Banda, Tateyama, Chiba Pref., 11 Dec 1996, 4 specimens (CMNH-ZG 201), 24 Feb 1997, 6 specimens (CMNH-ZG 3694), 15 May 2000, 2 specimens (CMNH-ZG 906); Nojima, Otsuchi, Iwate Pref., 8 Aug 2001, 4 specimens (CMNH-ZG1060), 4 specimens (CMNH-ZG 1061); Hadaka-jima, Asamushi, Aomori Pref., 22 Jun 1998, 60 specimens (CMNH-ZG 3698), 5 specimens (KUMNH 1809–1810), 3 specimens (NSMT-Co 1375–1378).

Description.—Column and pedal disc: Freshly collected specimens brown or bluish-green, proximal verrucae whitish (Fig. 2A–C). In living, expanded animals, column width 6–12 mm, almost equal to height (Fig. 2A–C); oral and pedal disc of almost equal width. Column of contracted animals dome-like (Fig. 2A, C). Adhesive endocoelic verrucae in regular vertical rows from margin to limbus; in some individuals, becoming dense and irregular distally (Fig. 2B); number of rows 24–39 (37 in holotype) distally, 24 proximally. Diameter of verrucae increases proximally: 0.4 mm at margin, 0.6–1.2 mm at limbus. In life, verrucae hold bits of gravel and broken shells. Marginal endocoels bear 9–32 pale, opaque, spherical acrorhagi that curve into fosse (Table 1). Pedal disc weakly adherent,

Table 1.—Morphological variability of 11 specimens of *Anthopleura atodai*, n. sp. collected from three localities. “—” indicates that an attribute was not measured or counted for that specimen.

Specimen	Diameter of pedal disc (in mm)	Height of column (in mm)	Number of acrorhagi	Number of pairs of mesenteries		Number of pairs of disjunctive mesenteries	Number of siphonophoryps
				Distal column	Proximal column		
holotype (CMNH-ZG 64)	12.0	10.7	32	28	28	2	2
paratype (CMNH-ZG 65)	12.4	9.7	23	28	28	2	2
paratype (NSMT-Co 1373)	10.0	14.4	—	34	34	2	2
paratype (KUMNH 1808)	11.7	11.9	—	34	34	2	2
paratype (CMNH-ZG 3693)	—	—	—	39	39	2	2
paratype (CMNH-ZG 209)	9.3	12.1	14	24	24	2	2
paratype (KUMNH 1808)	6.1	7.9	8	20	20	2	2
paratype (CMNH-ZG210)	9.5	9.8	15	28	28	2	2
paratype (CMNH-ZG44)	11.8	9.7	11	38	38	2	2
paratype (CMNH-ZG115)	7.8	11.9	9	34	34	2	2
paratype (CMNH-ZG 3696)	—	—	11	35	35	2	2

circular in outline, paler in color than column.

Oral disc and tentacles: Diameter of oral disc of slightly contracted, fixed anemone approximately equal to that of pedal disc and column. Center of oral disc somewhat elevated into oral cone that bears mouth; mouth elongate along directive axis. Each siphonoglyph marked with a bright cobalt-blue spot in life (Fig. 2A, B); color fades in preservation. Tentacles marginal, slender, shorter than oral disc diameter, number 40 to 62 (59 in holotype). Each tentacle translucent whitish to gray, with parallel longitudinal grayish streaks and/or white flecks on oral surface (Fig. 2A, B). Circular muscles of tentacles endodermal, longitudinal muscles of tentacles ectodermal (Fig. 3B). Numerous zooxanthellae in endoderm.

Marginal sphincter muscle: Endodermal, circumscribed-pinnate to circumscribed-diffuse, with highly branched mesogleal processes (Fig. 4B, C).

Mesenteries and internal anatomy: Actinopharynx whitish, half to two-thirds length of column, with two siphonoglyphs each attached to a pair of directive mesenteries. Distinct marginal stomata; oral stomata not seen. Mesenteries in 24–39 pairs, arranged hexamerously in three to four cycles, same number proximally and distally (Table 1). Mesentery arrangement irregular in specimens that have regeneration scars. All older mesenteries, including directives, fertile; all specimens hermaphroditic, with gametes of both sexes on same mesenteries or not (Fig. 3C). Zooxanthellae more numerous in endoderm of column than in endoderm of mesenteries. Each specimen may contain as many as 22 brooded young, early embryos through young adults with two cycles of mesenteries and tentacles (Fig. 3D–F); brooded young possess zooxanthellae.

Mesenterial retractor muscles strong, diffuse to restricted (Fig. 4A). Parietobasilar muscles well developed, extend half to entire distance between column wall and retractor muscle, with small free pennon distally (Fig. 4A). Basilar muscles distinct

(Fig. 3A). Cnidom: Spirocysts, basitrichs, holotrichs, heterotrichs, microbasic *p*-mastigophores, microbasic *p*-amastigophores (Fig. 5). Sizes and distribution of cnidae given in Table 2.

Distribution and habitat.—Known from the middle to northern Pacific coasts of Honshu, Japan (Fig. 1). Found in high intertidal, attached to *Mytilus* or in crevices of rock. Typically forms dense populations.

Etymology.—The species is named after Dr. K. Atoda, who first identified this as a new species.

Anthopleura hermaphroditica

(Carlgren, 1899)

Figs. 2, 5, 6

Bunodes hermaphroditicus Carlgren, 1899: 23.

Anthopleura hermaphroditica Carlgren, 1899.—Carlgren 1927: 32.—England 1987: 245.

Anthopleura hermafroditica Carlgr. Carlgren 1949: 54.—1959: 22.

non *Cribrina hermaphroditica* Carlgren, 1899.—McMurrich, 1904: 287.—Dawson, 1992: 38.

Material examined.—SMNH 1177 (syntype), SMNH 40829, 40830; ZSM (unnumbered)

Description.—Column and pedal disc: Freshly collected specimens olive green to rosy pink, proximal verrucae paler (Fig. 2D). In living, expanded specimens, column width 15–20 mm, height 17–25 mm. In contraction, column dome-like, width 4–10 mm, height 3–12.5 mm. Adhesive, endocoelic verrucae (Fig. 6A) in regular vertical rows from margin to limbus; number of rows 23–42. Verrucae larger and more prominent distally than proximally; maximum diameter of distal verrucae 0.5 mm in preserved specimens. In life, verrucae hold small stones and pieces of shells. Margin denticulate, with endocoelic conical projections that bear 1–3 verrucae on the outer surface; projection may bear a swollen acrorrhagus on the inner surface. Acrorrhagi

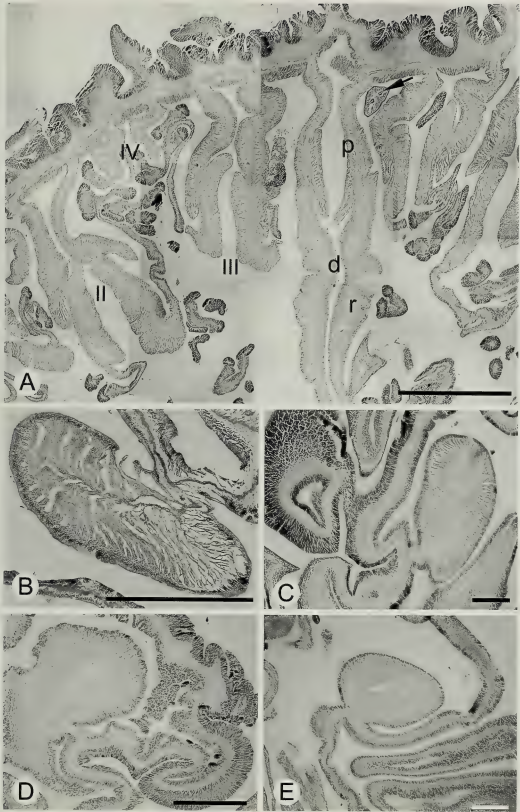


Fig. 3. *Anthopleura atodai*, new species (A, B, holotype CMNH-ZG 64; C, paratype CMNH-ZG NSMT-Co 1373; D, paratype CMNH-ZG 3692; E, paratype CMNH-ZG 3695): A, cross section of proximal column showing directive mesenteries flanked by those of the second (II), third (III) and fourth (IV) cycles; B-E, cross sections through circumscribed marginal sphincter. Scale Bars: A = 1 mm; B-E = 200 μ m. Abbreviations.—d, directive mesentery; p, parietobasilar muscle; r, retractor muscle. Arrow indicating brooded young.

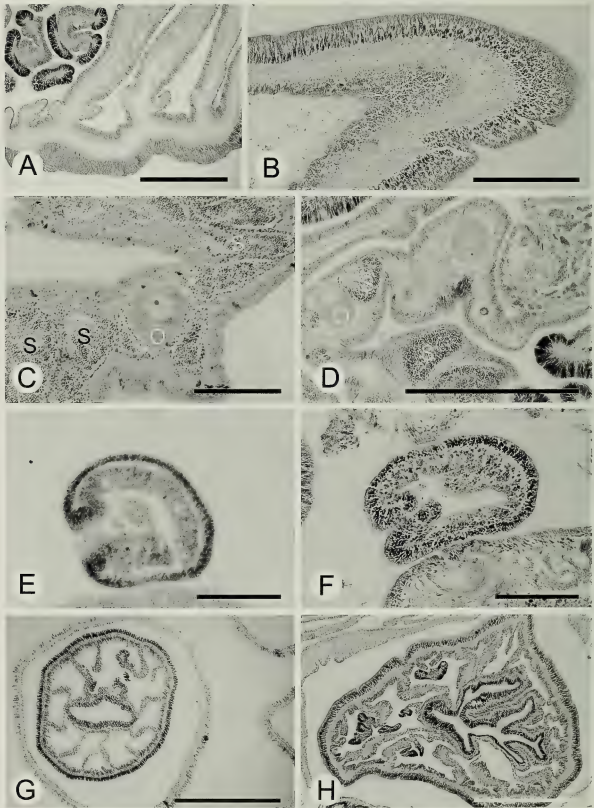


Fig. 4. *Anthopleura atodai*, new species (A, E, paratype CMNH-ZG 3692; B-C, holotype CMNH-ZG 64; D, paratype CMNH-ZG 3969; G, paratype CMNH-ZG 3696; H, paratype CMNH-ZG 209): A, longitudinal section through pedal disc showing basilar muscles; B, longitudinal section through a tentacle; C-D, cross sections through a mesentery showing both spermatocysts and oocytes; E-H, internally brooded young in the enteron (E, F, H), and tentacles (G). Scale Bars: A, C, D = 200 μ m; B, G, H = 500 μ m; E, F = 100 μ m (E-F Abbreviations.—o, oocyte; s, spermatocysts).

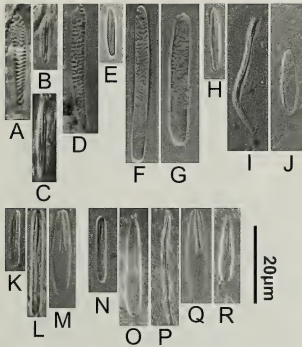


Fig. 5. Cnidae of *Anthopleura atodai*, new species (paratype CMNH-ZG65); see Table 2 for size ranges. The cnidae of *A. hermaphroditica* are identical in morphology and in distribution in the body, but differ in size; see Table 3 for sizes. A-C from tentacles, D-G from acrorhagus, H-J from column, K-M from actinopharynx, N-R from filaments. A, spirocyst; B, basitrich-1; C, basitrich-2; D, spirocyst; E, basitrichs; F, Holotrich; G, Holotrich; H, basitrich-1; I, S-basitrich; J, heterotrich; K, basitrich-1; L, basitrich-2; M, microbasic *p*-mastigophore; N, basitrich-1; O, basitrich-2; P, S-basitrich; Q, microbasic *p*-mastigophore; R, microbasic *p*-mastigophore. Scale Bar = 20 μ m.

endocoelic, opaque, tan to white, approximately 0.5 mm tall. Fosse deep. Pedal disc adherent, roughly circular in outline, paler in color than distal column.

Oral disc and tentacles: Oral disc diameter of expanded individuals slightly greater than pedal disc diameter. center of disc elevated into an oral cone that bears mouth; mouth elongate along directive axis, pale gray to rosy pink in life. Oral disc with opaque marks; marks grouped into six wedge-shaped zones or forming a stellate pattern of concentric, lighter and darker stripes (Fig. 2D, E); pattern fades in preservation. Tentacles slender, marginal, conical, shorter than oral disc diameter: approximately 4 mm long in an expanded preserved individual; innermost tentacles

slightly longer than outermost tentacles. Tentacles number 34–80, in three to five cycles. In life, tentacles translucent, typically with opaque white base and cross-bars on oral surface (Fig. 2D, E). Circular muscles of tentacles endodermal, longitudinal muscles ectodermal. Zooxanthellae in endoderm.

Marginal sphincter muscle: Endodermal, circumscribed-pinnate, pedunculate, asymmetrical, with closely spaced, highly branched mesogleal processes (Fig. 6C).

Mesenteries and internal anatomy: Actinopharynx one-half to two-thirds length of column, with two aborally prolonged siphonoglyphs each attached to a pair of directive mesenteries. Marginal stoma slightly larger than oral stoma. Mesenteries in 24–48 pairs, arranged hexamerously into three to five cycles, same number proximally and distally. Mesenteries of first three cycles typically perfect, those of fourth cycle imperfect. All perfect mesenteries, including directives, fertile, each typically bears both male and female gametes (Fig. 6D). Mesenteries of specimens that contain many brooded young typically lack gametic tissue. Zooxanthellae more numerous in endoderm of column than in that of mesenteries. A specimen may contain as many as nine brooded young; brooded young up to 2 mm long, with an oral disc diameter of 1 mm, and as many as 20 tentacles. Largest brooded young zooxanthellate, with small endocoelic verrucae and marginal projections.

Mesenterial retractor muscles diffuse-restricted; retractor typically abuts parietal muscle pennon (Fig. 6E). Parietobasilar muscles strong, each with a broad pennon and many short, thick, lateral processes. Parietal muscle may span as much as half the distance between the column and the free edge of the mesentery. Basilar muscles strong (Fig. 6B).

Cnidom: Spirocysts, basitrichs, heterotrichs, holotrichs, microbasic *p*-amastigophores, microbasic *p*-mastigophores. Sizes

Table 2.—Cnidae of *Anthopleura atotada*. Letter refer to Fig. 5. Sizes are given as ranges of length and width; measurements of exceptionally large or small capsules are in parentheses. "N" is the number of specimens examined containing that type of cnidae, "n" is the number of capsules measured, including data from holotype. Data for holotype (CMNH-ZG64) are given in separate column.

Location	Type of cnida	N	n	Size (μm)	Holotype (CMNH-ZG64) Range (Mean/SD)
Tentacle	Spirocyst (A)	4/4	99	15.0–29.8 \times 1.8–4.1	22.0–28.5 (25.2/1.63) \times 2.5–4.1 (3.0/0.32), n = 20
	Basitrich-1 (B)	4/4	18	9.5–13.2 \times 1.5–2.3	10.0–13.2 (11.4/11.7) \times 2.0–2.1 (2.0/0.05), n = 5
	Basitrich-2 (C)	4/4	118	15.2–23.0 \times 1.9–2.8	18.2–23.0 (25.9/1.23) \times 1.9–2.5 (2.1/0.14), n = 21
Acrothagi	Spirocyst (D)	4/4	66	14.8–33.9 \times 2.0–3.8	20.0–33.3 (25.9/3.48) \times 2.0–3.0 (2.4/0.42), n = 10
	Basitrich (E)	4/4	29	10.8–20.6 \times 1.6–2.3	15.2–16.0 (15.6/0.57) \times 2.0–2.3 (2.2/0.21), n = 2
	Holotrich (F, G)	4/4	266	20.3–48.2 \times 2.1–5.8	30.0–42.0 (36.9/3.12) \times 3.0–5.0 (3.9/0.50), n = 42
Distal column	Basitrich (H)	3/3	84	12.1–17.8 \times 1.7–2.6	13.0–16.7 (14.6/0.87) \times 2.0–2.2 (2.0/0.06), n = 15
	Basitrich-1 (H)	4/4	121	9.0–18.8 \times 1.3–2.6	10.5–16.3 (14.3/1.65) \times 1.8–2.5 (2.0/0.16), n = 20
Proximal column	S-basitrich (I)	4/4	19	21.0–60.9 \times 0.9–2.2	21.0–26.0 (23.5/3.53) \times 1.0, n = 3
	Heterotrich (J)	4/4	71	14.5–19.8 \times 2.8–4.1	14.5–18.0 (16.5/1.08) \times 3.9–3.9 (3.5/0.33), n = 10
Pharynx	Basitrich-1 (K)	4/4	36	11.7–21.3 \times 1.6–2.2	18.0–21.3 (15.3/1.03) \times 1.8–2.1 (2.0/0.8), n = 10
	Basitrich-2 (L)	4/4	103	22.0–28.2 \times 1.9–3.2	22.0–28.2 (24.9/0.48) \times 2.0–2.8 (2.3/0.27), n = 20
Filament	Microbasic <i>p</i> -amastigophore (M)	4/4	110	15.2–26.5 \times 3.2–5.6	18.0–21.3 (19.8/1.03) \times 4.0–5.2 (4.6/0.40), n = 20
	Basitrich-1 (N)	4/4	59	11.0–20.1 \times 1.8–2.6	14.0–17.0 (15.3/0.46) \times 1.8–2.1 (2.0/0.09), n = 15
	Basitrich-2 (N)	4/4	110	21.0–28.4 \times 2.9–4.6	21.5–25.5 (24.2/11.9) \times 3.2–4.0 (3.6/0.27), n = 20
	S-basitrich (S)	4/4	60	24.2–36.7 \times 0.9–1.7	28.0–35.5 (31.5/2.35) \times 0.9–1.2 (1.0/0.07), n = 20
	Microbasic <i>p</i> -amastigophore (Q)	4/4	118	17.3–25.0 \times 3.9–5.5	20.0–23.0 (21.5/0.99) \times 3.9–5.0 (4.4/0.36), n = 20
Microbasic <i>p</i> -mastigophore (R)	4/4	74	12.0–22.8 \times 2.3–4.9	13.5–18.5 (16.5/1.66) \times 2.8–3.2 (2.9/0.15), n = 10	

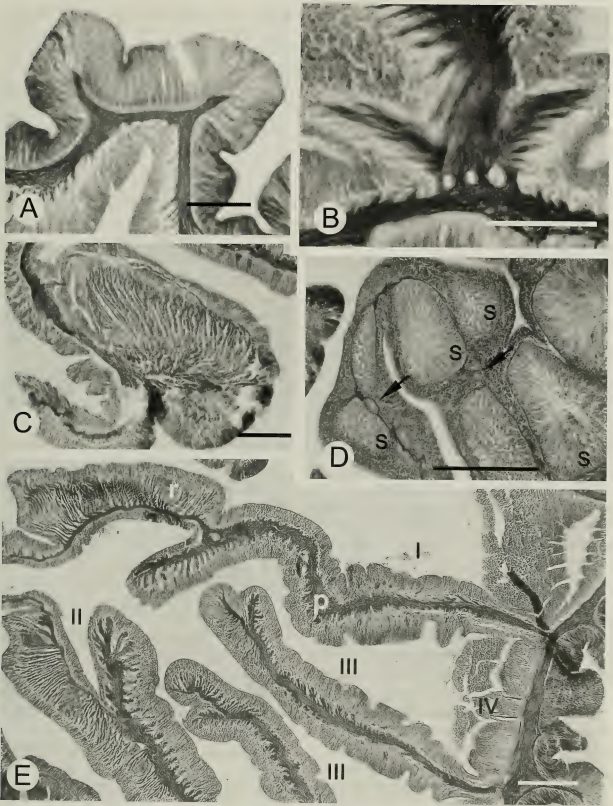


Fig. 6. Internal anatomy and histology of *Anthopleura hermaphroditica*. A, longitudinal section through a verruca; B, longitudinal section through pedal disc showing basilar muscles; C, cross section through sphincter muscle; D, cross section through a mesentery showing both spermatocysts and oocytes; E, cross section through proximal to actinopharynx showing mesenteries of first (I), second (II), third (III), and fourth (IV) cycles. Scale Bars: A = 150 μ m; B, C = 100 μ m; D = 200 μ m; E = 600 μ m. Abbreviations.—p, parietobasilar muscle; r, retractor muscle; s, spermatocyst. Arrow indicating oocyte.

and distribution of cnidae given in Table 3; cnidae illustrated in Fig. 5.

Distribution and habitat.—Known only from high intertidal zone of Chile.

Discussion

Differential diagnosis.—*Anthopleura atodai* and *A. hermaphroditica* belong to the genus *Anthopleura* by virtue of possessing verrucae, acrorhagi, and columnar heterotrichs. The hermaphroditism and brooding habit of *A. atodai* distinguishes it from other species of *Anthopleura* from waters around Japan, viz. *A. mcmurrici* Wasilief, 1908; *A. pacifica* Uchida, 1938; *A. fuscoviridis* Carlgren, 1949; *A. asiatica* Uchida & Muramatsu, 1958; *A. kurogane* Uchida & Muramatsu, 1958; *A. uchidai* England, 1992, and from most other nominal species of *Anthopleura*. It is distinguished from *A. aureoradiata* by the character of verrucae at the lower column and the coloration of the column: in *A. aureoradiata*, the verrucae diminish in size proximally (Parry 1951), and "near the bottom of the column these become mere markings" (Stuckey 1909a: 369); in *A. atodai*, the verrucae increase in size proximally. In *A. aureoradiata*, the coloration of the column differs distally and proximally (Stuckey 1909a, Parry 1951), whereas in *A. atodai*, the coloration of the column is uniform. *Anthopleura atodai* is distinguished from *A. handi* in its hermaphroditism, possession of zooxanthellae, and circumscribed marginal sphincter muscle.

Anthopleura atodai and *A. hermaphroditica* are both hermaphroditic, and brood young internally. However, they are distinguished by number of tentacles, coloration, size of cnidae, and geographical distribution. The maximum number of the tentacles observed in members of *A. atodai* is 62, whereas Carlgren (1899) reported a maximum of 90 in specimens of *A. hermaphroditica*. The column of living specimens of *A. atodai* is bluish-green or brown; in specimens of *A. hermaphroditica*, the column is

Table 3.—Cnidae of *Anthopleura hermaphroditica*. Letters refer to Fig. 5. Sizes are given as a length by width range, in μm ; measurements of exceptionally large or small capsules in parentheses. "N" is the number of specimens examined containing that type of cnidae, "n" is the number of capsules measured. The size range of cnidae for *A. handi*, combined from Dunn (1974) and England (1987) is given for comparison.

Location	Type of cnidae	N	n	Size (μm)	<i>A. handi</i>	
					N	n
Tentacle	Spirocyst (A)	6/6	57	15.2–23.9 × 1.8–3.5	11.3–24.3 × 1.4–3.7	
	Basitrich-2 (C)	6/6	98	(13.0) 15.0–23.7 × 1.6–3.2	14.1–24.7 × 1.8–3.6	
	Holotrich (F)	5/5	49	32.6–45.8 × 3.0–4.3	29.5–48.2 × 2.6–4.0	
Acrorhagi	Holotrich (G)	5/5	67	31.3–44.8 × 4.0–7.1	38.9–49.5 × 3.6–4.8	
	Basitrich-1 (H)	5/5	100	9.0–19.7 × 1.0–3.0 (3.8)	9.4–20.7 × 1.8–3.1	
Distal column	Basitrich-1 (H)	5/5	100	(10.0) 12.8–22.0 × 1.5–3.0	9.4–20.7 × 1.8–3.1	
	Proximal column	5/5	81	16.7–24.0 × (2.2) 3.0–4.6	14.2–28.8 (34.2) × 2.7–4.1 (5.7)	
Pharynx	Heterotrich (J)	5/5	28	12.2–17.9 × 1.3–2.7	11.8–17.7 × 1.8	
	Basitrich-1 (K)	4/5	81	21.6–27.3 × 2.1–2.8 (3.5)	15.3–24.8 × 2.4–3.0	
Filament	Basitrich-2 (L)	5/5	52	(15.7) 17.1–23.0 × (3.3) 3.7–5.3	16.5–22.7 (24.7) × 3.3–6.2	
	Microbasal <i>p</i> -mastigophore (M)	5/5	50	10.4–21.8 × 1.5–3.2	8.2–20.0 × 1.8–3.2	
Filament	Basitrich-1 (N)	5/5	95	23.7–30.1 × (3.3) 3.4–4.9 (5.4)	23.6 × 37.1 (39.1) × 3.2–5.4	
	Basitrich-2 (O)	5/5	54	19.7–29.5 × 1.3–2.0		
	S-basitrich (S)	4/5	11	16.1–27.3 × 2.4–5.6 (5.9)		
	Microbasal <i>p</i> -amastigophore (Q)	5/5	59	14.8–22.8 × 2.3–3.7		
	Microbasal <i>p</i> -mastigophore (R)	3/3	20		14.0–21.2 × 3.0–5.8	
					10.6–17.7 × 2.4–3.0	

Table 4.—Summary of differences in size and distribution of cnidae between *Anthopleura atodai* and *A. hermaphroditica*.

Cnidae type and location	Difference
Tentacle basitrichs	One size class in <i>A. hermaphroditica</i> ; two distinct classes in <i>A. atodai</i>
Acorrhagus holotrichs	Narrower in <i>A. atodai</i>
Proximal column heterotrichs	Shorter in <i>A. atodai</i>
Proximal column basitrichs	One size class in <i>A. hermaphroditica</i> ; two distinct classes in <i>A. atodai</i>
Filament basitrich-2	Shorter in <i>A. atodai</i>

gray or pink. The nematocysts of the tentacles, acrorhagi, column, and filaments further distinguish the two (Table 4).

Taxonomy of Anthopleura hermaphroditica.—The taxonomy of *Anthopleura hermaphroditica* has been confused because of a series of misidentifications and because of a proposed synonymy between *A. hermaphroditica* and *A. handi*. In the original description of the species, as *Bunodes hermaphroditicus*, Carlgren (1899) mentioned two notable features: hermaphroditism and acrorhagi. McMurrich (1904) found specimens of a hermaphroditic actiniid from Chile that had pseudoacrorhagi, rather than true acrorhagi and identified these as *Cribrina hermaphroditica*, changing the generic assignment of Carlgren's species and contesting Carlgren's (1899) assertion that the species had acrorhagi. Carlgren (1927) transferred the species to *Anthopleura*, a genus characterized as having acrorhagi, but maintained that the species he had originally called *Bunodes hermaphroditica* and the specimens described by McMurrich (1904) as *C. hermaphroditica* were the same species. However, after examining additional material from Chile, Carlgren (1959) reversed this opinion, and erected a new species, *B. hermaphroditica*, which he attributed to McMurrich.

Carlgren's (1959) description constitutes a new combination for *C. hermaphroditica* McMurrich 1904, rather than an original description. According to the International Code of Zoological Nomenclature (ICZN 1999: Art. 11.6), the name *C. hermaphroditica* was made available by its subsequent use as valid (e.g., Clubb, 1908), and its au-

thorship dates from its publication by McMurrich (1904) as a synonym of *Bunodes hermaphroditica* (International Code of Zoological Nomenclature: Art. 50.7; ICZN 1999). Therefore, the specimens McMurrich examined constitute the type series for *C. hermaphroditica* McMurrich, 1904; the type specimens of *Bunodes hermaphroditicus* Carlgren, 1899 (SMNH 1177) belong to *Anthopleura* as they have true acrorhagi with holotrichous nematocysts.

The surviving material from the Lund University Chile Expedition includes two recognizable species: *A. hermaphroditica* (Carlgren, 1899) and *Bunodactis hermaphroditica* (McMurrich, 1904). There are many more specimens belonging to *Bunodactis hermaphroditica* than to *A. hermaphroditica*; the difference in number of specimens collected reflects their abundance in the field (V. Häussermann, pers. comm.). Specimens belonging to *Bunodactis hermaphroditica* lack holotrichous nematocysts in the distal column and in the proximal column; both of these features are diagnostic at the level of genus (e.g., England, 1987). Specimens of *Bunodactis hermaphroditica* have more prominent verrucae than specimens of *A. hermaphroditica*, especially proximally.

England (1987) suggested that *A. hermaphroditica* might be synonymous with *A. handi*. We disagree with this proposition of synonymy because *A. hermaphroditica* and *A. handi* differ in several important respects. Most importantly, members these two species differ in key life history features: members of *A. hermaphroditica* are hermaphroditic and zooanthellate, mem-

bers of *A. handi* are gonochoric and azoouxanthellate. Furthermore, the basitrichs in both the distal and proximal column are larger in members of *A. handi* than in members of *A. hermaphroditica*. Finally, there is a considerable disparity in the geographic range and habitat of the two species: *A. handi* is found in the tropical Indo-Pacific around Malaysia, Singapore, and New Guinea (Dunn 1978, 1982b; England 1987; Fautin 1988); *A. hermaphroditica* is restricted to cold waters of the western Pacific (Carlgren 1899, 1959).

Biology of Anthopleura atodai.—*Anthopleura atodai* clearly corresponds to Atoda's *Anthopleura* sp.: the two have identical distributions, life history, and coloration. All specimens examined, regardless of size, were simultaneously hermaphroditic. In actiniarians, hermaphroditism is unexpectedly rare (Shick 1991) in view of the "low density model" of Ghiselin (1969). Among hermaphrodites, simultaneous hermaphroditism is the most common mode; known exceptions include the protandrous hermaphrodite *Sicyopsis* (= *Kadosactis*) *commensalis* (Gravier, 1918) and the gynodioecious species *Epiactis prolifera* (Verrill, 1869) and *Cereus pedunculata* (Pennant, 1777) (see Bronsdon et al. 1993, Dunn 1975, Rossi 1971).

The reproductive biology of *A. atodai* remains ambiguous. Isomura et al (2003) were unable to find gametogenic tissue in any specimens that they identified as *Anthopleura* sp. sensu Atoda, although they regularly found brooded young. The mesenteries of some specimens bore spherical protuberances proximally that were interpreted to be early stages of the brooded young; from this they inferred that the brooded young were asexually produced (Isomura et al. 2003). None of our results refute an asexual origin for the brooded young. However, our finding of fertile specimens from the study site of Isomura et al. (2003), including those that contained both gametes and brooded young (e.g., Fig. 4A), indicates that the species is not exclusively

asexual, and lends support to the contention by Isomura et al. (2003) that the Mutsu Bay population is remarkable in lacking fertile individuals. In general, the gametes and the gametogenic region are small in *A. atodai*, making it possible that Isomura et al. (2003) overlooked them in the specimens they examined. The presence of gametes does not rule out an asexual origin for the brooded young; some species of *Actinia* have both gametes and asexually produced young in their enteron (Yanagi et al., 1999). Therefore, further investigation is necessary to definitively demonstrate the asexual origin of the brooded young and to clarify reproductive ecology of *A. atodai*.

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**New species and new combinations in *Rhysolepis*
(Heliantheae: Asteraceae)**

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Abstract.—A narrow circumscription of the genus *Viguiera* Kunth results in transfer of 58 species of Helianthinae with glabrous stamen filaments, exappendiculate style appendages, and a persistent pappus into *Rhysolepis* S.F.Blake. *Rhysolepis dillonorum* from Peru, *R. emaciata* from Bolivia, and *R. goyasensis*, *R. hatschbachii*, *R. laxicymosa*, *R. santacatarinensis*, and *R. subtruncata* from Brazil are new species. *Viguiera pazensis* and *V. procumbens* are placed in synonymy under *Rhysolepis helianthoides*, and *V. misionensis* is combined with *R. pilosa*.

The present study began with a project by the junior author to clarify the limits of two Andean species of *Viguiera* Kunth in H.B.K. and join in the description of a species from Brazil known to be undescribed. The project was undertaken with the knowledge that none of the species involved were truly congeneric with the type species of *Viguiera*, *V. helianthoides* Kunth in H.B.K. = *V. dentata* (Cav.) Spreng. The arrival of additional material from Gert Hatschbach of the Museo Botánico Municipal de Curitiba, led to review of other species problems and discovery of additional species needing description. In view of the number of species involved and because of the generic redelimitations of Schilling and Panero (2002), the decision has been made to abandon the long misapplied name *Viguiera* and use a more phylogenetically appropriate generic concept for the species in this study.

Viguiera traditionally has contained species related to *Helianthus* L., but differing by a more persistent pappus with squamellae. The most recent treatment of *Viguiera* in the broad sense was that of Blake (1918). Blake's treatment excluded some genera such as *Tithonia* Desf. with broadened, fistulose peduncles (La Duke 1982); *Syncre-*

tocarpus S. F. Blake (1916) with a glabrous strip just inside the lateral margins of its achenes that was misinterpreted as a wing; and *Rhysolepis* S. F. Blake (1917) with transverse corrugations on its paleae. The broad Blake concept of *Viguiera* included some elements now placed in *Hymenostephium* Benth. in Benth. & Hook.f., but excluded others (Schilling and Panero 2002). Some single species once placed in *Viguiera* have been moved to other genera, in example a Peruvian species named by Blake in 1918, *Viguiera acutifolia*, has been transferred to *Pappobolus* (Panero 1992) and a Mexican species included in *Viguiera* by Blake (1924) was subsequently transferred to *Stuessya* (Turner & Davies 1980).

In a brief review of members of the *Hymenostephium* group, Robinson (1977) retained the broad concept of *Viguiera* in spite of the realization that the type species of *Viguiera* was individually distinctive with pubescent anther filaments and a small apical appendage on the branches of the style. *Hymenostephium* was retained in *Viguiera* because it had an apical appendage on the style branches and was technically closer to the type of *Viguiera* than most other species placed in the latter genus. The

needed generic revisions of the concept of *Viguiera* were fully initiated by Schilling and Panero (2002); but the South American species and their relatives in Mexico with exappendiculate styles have not yet been treated.

The South American species are in need of transfer to some genus other than *Viguiera*. The problem has been that none of the synonyms given by Blake (1918) seems to be applicable. *Leighia* Cass. belongs to the group, but that name is a later homonym of *Leighia* Scop. As noted by Blake, the type of *Harpalium* Cass., *H. rigidum* (Desf.) Cass. (= *Helianthus rigidus* Desf.), is not a *Viguiera*. Other Blake synonyms, *Heliomeris* Nutt. and *Bahiopsis* Kellogg, are considered separate genera (Schilling & Panero 2002). The type of *Gymnolomia* Kunth in H.B.K., after some confusion, proved to belong to *Eleutheranthera* Poit. ex Bosc. (Robinson 1992). Thus, none of the synonyms from Blake (1918) can be used. A name is found, however, outside the synonymy of *Viguiera* as circumscribed by Blake in 1918. His genus *Rhysolepis*, in spite of its sometimes weakly transversely corrugated paleae, is not distinct from the group treated here, and so the name can be applied.

Rhysolepis S. F. Blake, Contr. Gray Herb. 52: 36 (1917).—Type: *Viguiera palmeri* A. Gray

Leighia Cass. in F. Cuvier, Dict. Sci. Nat. ed. 2. 25: 435 (1822).—Type: *Helianthus linearis* Cav. Not *Leighia* Scop. (1777). = *Ethulia* L.f.

Annual to perennial herbs or shrubs; often with tubers or with fusiform nodes on roots. Stems and leaves usually strigose, pilose, or hispid. Leaves alternate or opposite, sessile or petiolate, filiform to ovate, lanceolate, oblong, or broadly rounded; blade often trinervate with secondary veins near and subparallel to lower margin; margins entire to serrate. Inflorescences usually with 1–6 heads, sometimes heads over 50; peduncles usually elongate, 3–30 cm long, of-

ten stout, not enlarged and fistulose distally; involucre broadly campanulate; bracts in 2–5 series, gradate to subequal, oblong to ovate or lanceolate, at base usually with indurated ribs, at tips herbaceous, appressed or reflexed to acute; receptacle convex to conical; pales persistent, partially enclosing achenes, mostly ribbed and indurate, sometimes transversely corrugated, usually with blunt apex. Ray florets usually 8–24, sterile, sometimes lacking; corollas yellow, with yellow or orange resin ducts along veins. Disk florets usually 40–200, tightly packed, bisexual; corollas yellow or greenish-yellow, 5-lobed, with basal tube usually 0.5–1.0 mm long and narrow, usually scabrid on abruptly broadened base of throat and on backs of lobes, with yellow or orange resin ducts along 5 veins of throat; anther filaments without hairs or papillae; thecae blackish, shortly hastate at base; endothelial cells with nodes on transverse walls; apical appendage usually yellow, blackish in some annual species, ovate, concave abaxially often with cluster of glands in concavity; style with resin ducts outside of veins not restricted to branches; style branches spreading radially, with tuft of hairs or papillae at tip, without apical appendage, with stigmatic papillae covering whole inner surface. Achenes compressed, with or without setulae, without differentiated intramarginal bare strip; walls with phytomelanin interrupted by striations of pale cells; pappus mostly persistent, with pair of awns usually longer than squamellae on margins between awns, but awns sometimes not longer than squamellae. Chromosome numbers $n = 17, 34$.

Rhysolepis was described from Mexico and has previously been credited with only three Mexican species as recognized by Robinson (1972):

Rhysolepis kingii H. Rob., Phytologia 24: 210 (1972).

Rhysolepis morelensis (Greenm.) S. F. Blake, Contr. Gray Herb. 52: 36 (1917).

Viguiera morelensis Greenm., Proc. Amer. Acad. 40: 40 (1904).

Rhysolepis palmeri (A. Gray) S. F. Blake, Contr. Gray Herb. n.s. 52: 37 (1917).

Viguiera palmeri A. Gray in S. Watson, Proc. Amer. Acad. 22: 427 (1887).

The broadened concept of *Rhysolepis* recognized here includes the rather overlapping Blake (1918) sections and series, *Tenuifoliae* consisting of perennial herbs with linear leaves, solitary heads and involucre bracts 2-seriate and subequal; *Revolvatae* with perennial herbs or subshrubs of the Chilean and Argentine Andes with large solitary heads and involucre bracts 2-5-seriate, gradate and lanceolate; *Grandiflorae* with perennial herbs having one or few large, long-pedunculate heads and having few leaves with the lowest opposite and scale-like; *Aureae*, primarily Andean, including annuals to shrubby perennials with broad leaves and involucre bracts mostly 3-5-seriate, usually gradate, lanceolate, and with herbaceous tips not strongly differentiated; *Bracteatae*, mostly of Brazil and Paraguay, including herbaceous perennials similar to the *Aureae* but with involucre bract tips shortly and abruptly herbaceous and blunt; *Leighia*, mostly Mexican, but similar to the *Aureae* and *Bracteatae* with involucre bracts strongly gradate, oblong and usually with an abrupt herbaceous tip; *Trichophylla* consisting of slender virgate perennials with linear to filiform leaves, revolute leaf margins and involucre bracts lanceolate to linear-lanceolate; and subgenus *Verbalesia* containing perennial herbs with pappus awns equalled in length by and partially fused to the squamellae. The following new combinations agree, to a considerable extent, with species concepts of Blake (1918), although that work left questions about the real distinctions of many species. As a result, more recent synonymies are taken into account, and other synonymies are to be expected. Many poorly known species are omitted.

Rhysolepis anchusifolia (DC.) H. Rob. & A. J. Moore, comb. nov.

Leighia anchusaefolia DC., Prodr. 5: 580 (1836).

L. dissitifolia DC., Prodr. 5: 581 (1836).

L. immarginata DC., Prodr. 5: 581 (1836).

L. lomatoneura DC., Prodr. 5: 581 (1836).

L. stenophylla Hook. & Arn., J. Bot. 3: 313 (1841).

L. baldwiniana Nutt., Trans. Amer. Philos. Soc. ser. 2, 7:365 (1841).

Viguiera stenophylla (Hook. & Arn.) Griseb., Goett. Abh. 24: 193 (1879).

V. anchusaefolia (DC.) Baker in Mart., Fl. bras. 6(3): 222 (1884). Argentina, Brazil, Uruguay.

Rhysolepis arenaria (Baker) H. Rob. & A. J. Moore, comb. nov.

Viguiera arenaria Baker in Mart., Fl. bras. 6(3): 228 (1884). Brazil, north central São Paulo.

Rhysolepis aspilioides (Baker) H. Rob. & A. J. Moore, comb. nov.

Viguiera aspilioides Baker in Mart., Fl. bras. 6(3): 228 (1884). Brazil, Matto Grosso.

Rhysolepis atacamensis (Phil.) H. Rob. & A. J. Moore, comb. nov.

Viguiera atacamensis Phil., Anales Mus. Nac. Chile, Segunda Secc., Bot. 1891: 48 (1891). Chile.

Rhysolepis australis (S.F.Blake) H. Rob. & A. J. Moore, comb. nov.

Viguiera australis S. F. Blake, Contr. Gray Herb. n.s. 54: 148 (1918). Chile.

Rhysolepis bakeriana (S. F. Blake) H. Rob. & A. J. Moore, comb. nov.

Viguiera bakeriana S. F. Blake, Contr. Gray Herb. n.s. 54: 130 (1918). Brazil, Minas Gerais.

- Rhysolepis bishopii** (H. Rob.) H. Rob. & A. J. Moore, comb. nov.
- Viguiera bishopii* H. Rob., *Phytologia* 45: 458 (1980). Bolivia.
- Rhysolepis bracteata** (Gardn.) H. Rob. & A. J. Moore, comb. nov.
- Viguiera bracteata* Gardn., *London J. Bot.* 7: 404 (1848). Brazil. Distrito Federal, Goiás, Minas Gerais.
- Rhysolepis breviflosculosa** (S. F. Blake) H. Rob. & A. J. Moore, comb. nov.
- Viguiera breviflosculosa* S. F. Blake, *Contr. Gray Herb.* n.s. 54: 158 (1918). Uruguay.
- Rhysolepis brittonii** (Hochr.) H. Rob. & A. J. Moore, comb. nov.
- Viguiera brittonii* Hochr., *Bull. New York Bot. Gard.* 6: 294 (1910). Peru.
- Rhysolepis discolor** (Baker) H. Rob. & A. J. Moore, comb. nov.
- Viguiera discolor* Baker in *Mart., Fl. bras.* 6(3): 228 (1884). Brazil, Minas Gerais.
- Rhysolepis ellenbergii** (Cuatrec.) H. Rob. & A. J. Moore, comb. nov.
- Viguiera ellenbergii* Cuatrec., *Proc. Biol. Soc. Wash.* 77: 146 (1964).
- Peru. A second specimen from the type locality is as follows: Peru. Cuzco: Prov. Urubamba, ruinas de Machu Picchu, high above Río Urubamba, 80 km WNW of Cuzco, rock walls, rock piles, terraces & cliffs, Intyhuatana (Solar Observatory); 2500–2600 m, 27 May 1963, *Ugent 5376* (US).
- Rhysolepis fabrisii** (Saenz) H. Rob. & A. J. Moore, comb. nov.
- Viguiera fabrisii* Saenz, *Darwiniana* 22: 50 (1979). Argentina.
- Rhysolepis fusiformis** (S. F. Blake) H. Rob. & A. J. Moore, comb. nov.
- Viguiera fusiformis* S. F. Blake, *Contr. Gray Herb.* n.s. 54: 145 (1918). Bolivia.
- Rhysolepis gardneri** (Baker) H. Rob. & A. J. Moore, comb. nov.
- Viguiera gardneri* Baker in *Mart., Fl. bras.* 6(3): 224 (1884).
- Originally described from Brazil, Goiás. Two more recent collections matching the type photograph are: Brazil. Goiás, Pirenópolis (Morro da Caixa D'água); cerrado seco, arborizado, com pedras no solo, sujeito ao fogo periódico; planta com 80 cm, ramificada inflorescência terminais, flores roxas, 23 Apr 1976, *Heringer 15560* (UB, US); Município de Niquelândia, entrada no km 8 da Rodovia Niquelândia/Uruaçu; Fazenda Traíras. Morro. Relêvo ondulado; 14°29'19"S, 48°33'19"W. Cerrado com muitas pedras de cor branca; arbusto, ca. 70 cm de altura; flores com corola amarela e anteras alaranjadas. Nome comum: margarida; 13 Apr 1996; *Mendonça, Marquete, Fonseca & Oliveira 2453* (UB, US).
- Rhysolepis gilliesii** (Hook. & Arn.) H. Rob. & A. J. Moore, comb. nov.
- Leighia gilliesii* Hook. & Arn., *J. Bot. (Hooker)* 3: 313 (1841).
- Helianthus heteropappus* Gill. ex Hook. & Arn., *J. Bot. (Hooker)* 3: 314 (1841), nom. nud.
- Viguiera gilliesii* (Hook. & Arn.) Hieron., *Actas Acad. Nac. Ci. Cordoba* 4: 39 (1882).
- Flourensia hispida* Phil., *Anales Univ. Chile* 36: 186 (1870). Argentina, Chile.
- Rhysolepis grandiflora** (Gardn.) H. Rob. & A. J. Moore, comb. nov.
- Leighia grandiflora* Gardn. in *Field & Gardn., Sert. Pl.* t. 54–55 (1844).
- Viguiera grandiflora* (Gardn.) Gardn., *London J. Bot.* 7: 404 (1848).

Rhysolepis guaranitica (Chod.) H. Rob.
& A. J. Moore, comb. nov.

Viguiera guaranitica Chod., Bull. Herb. Boiss. ser. 2, 3: 724 (1903). Argentina, Brazil, Paraguay.

Rhysolepis helianthoides (L. Rich.) A. J. Moore & H. Rob., comb. nov.
Fig. 1

Sanvitalia helianthoides L. Rich. in Willd., Sp. Pl. 3: 2190 (1803).

Helianthus procumbens Pers., Syn. Pl. (Perseon) 2: 475 (1807).

Viguiera pazensis Rusby, Mem. Torrey Bot. Club 3(3): 59 (1893).

Viguiera pflanzii Perkins, Bot. Jahrb. Syst. 49: 226 (1913).

Viguiera punensis S. F. Blake, Bot. Jahrb. Syst. 54, Beibl. 119: 48 (1916). Argentina, Bolivia, Peru.

The present complex was maintained as two separate species by Blake (1918) based on longer, relatively narrower leaf shape and more prominent leaf venation in *V. pazensis*. Separation was maintained by Saenz as recently as 1979 based on larger, ovate-lanceolate rather than ovate to oblong leaves, multiple rather than single heads per stem, and smaller involucre in *V. pazensis*. We could not separate the species using these characters, nor pubescence type or shape of the involucre bracts. Tips of the involucre bracts were sometimes reflexed and thus looked different from bracts without reflexed tips, but the lengths and shapes were the same.

The broadened concept of *Rhysolepis helianthoides* is characterized by leaves tuberculate-pilose adaxially, pilose abaxially with hairs denser on veins; stems ribbed and villous; and involucre bracts oblanceolate, subequal, often recurved, and with an indurate base and herbaceous apex. In addition, the achenes tend to have rather readily deciduous awns and squamellae, a character reportedly shared with *R. lanceolata* (Blake 1918).

The concept of *Viguiera pazensis* in this study includes two isotypes, *Bang 44* (US). Some more southern material might prove distinct, and the name *Helianthus atacamensis* Phil. (not *Viguiera atacamensis* Phil.) is for the present omitted from the synonymy. For an additional specimen that was determined as *V. pazensis*, but is not this species, see *Rhysolepis dillonorum* A. J. Moore & H. Rob. below.

Rhysolepis hilairei (S. F. Blake) H. Rob.
& A. J. Moore, comb. nov.

Viguiera hilairei S. F. Blake, Contr. Gray Herb. 54: 153 (1918). Brazil, Minas Gerais.

Rhysolepis hypoleuca (S. F. Blake) H. Rob. & A. J. Moore, comb. nov.

Viguiera hypoleuca S. F. Blake, Contr. Gray Herb. n.s. 54: 165 (1918). Brazil, Matto Grosso.

Rhysolepis incana (Pers.) H. Rob. & A. J. Moore, comb. nov.

Helianthus incanus Pers., Syn. Pl. 2: 475 (1807).

Helianthus aureus Kunth in H.B.K., Nov. Gen. Sp., ed fol. 4: 176 (1818).

Harpalium aureum (Kunth) Cass., Dict. Sci. Nat. 25: 438 (1822).

Viguiera chimboensis Hieron., Bot. Jahrb. Syst. 29: 38 (1900).

Viguiera lehmannii Hieron., Bot. Jahrb. Syst. 29: 38 (1900).

Viguiera aurea (Kunth.) Hieron., Bot. Jahrb. Syst. 28: 608 (1901).

Viguiera incana (Pers.) S. F. Blake, Contr. U. S. Nat. Herb. 26: 252 (1930). Ecuador.

Rhysolepis kunthiana (Gardn.) H. Rob.
& A. J. Moore, comb. nov.

Viguiera kunthiana Gardn., London J. Bot. 7: 399 (1848). Brazil, Goiás.



Fig. 1. *Rhysalepis helianthoides* (L. Rich.) A. J. Moore & H. Rob., A. Habit. B. Head with ray florets removed and involucre bracts not recurved. C. Head showing ray florets. D. Receptacular pale. E. Ray corolla showing lack of style. F. Disk floret showing striated achene with pappus of awns and squamellae. G. Disk corolla in section, showing filaments and anthers with small glands on outer surfaces of anther appendages. H. Disk style showing branches with continuous stigmatic area on inner surfaces and apex with hairs but no appendage. Drawn mostly from *Bang 44* (US, isotype of *Viguiera pazensis* Rusby); C. from *Buchtien 8579* (US).

Rhysolepis lanceolata (Britton) H. Rob.
& A. J. Moore, comb. nov.

Viguiera lanceolata Britton, Bull. Torrey Bot. Club 19: 149 (1892).

V. mandonii Sch.Bip. ex Rusby, Mem. Torrey Bot. Club 3(3): 60 (1893).

Helianthus szyszyłowiczii Hieron., Bot. Jahrb. Syst. 36: 491 (1905). Bolivia, Peru.

Rhysolepis linearifolia (Chod.) H. Rob.
& A. J. Moore, comb. nov.

Viguiera linearifolia Chod., Bull. Herb. Boiss. ser. 2, 2: 392 (1902).

Viguiera trichophylla Dusén, Ark. Bot. 9(15): 30, f. 12 & t. 7. f. 4 (1910). Brazil, Goiás, Matto Grosso, Paraná; Paraguay.

Rhysolepis linearis (Cav.) H. Rob. & A. J. Moore, comb. nov.

Helianthus linearis Cav., Icon., 3: 9, t. 218 (1794)[1795].

Helianthus squarrosus Kunth in H.B.K., Nov. Gen. & Sp., ed. fol. 4: 174, t. 377 (1818).

Leighia elegans Cass., Dict. Sci. Nat. 25: 435 (1822).

Leighia linearis (Cav.) DC., Prodr. 5: 581 (1836).

Viguiera linearis (Cav.) Sch.Bip. ex Hemsl., Biol. Centr.-Amer., Bot. 2: 178 (1881). Mexico.

Rhysolepis macbridei (S. F. Blake) H. Rob. & A. J. Moore, comb. nov.

Viguiera macbridei S. F. Blake, J. Wash. Acad. Sci. 16: 218 (1926). Peru.

Rhysolepis macrocalyx (S. F. Blake) H. Rob. & A. J. Moore, comb. nov.

Viguiera macrocalyx S. F. Blake, Contr. Gray Herb. 54: 171 (1918). Brazil, Minas Gerais.

Rhysolepis macropoda (S. F. Blake) H. Rob. & A. J. Moore, comb. nov.

Viguiera macropoda S. F. Blake, Contr. Gray Herb. 54: 128 (1918). Brazil, Minas Gerais.

Rhysolepis macrorhiza (Baker) H. Rob. & A. J. Moore, comb. nov.

Viguiera macrorhiza Baker in Mart., Fl. bras. 6(3): 225 (1884). Paraguay.

Rhysolepis media (S. F. Blake) H. Rob. & A. J. Moore, comb. nov.

Viguiera media S. F. Blake, Contr. Gray Herb. 54: 138 (1918). Ecuador.

Rhysolepis mollis (Griseb.) H. Rob. & A. J. Moore, comb. nov.

Viguiera mollis Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 183 (1874).

Helianthus argentinus Saenz, Darwiniana 22: 64 (1979) Argentina.

We do not know why Saenz (1979) excluded the species from *Viguiera* in his treatment, creating the new name *Helianthus argentinus*. Panero (1992) was correct in returning the species to *Viguiera* as then delimited.

Rhysolepis nervosa (Gardn.) H. Rob. & A. J. Moore, comb. nov.

Viguiera nervosa Gardn., London J. Bot. 7: 403 (1848). Brazil, Goiás.

Rhysolepis nudibasilaris (S. F. Blake) H. Rob. & A. J. Moore, comb. nov.

Viguiera nudibasilaris S. F. Blake, Contr. Gray Herb. 54: 149 (1918). Brazil, Minas Gerais.

Rhysolepis nudicaulis (Baker) H. Rob. & A. J. Moore, comb. nov.

Viguiera nudicaulis Baker in Mart., Fl. bras. 6(3): 228 (1884). Uruguay.

Rhyssolepis oblongifolia (Gardn.) H. Rob. & A. J. Moore, comb. nov.

Viguiera oblongifolia Gardn., London J. Bot. 7: 402 (1848).

Rhyssolepis oblongifolia was described from Brazil, Goiás. Some more recent collections include: Brazil. Matto Grosso: Serra do Roncador, Mun. de Barra do Garças, 230 km along new road NNE of village of Xavantina, 6.0 km S of Córrego dos Porcos, 30 km due S of 12°51'S, 51°45'W. ca. 450 m, 26 Nov 1969, Eiten & Eiten 9547 (SP, US); 209 km NNE of Xavantina; 9 Dec 1969; Eiten & Eiten 9818 (SP, US); Minas Gerais. 56 km along road NE of Barroão, towards Porteirinha, 2400 ft.; 21 Jan 1981, King & Bishop 8585 (MO, US); Brasilândia de Minas, 1 Jun 2001, Soares 321 (BHCB, US); Maranhão, Balsas, approx. 25 km along road west from Balsas to fazenda of Sr. Damião; 7°40'S, 46°10'W; 4 Dec 1981; Jangoux et al. 1783 (US).

Rhyssolepis obtusifolia (Baker) H. Rob. & A. J. Moore, comb. nov.

Viguiera obtusifolia Baker in Mart., Fl. bras. 6(3): 226 (1884). Brazil, Goiás?

Rhyssolepis ovatifolia (DC.) H. Rob. & A. J. Moore, comb. nov.

Leighia ovatifolia DC., Prodr. 5: 583 (1836).

Viguiera ovatifolia (DC.) Baker in Mart., Fl. bras. 6(3): 226 (1884).

The type is from Brazil, São Paulo. Additional specimens seen from Paraná match the type photograph: Jaguariahyva, ad marginem silvulae, 19 Apr 1910; Dusén 9723 (US)(det. Dusén as *Viguiera robusta*). Jaguariahyva opp., in campo, 740 m.s.m., 5 May 1914, G. Jönsson 262a (US)(det. Malme as *V. robusta*).

Rhyssolepis peruviana (A. Gray) H. Rob. & A. J. Moore, comb. nov.

Viguiera peruviana A. Gray, Proc. Amer. Acad. Arts 5: 124 (1861–62).

Viguiera weberbaueri S. F. Blake, Bot. Jahrb. Syst. 54, Beibl. 119: 49 (1916). Peru.

Rhyssolepis pilicaulis (S. F. Blake) H. Rob. & A. J. Moore, comb. nov.

Viguiera pilicaulis S. F. Blake, Contr. Gray Herb. 54: 164 (1918).

Rhyssolepis pilicaulis was described from Paraguay. A recent collection has been seen from Brazil: Matto Grosso do Sul. Rod. BR-267, próximo do km 447, descida da chapada (Mun. Guia Lopes de Laguna, 9 Mar 2003, G. & H. Hatschbach & Barbosa 74393 (MBM, US). The Brazilian specimen is most like the Field Museum type photograph of the now destroyed, broad-leaved Berlin specimen. The inflorescence is characteristically rather profusely branched with short peduncles, and there are only 8 or 9 short, slender rays while Blake cited 10 to 11. The species has antrorse prurosity inside the disk corolla throat.

Rhyssolepis pilosa (Baker) H. Rob. & A. J. Moore, comb. nov.

Viguiera pilosa Baker in Mart., Fl. bras. 6(3): 223 (1884).

Viguiera malmei S. F. Blake, Contr. Gray Herb. 54: 151 (1918).

Viguiera misionensis Saenz, Darwiniana 22: 62 (1979).

Viguiera misionensis of northern Argentina shows no obvious differences from *R. pilosa* from southern Brazil in Paraná, Rio Grande do Sul, Santa Catarina.

Rhyssolepis pusilla (A. Gray) H. Rob. & A. J. Moore, comb. nov.

Tithonia pusilla A. Gray, Proc. Amer. Acad. Arts 5: 124 (1861–62).

Viguiera pusilla (A. Gray) S. F. Blake, Contr. Gray Herb. 54: 160 (1918). Peru.

Rhysolepis radula (Baker) H. Rob. & A. J. Moore, comb. nov.

Viguiera radula Baker in Mart., Fl. bras. 6(3): 223 (1884). Brazil, Minas Gerais.

Rhysolepis retroflexa (S. F. Blake) H. Rob. & A. J. Moore, comb. nov.

Viguiera retroflexa S. F. Blake, Contr. Gray Herb. 54: 146 (1918). Bolivia.

Rhysolepis revoluta (Meyen) H. Rob. & A. J. Moore, comb. nov.

Helianthus revolutus Meyen, Reise Erde 1: 311 (1834).

Helianthus lanceolatus Meyen, Reise Erde 1: 311 (1834), not *V. lanceolata* Britton
Flourensia corymbosa DC., Prodr. 5: 592 (1836).

Viguiera poeppigii A. Gray, Proc. Amer. Acad. Arts 19: 6 (1883).

Viguiera corymbosa (DC.) S. F. Blake, Proc. Amer. Acad. Arts 49: 349 (1913).

Viguiera revoluta (Meyen) S. F. Blake, Contr. Gray Herb. 54: 121 (1918). Argentina, Chile.

Rhysolepis robusta (Gardn.) H. Rob. & A. J. Moore, comb. nov.

Viguiera robusta Gardn., London J. Bot. 7: 403 (1848). Brazil, Goiás.

Rhysolepis rojasii (S. F. Blake) H. Rob. & A. J. Moore, comb. nov.

Viguiera rojasii S. F. Blake, Contr. Gray Herb. 54: 179 (1918). Paraguay.

Rhysolepis salicifolia (Hassl.) H. Rob. & A. J. Moore, comb. nov.

Viguiera salicifolia Hassl., Repert. Spec. Nov. Regni Veg. 14: 274 (1916).

Viguiera villaricensis S. F. Blake, Contr. Gray Herb. 54: 152 (1918). Argentina, Paraguay.

Rhysolepis simsioides (S. F. Blake) H. Rob. & A. J. Moore, comb. nov.

Viguiera simsioides S. F. Blake, Bot. Jahrb. Syst. 54. Beibl. 119: 48 (1916). Peru.

Rhysolepis sodiroi (Hieron.) H. Rob. & A. J. Moore, comb. nov.

Helianthus sodiroi Hieron., Bot. Jahrb. Syst. 29: 41 (1900).

Viguiera sodiroi (Hieron.) S. F. Blake, Contr. Gray Herb. 54: 139 (1918). Ecuador.

Rhysolepis speciosa (Hassl.) H. Rob. & A. J. Moore, comb. nov.

Viguiera speciosa Hassl., Repert. Spec. Nov. Regni Veg. 14: 272 (1916).

Viguiera simulans S. F. Blake, Contr. Gray Herb. 54: 127 (1918).

Rhysolepis speciosa has been known from Paraguay; Brazil, Matto Grosso. It also occurs in the Distrito Federal with specimens previously identified as *Viguiera squalida* as follows: Peunsula Norte, 1000 m, s. d., Valério de Carvalho dos grupos 11 (UB, US); Reserva Ecológica do IBGE, 7 Nov 1977, Heringer et al. 249 (IBGE, US); Area do Cristo Redentor: 15°57'07"S, 47°53'37"W, 19 Oct 1988, Azevedo 180 (IBGE, US); Reserva Ecológica do IBGE, Campo Limpo; 21 Aug 1990, Silva et al. 1009 (IBGE, US); Cristo Redentor, 10 Oct 1990, Brochado 70 (IBGE, US); Tampão das parcelas de campo sujo do Projeto Fogo—IBGE, 9 Dec 1991, Landim de Souza 83 (IBGE, US); Ecológica do IBGE, 15°56'41"S, 47°53'07"W, 7 Nov 1994, Aparecida da Silva 2457 (IBGE, US).

Rhysolepis squalida (S. Moore) H. Rob. & A. J. Moore, comb. nov.

Viguiera squalida S. Moore, J. Bot. 42: 37 (1904). Brazil, Goiás, Matto Grosso, Matto Grosso do Sul.

Rhyssolepis subdentata (S. F. Blake) H. Rob. & A. J. Moore, comb. nov.

Viguiera subdentata S. F. Blake, Contr. Gray Herb. 54: 131 (1918). Brazil, Minas Gerais.

Rhyssolepis tenuifolia (Gardn.) H. Rob. & A. J. Moore, comb. nov.

Viguiera tenuifolia Gardn., London J. Bot. 7: 400 (1848). Brazil, Minas Gerais.

Rhyssolepis tuberculata (S. F. Blake) H. Rob. & A. J. Moore, comb. nov.

Viguiera tuberculata S. F. Blake, Contr. Gray Herb. 54: 151 (1918). Brazil, Minas Gerais.

Rhyssolepis tuberosa (Griseb.) H. Rob. & A. J. Moore, comb. nov.

Viguiera tuberosa Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 192 (1879). Argentina; Brazil, Rio Grande do Sul, Uruguay.

Rhyssolepis tucumanensis (Hook. & Arn.) H. Rob. & A. J. Moore, comb. nov.

Leighia tucumanensis Hook. & Arn., J. Bot. (Hooker) 3: 314 (1841)

Viguiera stenophylla (Hook. & Arn.) Griseb. var. *discoidea* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 193 (1879).

Viguiera discoidea (Griseb.) S. F. Blake, Contr. Gray Herb. 54: 157 (1918).

Viguiera oligodonta S. F. Blake, Contr. Gray Herb. 54: 146 (1918). Argentina.

Rhyssolepis weddellii (Sch.Bip. ex S. F. Blake) H. Rob. & A. J. Moore, comb. nov.

Viguiera weddellii Sch.Bip. ex S. F. Blake, Contr. Gray Herb. 54: 126 (1918). Bolivia; Brazil, Goiás-Matto Grosso.

In addition to the species listed above we include the following seven previously un-

described species. Of the new species, the ones from Bolivia and Santa Catarina, Brazil, seem to fit Blake's series *Aureae*; whereas the others fit his series *Bracteatae*. One character seen in the new species seems to partially reinforce the distinction. All of the new members of the *Bracteatae* except *R. subtruncata* have bands of prorulose cells on the inner surface of the disk corolla throats, midway between the veins and often also along the veins. Prorulosity is the condition where elongate cells have the upper ends projecting as papillae. The two new species in the *Aureae* lack such prorulose bands. The specimens were described partially from dissections of florets mounted in Hoyer's solution (Anderson 1954).

Rhyssolepis dillonorum A. J. Moore & H. Rob., sp. nov.
Fig. 2

Type: Peru. Arequipa: Prov. Caraveli, Lomas of Atiquipa, ca. 10.5 km N of turn-off to Atiquipa, 584 km S of Lima; ca. 150–200 m, 1 Nov 1983, *M. O. Dillon* & *D. Dillon* 3775 (holotype US; isotype F).

E speciebus omniibus in habitis fruticosis et in indumento appresse strigulosis et in bracteis involucri plerumque obtusis distincta.

Shrub to 1 m high, moderately and alternately branched at 30–45° angles; roots not seen; stem tan to dark brown, closely appressed-strigulose, glabrescent with age. Leaves usually opposite in middle of branches, alternate at base of branches and distally, not decrescent except near heads; petioles none to 0.2 cm long, bases sometimes continuous across node; blades ovate to oblong-ovate, 1.5–4.2 cm long, 0.7–2.2 cm wide, base broadly acute to rounded, margins entire, apex acute, both surfaces densely appressed-strigulose, abaxially with scattered glandular dots, triplinervate from near base, secondary veins reaching distal 1/3. Heads borne singly on long branches or with 2 or 3 heads on short branches; brac-



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DEPTO AREQUIPA PROV CARAVELI

ASTERACEAE

Rhysolepis dillonorum A. J. Moore & H. Rob.
Holotype

Viguiera pozensis Rusby

UNITED STATES

3026289

NATIONAL HERBARIUM



Lomas of Atiquipa, ca. 10.5 km N of turn-off to
Atiquipa, RM 594 S of Lima, ca. 150-200 m.

Erect shrub to 1 m.; ray & disc florets yellow.

1 Nov 1983

M. G. Dillon & D. Dillon 3775

Plant collected under the sponsorship of the National Geographic Society [Sheet No. 3786-01]
Digitized by Field Museum of Natural History

Fig. 2. *Rhysolepis dillonorum* A. J. Moore & H. Rob., holotype, Dillon & Dillon 3775 (US).

teoles decrescent, oblong, 1.1–0.4 cm long; peduncles 3.5–17 cm long, 0.5–5.0 cm from last bracteole, appressed-strigulose. Involucre 0.4–0.6 cm high, 1.2–1.5 cm diam.; bracts 2–3-seriate, obovate, gradate, 4–8 mm long, 2–4 mm wide, 3–5-nerved, tips obtuse to short-acuminate, indurate in proximal $\frac{1}{2}$ to $\frac{3}{4}$, distally herbaceous, abaxially and adaxially appressed-strigulose especially on tips; paleae obovate, indurate, ca. 7.5 mm long, ca. 1.0–1.5 mm wide, scabridulous on tip, apex short-acute. Ray florets 13–14; corollas yellow, tube ca. 1.2 mm long, sparsely scabridulous; limb oblong-elliptical, 1.5 cm long, 0.5–0.8 cm wide, sparsely scabridulous abaxially, apex 3-lobed. Disk florets at least 50; corolla yellow, ca. 5 mm long, tube 1 mm long, scabridulous; throat 3 mm long, slightly campanulate at base, scabridulous proximally, glabrous distally, with vertical bands of antrorsely prulose cells inside, lobes 1 mm long, glabrous outside, papillose inside especially near margins; anther thecae 2 mm long; appendages yellow, 0.6–0.75 mm long, ca. 0.45 mm wide. Ray achenes ca. 3.5 mm long, ca. 0.7 mm wide, sericeous on margins, with pappus crown ca. 0.1 mm high. Disk achenes 3.5 mm long, 0.9 mm wide, sericeous with setulae over whole surface; pappus awns 2.0–2.2 mm long, fimbriate-margined, squamellae ca. 4, 1.0–1.2 mm long, ca. 1 mm wide, margins fimbriate. Pollen 30–33 μ m in diam. in Hoyer's solution.

Rhysolepis dillonorum is presently known only from the type collection. The specimen was earlier identified as *Viguiera pazensis*; it was seen as distinct in a recent review of the latter by the senior author of the new species. The low elevation at 150–200 m near the coast, the shrubby habit, the appressed minute hairs on the stems, leaves, and involucre bracts, and the blunt tips of the involucre bracts are all distinctive. The supposed Andean relatives are found at 2000 m or above, are more herbaceous, have longer, mostly spreading hairs, and

have more lanceolate, subequal involucre bracts.

The blunt involucre bracts and the vertical bands of prulose cells inside the disk corolla throat seem to relate the new species to members of Blake's section *Bracteatae* that are most common in Brazil and distinguish the species from the section *Aureae* to which *V. pazensis* (= *R. helianthoides*) belongs. Opposite leaves are common on the specimen, but the branching is alternate, and the basal nodes of the branches have alternate leaves.

Rhysolepis emaciata H. Rob. & A. J.

Moore, sp. nov.

Fig. 3

Type: Bolivia. Cochabamba: 10 NE; 2465 m; Campero, pajonal de *Elyonurus tripsacoides*, 2 May 1999, Antezana 1276 (holotype US, isotype MO).

E speciebus aliis boliviensis in seriebus *Aureis* in ramis nullis in foliis dense spiralter insertis et in bracteis involucri ca. triseriatis gradatis differt.

Slender subshrub or shrub 0.4–0.6 m tall, apparently unbranched above base; roots not seen; stems reddish-brown, densely hispid with long hairs. Leaves rather densely spirally inserted, sessile; laminae herbaceous, lanceolate, 1.5–2.8 cm long, 0.5–0.8 cm wide, base rounded, margins often with single blunt tooth near basal $\frac{1}{4}$, subtire to remotely undulate distally, apex acute, mucronulate, adaxial surface densely scabrous with slender hairs, abaxially densely villous with white hairs and densely gland-dotted; triplinerved from near base, reaching to $\frac{1}{2}$ leaf length. Inflorescence example seen with single terminal head, with leaves on 7 cm below head becoming smaller, uppermost bractlike; peduncle 2.5 cm long from last foliiform bract, densely villous. Head with involucre 1 cm high, 2 cm wide; bracts ca. 3-seriate, oblong-lanceolate, gradate, 6–10 mm long, 1.5–2.0 mm wide, appearing herbaceous throughout, villous with white hairs abaxially, without distinct cilia on



Fig. 3. *Rhysalepis emaciata* H. Rob. & A. J. Moore, holotype, Antezana 1276 (US).

margins distally, tips acute to slightly mucronulate, erect on inner bracts, shortly recurved on other bracts, scabridulous on both surfaces; paleae yellowish-tan, indurate, oblong, 7.5 mm long, ca. 2.5 mm wide, tip minutely hispidulous, acute to, sometimes, trifid. Ray florets 17–18; corollas yellow, tube 1.5 mm long, hispidulous, limb oblong, ca. 1.0–1.1 cm long, 0.4 cm wide, abaxial surface strigose and gland-dotted, apex 2- or 3-lobed. Disk florets 50 or more; corollas darker yellow, ca. 6 mm long, tube ca. 1 mm long, scabridulous, throat ca. 4 mm long, campanulate and scabridulous at base, smooth inside, lobes 1.0–1.2 mm long, strigulose outside, papillose inside; anther thecae 2.5–3.0 mm long, with slender basal hastation much longer than collar, essentially short-tailed; appendage 0.58–0.70 mm long, 0.35–0.41 mm wide. Achenes ca. 2.5–3.0 mm long, 0.8 mm wide, sparsely strigulose with stiff setulae; pappus color a very light tan, awns 3.0–3.5 mm long, with fimbriate margins, squamellae ca. 5, 1.0–1.5 mm long, 0.2–0.5 mm wide, deeply fimbriate. Pollen grains 25–28 μm in diam. in Hoyer's solution.

Rhysolepis emaciata is known only from the type collection. Relation might be expected to *R. australis*, *R. fusiformis*, *R. helianthoides*, and *R. lanceolata* of the Bolivian Andes, but the latter all have thicker stems, more obvious branching, and only about 2 series of subequal involucre bracts. The spirally inserted leaves of *R. emaciata* characteristically seem to contract slightly in width near the basal fourth. The bases of the anthers seem unusually long and tailed for a member of the Heliantheae.

Rhysolepis goyasensis H. Rob. & A. J. Moore, sp. nov.
Fig. 4

Type: Brazil. Goiás: Serra Geral do Paraná, ca. 3 km S of São João da Aliança, near Riacho, ca. 850 m, gallery forest and adjacent cerrado, 15 Mar 1971, *Irwin, Har-*

ley & G. L. Smith 31821 (holotype US; isotypes NY, UB, US).

A *R. breviflosculosam* in pubescentibus caulis et involucri similis sed in foliis superioribus decrescentibus et in laminis base non cordatis differt.

Subshrub to 1 m high; usually unbranched between base and inflorescence; part of rhizome seen, roots moderately stout, spreading, without evident fusiform enlargements; stem reddish-brown to tan, pilose to lanulose, denser above, hairs spreading to retrorse. Leaves alternate, reduced to bracteoles distally, often gradually decrescent; petioles ca. 2 mm long; blades oblong-elliptical, 0.6–6.5 cm long, 0.3–2.1 cm wide, at base broadly acute, margins entire, apex short-acute to short-acuminate, adaxially villous with tubercle-based hairs, abaxially villous, triplinervate from near base, secondary veins reaching distal $\frac{1}{2}$ of blade. Inflorescences unbranched or with 1–3 branches on each side, conic to cylindrical when multibranching, elongate branches shorter than main axis, spreading at ca. 45° angles; bracteoles narrowly oblong-elliptical 0.7–3.0 mm long; peduncles 3.5–5.0 cm long, 1–2 mm long from last bracteoles, lanulose as in stems. Heads usually 1–5; involucre 0.9–1.1 cm high, 1.2–1.9 cm wide; bracts ca. 3-seriate, oblong to oblong-lanceolate, gradate, 10–15 mm long, 3–4 mm wide, 3-nerved, tips abruptly acute to slightly acuminate, slightly indurate at base or herbaceous throughout; paleae rather oblong, coriaceous, ca. 8 mm long, ca. 2 mm wide, apex short-acute to mucronulate. Ray florets 14–15; corollas yellow; tube 3.5 mm long, pilosulous; limb 1.5 cm long, 0.4 cm wide, pilosulous abaxially on veins, apex 2 or 3 lobed. Disk florets ca. 50; corolla yellow, ca. 5 mm long, tube 0.7–1.0 mm long, nearly glabrous; throat 2.5–3.0 mm long, slightly campanulate at base, glabrous, inside with vertical bands of antrorsely prorulose cells, lobes 0.7–1.0 mm long, acute, sparsely scabrid outside, papillose inside; anther thecae 2.5 mm long, appendages yellow, 0.55–0.60 mm long, 0.3–0.4 mm wide.



Rhysolepis goyasensis H. Rob. & A. J. Moore
 Holotype:

THE NEW YORK BOTANICAL GARDEN
 Herbarium of the University of Brazil

No. 31821 Serra Geral do Paraná

Figuiera quinqueramis Blake
 (ex Descript. of phyllaries)
 det. John Fernald (NY), 1992

Erect simple or few-branched subshrub
 ca. 1m tall. Ligules yellow; disc yellow-
 brown. Gallery forest and adjacent
 cerrado, ca. 1km S. of São João de Aliança,
 near Riacho, ca. 850m. elev.

H. S. Irwin, R. M. Harley, G. L. Smith 15 March 1971

Plant material deposited with the collections of the Universidade de Brasília and the Instituto de Pesquisas e Experimentação Agrícola de Brasília, supported in part by funds from the National Science Foundation.

UNITED STATES

3314050

NATIONAL HERBARIUM



Fig. 4. *Rhysolepis goyasensis* H. Rob. & A. J. Moore, holotype, Irwin, Harley & Smith 31821 (US).

Achenes 3 mm long, 0.8–1.0 mm wide, glabrous except few, small, marginal setulae; pappus awns 2.0–3.1 mm long, minutely scabrid on margins and keel, squamellae ca. 8, 1.1–1.7 mm long, 0.3–0.5 mm wide, margins fimbriate. Pollen 27–30 μm in diam. in Hoyer's solution.

Paratypes: Brazil. Goiás: São João de Aliança, estrada para Vãozinho, campo cerrado, solo rochoso, 9 Feb 1994, G. & M. Hatschbach 60230 & Silva (MBM, US); Corrente (Mun. São João da Aliança), campo cerrado, solo rochoso, 20 Feb 2000, G. & M. Hatschbach & O. S. Ribas 70471 (MBM, US).

Rhysolepis goyasensis has pubescence of the stems and involucre reminiscent of that in *R. breviflosculosa* far to the south in Uruguay. The new species differs by the leaf blades lacking cordate subamplexicaul bases and by the decrescent size of the distal leaves of the stem. The new species seems related to the *R. robusta* species group, but has few or single heads or a narrowly conic to cylindrical inflorescence borne well beyond the larger stem leaves.

Rhysolepis hatschbachii H. Rob. & A. J. Moore, sp. nov.

Fig. 5

Type: Brazil. Matto Grosso do Sul: Rodovia Bonito, Campo dos Índios, próximo de Três Morros (Mun. Bonito); encosta do morro; solo calcário, 10 Mar 2003, G. & M. Hatschbach & E. Barbosa 74469 (holotype MBM, isotype US).

A *R. gardneri* in formibus capituli similis sed in foliis abaxialiter dense pilosulis et in pedunculis ebracteatis longioribus et in limbis radii abaxialiter glabris distincta.

Perennial herb or subshrub to 1 m high, with lateral branches ascending at 35–40° angles; roots not seen; stems tan to dark brown, densely hispid to strigose. Leaves of main stems alternate, 4.5–8.5(11) cm long, 1.5–2.8(4.2) cm wide, on branches often opposite, 2.0–5.5 cm long, 0.5–1.5 cm wide; petioles 1–2 mm long; laminae her-

baceous, oblong-elliptical, base obtuse, margins entire to remotely serrulate, apex short-acute and apiculate, adaxial surface densely pilosulous with bases of hairs often enlarged, abaxial surface densely scabridulous on veins, less densely pilosulous between veins, gland-dotted; triplinervate with strongly ascending secondary veins reaching middle or distal $\frac{1}{3}$ of blade. Inflorescence of few heads terminal on stems and branches; peduncles 9–30 cm long without leaves or bracts, strigulose to hispid with white hairs, hairs denser below heads; involucre 10–13 mm high, 13–20 mm wide; bracts broadly 3–4-seriate, slightly unequal, oblong with obtuse to acute tips, 7–11 mm long, ca. 4 mm wide, bases of inner bracts indurate and strongly ribbed, abruptly shortly herbaceous and sometimes recurved at tips, outer bracts canescent with white, densely strigulose pubescence, margins densely fimbriate with short cilia, inner surface usually glabrous, rarely strigulose near tip; paleae oblanceolate, ca. 9 mm long, 1.5 mm wide, acute, essentially glabrous. Ray florets 9–14; corollas yellow, tube ca. 1 mm long, sparsely pilosulous; limb narrowly elliptical, ca. 1.7–2.4 cm long, 0.5–0.6 cm wide, abaxially glabrous, apex minutely bilobed. Disk florets 35–45 or more; corollas yellow, ca. 5 mm long, tube ca. 1 mm long, scabridulous, throat ca. 3 mm long, sparsely scabridulous on narrowly campanulate base, with vertical bands of antrorsely prurulose cells inside, lobes ca. 1 mm long, nearly glabrous abaxially, papillose inside; anther thecae ca. 2.3 mm long; appendage yellow, 0.6–0.7 mm long, ca. 0.4 mm wide. Sterile ray ovaries with pair of squamellae 0.5–0.9 mm long; disk achenes ca. 4 mm long, ca. 1.2 mm wide; awns 3.0–3.5 mm long, squamellae narrow, 0.5–0.8 mm long, fimbriate. Pollen grains ca. 32 μm in diam. in Hoyer's solution.

Paratype: Brazil. Matto Grosso do Sul: Serra de Bodoquena, Fazenda Bodoquena, Reserva da Tercola (Mun. Miranda); Mata, 5–8 m, Sopé de morro, solo argiloso raso,



UNITED STATES

Rhysolepis hatschbachii H. Rob. & A. J. Moore

3441382

Isotype:

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	PREFEITURA MUNICIPAL DE CURITIBA MUSEU BOTÂNICO MUNICIPAL	HERBÁRIO Nº
	Asteroceae Redovia Bonito—Campo dos Índios, próximo de Três Morros (Mun. Bonito) Mato Grosso do Sul G. Hatschbach, M. Hatschbach & E. Barbosa 74469, 10.III.2003 Ereta, 1m, capítulo amarelo. Encosta do morro, solo calcário.	

FMC - DPP 004

Fig. 5. *Rhysolepis hatschbachii* H. Rob. & A. J. Moore, isotype, G. & M. Hatschbach & Barbosa 74469 (US).

encharcado, 17 Mar 1995, A. Pott & *al.* 7026 (US, MBM).

Rhysolepis hatschbachii is known from only the two cited collections. The paratype was previously determined as near *R. gardneri* of Goiás, and the latter is possibly the closest relative. Differences include the long peduncles of the latter having many foliiform bracts, its involucre bracts being distinctly narrower and pale at the base, and its rays being shorter and puberulous abaxially. The general habit of the new species is closer to *R. ovatifolia* of São Paulo and Paraná, but that species has distinctive narrower involucre bracts that are essentially glabrous except for the densely ciliate margins.

Rhysolepis laxicymosa H. Rob. & A. J.

Moore, sp. nov.

Fig. 6

Type: Brazil. Minas Gerais: Serra do Cabral, estrada para Francisco Dumont (Mun. Joaquim Felício); campo rupestre, 950 m, 16 May 2001, G. & M. Hatschbach & Barbosa 72088 (holotype MBM, isotype US).

A speciebus novis *R. goyasensem* similis sed in caulibus non lanulatis et in inflorescentiis laxe cymiformibus et in limbis radii brevibus distinctis.

Erect perennial herb or shrub 50–90 cm high, apparently unbranched between base and inflorescence; roots not seen; stem reddish-tan, pilose to strigose or thinly villous. Leaves alternate; petioles ca. 1 mm long; laminae coriaceous, oblong-elliptical, 3.7–1.5 cm long, 1.6–0.6 cm wide, decrescent toward inflorescence, base rounded to broadly acute, margins entire or remotely 1–3-subserulate, apex short-acute and slightly mucronulate, adaxial surface sparsely strigose and densely scabridulous, abaxial surface with prominent veins and prominulous veinlets, densely strigose on veins, strigulous to subsericeous between veins, gland-dotted; triplinerved from near base, secondary veins reaching distal 1/3 or

more of blade. Inflorescences are sparingly branched, cymiform, branches long, ascending at ca. 30° angles; with bracteoles mostly at branch bases 1.5–0.7 cm long, 0.6–0.3 cm wide; peduncles 6–23 cm long, strigose, more densely villous near heads, with bracteoles 7–3 mm long, 3–1 mm wide. Heads ca. 5; involucre 0.5–0.6 cm high, 1.0–1.2 cm wide; bracts ca. 3-seriate, oblong, somewhat gradate, 3.0–6.5 mm long, 0.8–1.2 mm wide, tips obtuse to short-acute, outer bracts indurate in basal 1/2, herbaceous in distal 1/2, inner bracts almost completely indurate with broad sclerified bands between veins, exposed surfaces densely pilosulous; paleae pale tan, papery, lanceolate to oblong, ca. 7 mm long, ca. 1.5 mm wide, scaberulous at base and tip, gland-dotted at tip. Ray florets ca. 18; corollas yellow, tube ca. 1.2 mm long, scabridulous; limb broadly oblong, 6.5 mm long, 1.8–3.0 mm wide, puberulous abaxially on veins, apex trilobed. Disk florets 30–35 or more; corollas yellow, 4 mm long, basal tube 1 mm long, scabridulous, throat ca. 2.5 mm long, base slightly campanulate and scabridulous, with vertical bands of antrorsely prurulose cells inside, especially midway between veins, lobes ca. 0.7 mm long, pilosulous distally outside, papillose inside; anther thecae ca. 1.8 mm long; appendages yellow, 0.4–0.5 mm long, 0.33–0.38 mm wide. Achenes ca. 3.5 mm long, ca. 1.1 mm wide, sericeous with slender setulae; pappus whitish, awns mostly 2.0–2.5 mm long, fimbriate on margins and midrib; squamellae 5 or 6, ca. 1 mm long, 0.2–0.5 mm wide, margins fimbriate. Pollen grains 22–28 μm in diam. in Hoyer's solution.

Rhysolepis laxicymosa seems mostly closely related to *R. goyasensis*, but it is smaller in all parts. The pubescence of the stem is shorter, the inflorescence is more slender with fewer bracts, the involucre is smaller with narrowly oblong bracts, and the rays are scarcely twice as long as the involucre. In the length of its rays, *R. laxicymosa* is closer to *R. subtruncata*, also of Goiás, which has distinctive subtruncate

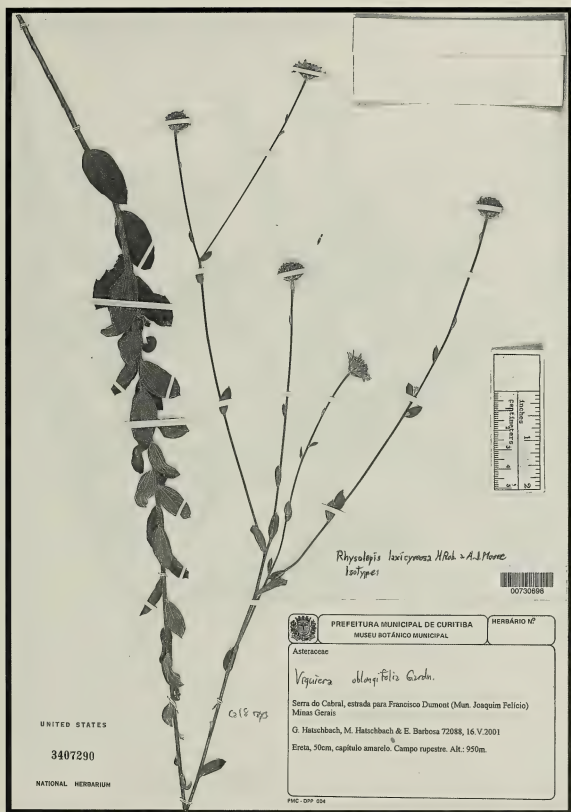


Fig. 6. *Rhysolepis laxicymosa* H. Rob. & A. J. Moore, isotype, G. & M. Hatschbach & Barbosa 72088 (US).

leaves that are not decrescent below the inflorescence.

Rhyssolepis santacatarinensis H. Rob. & A. J. Moore, sp. nov.

Fig. 7

Type: Brazil. Santa Catarina: Serra do Faxinal (Mun. Praia Grande), paredões rochosos, 1200 m, 15 Apr 1993, G. & M. Hatschbach 59135 & J. M. Silva (holotype MBM, 2 isotypes US).

A *R. pilosam* in foliis lanceolatis et bracteis involucris lanceolatis similis sed in foliis distincte petiolatis et in nervis pinnatis et in caulibus densius lanulatis differt.

Subshrub or shrub to 1 m high, moderately branched; roots not seen; stems tan to reddish-brown, villous, hairs denser near heads. Leaves alternate; petioles 0.2–1.7 cm long, sometimes slightly winged, villous; laminae herbaceous, lanceolate, 4–17 cm long, 0.4–3.5 cm wide, base and apex attenuate to acuminate, margins remotely crenate-serrulate, adaxially tuberculate-scabrous, abaxially densely canescent, pilose to subvillous, denser on veins, with glandular dots; venation pinnate or essentially pinnate. Inflorescence with 1 or 2 heads per branch, often overtopped by leaves; peduncles 0.2–2.0 cm long. Heads 4–8; involucre 0.75–1.25 cm high, 2–3 cm wide, 3.5 cm wide in fruit; bracts 2–3-seriate, narrowly lanceolate to narrowly oblanceolate, 12–22 mm long, 2–3 mm wide, apices acuminate to mucronulate, tips strongly recurved, basal $\frac{1}{4}$ to $\frac{1}{2}$ indurate, 5-ribbed, distally herbaceous, abaxially villosulous, adaxially at tip pilosulous to subglabrous, sparsely gland-dotted, margins finely ciliate; paleae oblong, ca. 9–11 mm long, ca. 2 mm wide, indurate, to 7-ribbed, apex acute and mucronulate, sometimes with teeth, glabrous with scabridulous midvein. Ray florets ca. 23; corollas yellow, tube ca. 1 mm long, sparsely puberulous; limbs narrowly elliptical, 1.5–3.5 cm long, 0.3–0.4 cm wide, apex 1- or 2-(-3-) lobed, abaxially puberulous, gland-dotted. Disk florets to 120 or

more; corollas yellow, 5–6 mm long, tube 1.5 mm long, glabrous, throat 3.5 mm long, base moderately campanulate, scabridulous on base and veins, smooth inside, lobes 0.5–1.0 mm long, acute, sometimes sparsely scabridulous outside, papillose on distal $\frac{1}{2}$ inside; anther thecae 2.5–3.0 mm long; appendage yellow, 0.7–0.8 mm long, 0.3–0.4 mm wide. Achenes 4 mm long, ca. 1 mm wide, glabrous except for marginal setulae near pappus; awns 2–3 mm long, squamellae separated into broad segments, ca. 0.5 mm long, fimbriate. Pollen 25–28 μ m in diam. in Hoyer's solution.

Paratypes: Brazil. Santa Catarina: Mun. Lauro Müller; 20 km west of Lauro Müller, lower and middle slopes of serra by Rio do Rastro, 700–1000 m, 3 Apr 1957, L. B. Smith & R. Klein 12339 (FLOR, US); Rod. SC-438, Serra do Rio do Rastro (Mun. Lauro Müller); Paredões rochosos; 1000 m, 7 Apr 1991, G. & M. Hatschbach & E. Barbosa 55311 (MBM, US).

Rhyssolepis santacatarinensis would belong to the series *Aureae* of Blake (1918) on the basis of its lanceolate involucre bracts, and it would key to various species in the Blake key depending on the emphasis given to the dense canescent pubescence of the abaxial faces of its leaves. Its distribution in southern Brazil and shape of its leaves suggest closest relation to *R. pilosa*, which has much sparser pilose pubescence, usually no petiole, and much smaller heads. The large heads with 120 or more disk florets distinguish the new species from most other members of the genus in Brazil and elsewhere. The venation of the leaves is also distinctive, lacking strongly ascending lateral veins at the base. The basal secondary veins are either strictly pinnate or only slightly more ascending.

Rhyssolepis subtruncata H. Rob. & A. J. Moore, sp. nov.

Fig. 8

Type: Brazil. Goiás: Chapada dos Veadoiros, ca. 42 km N of Alto do Paraíso, ca.



Fig. 7. *Rhysolepis santacatarinensis* H. Rob. & A. J. Moore, isotype, G. & M. Hatschbach 59135 & Silva (US).



Fig. 8. *Rhysalepis subtruncata* H. Rob. & A. J. Moore, holotype, Irwin, Harley & Smith 33151A (US).

125 m elev., riacho margin in cerrado, on rocky slopes and adjacent campo, 25 Mar 1971, Irwin, Harley & G. L. Smith 33151A (holotype US, isotypes NY, UB).

E speciebus aliis in foliis coriaceis saepe subtruncatis et in ramis inflorescentibus longis valde ascendentibus et in floribus radiis brevibus differt.

Subshrub to 2.5 m high, with few or no branches between base and inflorescence; roots not seen; stems tan to reddish-brown, strigose to stiffly pilose. Leaves alternate, petioles 0–1 mm long, 1–2 mm broad, densely villosulous abaxially; laminae coriaceous, obovate to cuneate, 1.8–4.5 cm long, 0.8–2.4 cm wide, scarcely smaller but more remote up to inflorescence, base cuneate, margins slightly crenulate-serrulate above, apex subtruncate to scarcely retuse, adaxial surface nearly smooth, hairs strigose with enlarged bases, abaxial surface with prominulous veinlets, pilose to thinly sericeous, triplinervate from near base, lateral veins reaching distal $\frac{3}{4}$. Inflorescence loosely corymbiform, with 2 or 3 long branches on each side, ascending at ca. 30° angles, pilose; bracts foliiform, mostly $\frac{1}{3}$ to $\frac{1}{2}$ as large as leaves, mostly at bases of branches, with few bracteoles on distal branches; peduncles 0.4–2.0 cm long beyond bracteoles. Heads ca. 9; involucre 0.8 cm high, ca. 1.5 cm wide; bracts ca. 2-seriate, lanceolate, 5–8 mm long, 1–2 mm wide, acute to slightly acuminate, basal $\frac{1}{4}$ to $\frac{3}{4}$ indurate, apices herbaceous, appressed to slightly spreading, abaxially puberulous, adaxially at tip pilosulous; paleae rather oblong, obtuse, ca. 5.5 mm long, ca. 1.5 mm wide, indurate, glabrous or with midvein strigulose. Ray florets ca. 20; corollas yellow, tube ca. 1.2 mm long, pilosulous; limb broadly oblong, 5–6 mm long, 3.5–4.0 mm wide, apex unlobed or 2-lobed, abaxially pilosulous mostly on veins, Disk florets ca. 50?; corollas yellow-brown, 4 mm long; tube 0.8 mm long, sparsely scabrid, throat 2.5 mm long, base scabrid, narrowly campanulate, glabrous distally, smooth inside, lobes deltate, ca. 1 mm long, scabrid out-

side; anther thecae 1.8–2.0 mm long; appendage yellow, 0.35–0.40 mm long, 0.45–0.55 mm wide. Achenes (immature) 2.5 mm long, 0.8–1.0 mm wide, setulae over whole surface, sericeous; pappus awns ca. 1.5 mm long, squamellae ca. 0.5 mm long, deeply fimbriate. Pollen grains 22–26 μ m in diam. in Hoyer's solution.

Rhysolepis subtruncata has distinctive cuneate, coriaceous leaves and ascending branches of the inflorescence reaching the level of the terminal central head. The rays are very short compared to many other species of the genus. The leaves below the inflorescence are not or are scarcely decrescent. The throats of the disk corollas lack the vertical bands of prorulose cells found in other species of sect. *Bracteatae*. Any additional collections should be readily identifiable by the leaf shape and by the overall habit of the leafy plants and inflorescence.

Acknowledgments

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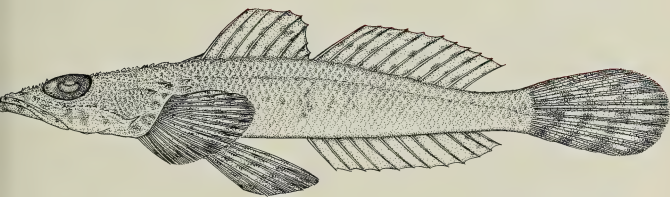
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**Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa).
Part 5: The genera *Plumarella* Gray, 1870; *Acanthoprimnoa*, n. gen.;
and *Candidella* Bayer, 1954**

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Abstract.—The nine western Atlantic species belonging to three genera, *Plumarella*, *Acanthoprimnoa*, and *Candidella*, are described and illustrated. Four new species of *Plumarella* are described, as well as one new species of *Acanthoprimnoa*; the genus *Acanthoprimnoa* is also described as new, differentiated from *Plumarella* by lacking tubercles on the undersurfaces of its sclerites. Two western Pacific species are transferred to *Acanthoprimnoa*: *A.serta* and *A.cristata*. Three varieties are recognized of the common *Plumarella pourtalesii*, one previously described as a variety (*P.p.robusta*) and another proposed herein (*P.p.var.obtusa*). A dichotomous key and table of comparisons is provided for the species and forms of *Plumarella*, as are a table of comparisons for the two Atlantic species of *Acanthoprimnoa*, and an indented key to the eleven genera of western Atlantic Primnoidae. Specimens of these genera were found to be extremely common at lower shelf and upper slope depths primarily in the temperate western Atlantic; over 1500 specimens were examined in this study, including types of all included species.

This is the fifth in a series of revisions (Cairns 2001; Cairns & Bayer 2002, 2003, 2004) of the western Atlantic deep-water octocorals, and the fourth dealing with the Primnoidae, a family consisting of about 205 species and 32 genera worldwide, of which approximately 33 species and 11 genera occur in the western Atlantic. Bayer's revision of western Atlantic *Calyptrophora* (2001) should also be considered as the first unnumbered part of this series, which also deals with primnoids. In order to facilitate identification at the generic level within this family a key is provided below for those 11 genera that occur in the western Atlantic. Two genera occur twice in the key since they have both dichotomous and pinnate branching. In this part we review the genera *Plumarella* and *Candidella*, as well as describe a new genus, *Acanthoprimnoa*, separated from *Plumarella* on the basis of its lacking tubercles on

the undersurfaces of its sclerites. Specimens of *Plumarella* and *Acanthoprimnoa* are extremely common at shelf and upper slope depths (137–1160 m) in the western Atlantic, occurring there opportunistically as weeds do on dry land. Ironically, species of these two genera were previously known from only 11 stations and as many specimens from the western Atlantic; this report lists approximately 1425 specimens from 145 localities. The third genus, *Candidella*, is known from deeper water (514–2139 m), and occurs farther north (New England Seamounts) as well as in the eastern Atlantic.

Indented Key to the 11 Western Atlantic Genera of Primnoidae (fraction indicates number of western Atlantic species/total number of species; genera in bold face treated in this part)

- I. Colonies unbranched or extremely sparsely branched: *Primnoella* (4/14)

- II. Branching in the form of a bottle-brush: *Thouarella* (1+/25)
- III. Colonies pinnately branched
- A. Polyps arranged in whorls: *Callogorgia* (3/28)
- B. Polyps arranged biserially and alternately
1. Tubercles not present on undersurfaces of sclerites: *Acanthoprimnoa* (2/4)
 2. Tubercles present on undersurfaces of sclerites
 - a. Undersurface of opercular scales with a prominent keel: *Amphilaphis* (1/6)
 - b. Undersurface of opercular scales without a longitudinal keel: *Plumarella* (6/20)
- IV. Colonies dichotomously branched
- A. Polyps arranged in whorls
1. Polyps face outward from branch; 4 marginal scales: *Candidella* (1/4)
 2. Polyps face up or down; 2 marginal scales
 - a. Polyps encased by only two pairs of large abaxial body wall scales
 - i. Members of two pairs of body wall scales inseparably fused to form a complete ring surrounding polyp; polyps face up or down: *Calyptrophora* (4/13)
 - ii. Body wall scales not fused; polyps face downward: *Paracalyptrophora* (3/6)
 - b. Polyps encased by 3 or 4 pairs of large abaxial body wall scales: *Narella* (7/25)
- B. Polyps arranged biserially and alternately
1. Tubercles not present on undersurfaces of sclerites: *Acanthoprimnoa* (2/4)
 2. Tubercles present on undersurfaces of sclerites: *Plumarella* (6/20)

- C. Polyps irregularly arranged: *Primnoa* (1/3)

Material and Methods

This study was based on the examination of approximately 1505 specimens, collected at 161 deep-water stations by 18 research vessels (Appendix: Station data). Except for those reported from the *Bibb* and *Atlantis*, which were borrowed from the MCZ, the specimens are deposited at the National Museum of Natural History (USNM). Synonymies for all species are purported to be complete for all previously published records. Unprefaced SEM stub numbers pertain to the series made by Bayer; those prefaced with C, to the series made by Cairns.

The following abbreviations are used: *Alb*—U.S.F.C.S. *Albatross*; *Atl*—R/V *Atlantis*; *BM*—British Museum (now The Natural History Museum, London); *CI*—R/V *Colombus Iselin*; *G*—R/V *Gerda*; *Gos*—R/V *Gosnold*; *H:W*—height to maximum width of an opercular or marginal scale; *JS*—Johnson-Smithsonian Deep-Sea Expedition (*Caroline*); *MCZ*—Museum of Comparative Zoology, Harvard, Cambridge; *O*—M/V and R/V *Oregon* and *Oregon II*; *P*—R/V *Pillsbury*; *SB*—R/V *Silver Bay*; *USNM*—United States National Museum (now the National Museum of Natural History, Smithsonian, Washington, D.C.).

Subclass Octocorallia

Order Gorgonacea

Suborder Calcaxonina

Family Primnoidae Gray, 1858

Genus *Plumarella* Gray, 1870

- Cricogorgia* Milne Edwards, 1857:6, pl. B2, fig. 6 (*nom. nud.*).—Gray, 1870:36–37.
- Plumarella* Gray, 1870:36.—Studer, 1887:51.—Wright & Studer, 1889:73–74, 281.—Versluys, 1906:13–14.—Kinoshita, 1908:6–8.—Kükenthal, 1915:144; 1919:340–342; 1924:255.—Deichmann, 1936:155–156.—Bayer, 1956:F220.—Fabricius & Alderslade, 2001:244–245.

Type species.—*Gorgonia penna* Lamarck, 1815, by subsequent designation (Kükenthal 1915:144).

Diagnosis.—Primnoidae with a well-defined operculum; polyps usually inclined apically, each polyp completely surrounded by 8 rows of body wall scales; polyps arranged biserially or irregularly, but never in whorls; 8 marginal scales, often pointed or spinose; undersurfaces of all sclerites tuberculate, opercular scales not keeled; colonies uniplanar, usually pinnately (plumose) branched but sometimes dichotomous.

Distribution.—Western Pacific; Patagonia; western Atlantic; 10–1914 m.

Remarks.—The only revision of the genus *Plumarella* was that of Kükenthal (1919), reiterated in 1924 (Kükenthal, 1924), which included the description and synonymy of all 17 species as well as a key to their identification. He used the following characters to distinguish species, as emphasized in his key: shape of distal edge of marginal scales, presence of a longitudinal keel on the body wall scales, number of scales in the ab- and adaxial body wall rows, polyp size, and texture of surface of body wall scales. These characters have also been used in this review (Table 1), along with the additional characters such as branching mode, terminal branchlet length and flexibility, number of polyps/cm branch length, shape of the operculars, presence of tubercles on the undersides of the sclerites, ornamentation on the edges of the opercular scales, and coarseness of coenenchymal granulation, the last three characters being used to distinguish a closely related new genus once confused with *Plumarella*.

Key to the Species and Forms of the Six Species of *Plumarella* known from the Western Atlantic

- 1. Distal edges of marginal scales straight, gently rounded or only slightly angular 2
- 1'. Distal edges of marginal scales prominently spined 7

- 2. Branching alternate pinnate; colonies often large (up to 33 cm) 3
- 2'. Branching dichotomous; colonies fairly small (less than 11 cm) *P. dichotoma*
- 3. Body wall scales smooth 4
- 3'. Body wall scales granular 5 (*P. pourtalesii*)
- 4. Closely-pinnate branching; opercular scales elongate and granular; 10–12 polyps/cm *P. pellucida*
- 4'. Loosely-pinnate branching; opercular scales shorter and smooth; 14–21 polyps/cm *P. laxiramosa*
- 5. Distal edges of marginal scales of some polyps in a colony slightly angled (but not spinose) *P. pourtalesii* var. *obtusata*
- 5'. Distal edges of marginal scales straight to slightly rounded 6
- 6. 11–13 polyps/cm; distance between polyps on one side of branch 1.0–1.2 mm *P. pourtalesii* var. typical
- 6'. 14–16 polyps/cm; distance between polyps 0.5–0.8 mm *P. pourtalesii* var. *robustata*
- 7. Each marginal scale with a prominent spine *P. aurea*
- 7'. Only 4–7 marginal scales with an elongate needle-shaped spine, those scales corresponding to operculars with at least one uncovered edge *P. aculeata*

Plumarella pourtalesii (Verrill, 1883)

Figs. 1A–B, 2A–C, 3A–C

Primnoa Pourtalesii Verrill, 1883:28–29, pl. 2, figs. 2, 2a–e (S. Carolina).—Not Hargitt & Rogers, 1901:281, fig. D (probably *A. goeisi*).

Plumarella pourtalesi.—Wright & Studer, 1889:73, 74, 280 (new comb.).—Versluys, 1906:15–16 (comments only).

Plumarella pourtalesii.—Versluys, 1906: 342 (key), 345–346 (German translation of Verrill); Kükenthal, 1919:345–346; 1924:257–258 (same as 1919).—Deichmann, 1936:156, pl. 25, figs. 17–18, pl. 26, figs. 10, 10a (two new records: *Bibb* 22, MCZ 4822 and *Bibb* 135, MCZ 4821).—Bayer, 1954a:281 (listed); 1956: F220, fig. 159-7; 1957:388 (two records, forma *obtusata*).—Bayer, Grasshoff & Versveldt, 1983: fig. 53.—Bayer, 1973: fig.

Table 1.—Table of comparisons of western Atlantic *Plumarella* and *Acanthoprimnoa* species and varieties.

	<i>P. pourtalesii</i> (typical) (Verrill, 1883)	<i>P. pourtalesii</i> var. <i>robusta</i> (Deichmann, 1936)	<i>P. pourtalesii</i> var. <i>obtusata</i>	<i>P. pellucida</i> , n. sp.	<i>P. laetramosa</i> , n. sp.
Branching: Maximum colony height	Regular, alternate, close-pinnate; 33 cm	Regular, alternate, close-pinnate; 30 cm	Regular, alternate, close-pinnate; 19 cm	Regular, alternate, close-pinnate; 17 cm	Regular, alternate, loose-pinnate; 24 cm
Branch length and flexibility	To 55 mm; flexible	To 50 mm; stiff	as in var. <i>robustata</i>	To 60 mm; stiff	To 80 mm; limp
Polyp height, diameter (mm); polyps/cm; orientation	0.9-1.2, 0.5-0.6; 11-13; inclined upward	1.1-1.2, 0.65; 14-16; inclined upward	as in var. <i>robustata</i>	1.1, 0.65; 10-12; inclined upward	1.1-1.2, 0.65; 14-21; inclined upward
Distal edge of marginals	Smooth, straight to rounded (scalloped)	as in typical var.	Triangular (obtuse angle)	Smooth, straight to rounded	Smooth, rounded
Scales per body wall row: abaxial/adaxial	5-6/4-5	as in typical var.	as in typical var.	6/5	6-7/5
H: W of operculars	1.5-1.9	as in typical var.	as in typical var.	1.7-2.4 (curved)	1.8-1.9
Scale ornamentation: opercular; bw; coenenchymal	Low apical ridges; granular, granular (fine sand paper)	as in typical var.	as in typical var.	Granular, no ridges; smooth; granular (translucent)	Smooth, no ridges; smooth
Tubercles present on underside of sclerites	Yes	Yes	Yes	Yes	Yes
Distribution	off N. Carolina to Cuba; 196-882 m	off N. Carolina through Straits of Florida; 183-850 m	off Georgia through Straits of Florida; 183-743 m	off N. Carolina through Straits of Florida; Bahamas; 549-1160 m	off N. and S. Carolina; 348-572 m
Branching: Maximum colony height	Dichotomous (lyrate); 11 cm	Dichotomous; 13 cm	Dichotomous, pinnate and lyrate; 12 cm	Dichotomous (4 cm) to pinnate (30 cm)	Loose pinnate (or lyrate) and dichotomous; 22 cm
Branch length and flexibility	To 40 mm; wiry to limp	To 100 mm; flexible	To 50 mm; stiff	To 40 mm; flexible	Long (to 55 mm); flaccid
Polyp height, diameter (mm); polyps/cm; orientation	1.1-1.3, 0.65; 8-10; perpendicular on large branches	0.8-1.2, 0.8-0.9; 14-22; often perpendicular	1.4-1.8, 0.7-0.8; 10-12; perpendicular	0.8-1.2, 0.50; 13-15; inclined slightly upward	Slender, 0.8-0.9, 0.4-0.45; 11-13; slightly inclined
Distal edge of marginals	Smooth	Usually 8 prominent, marginal spines	Usually 5-6 (4-7) long, needle-shaped spines	7 tall, slender, bent spines	Straight or slight angle inclined
Scales per body wall row: abaxial/adaxial	5-6/5-6	6-7/5-6	3-4/3-4	5-6/4-5	8-10

Table 1.—Continued.

	<i>P. dichotoma</i> , n. sp.	<i>P. anura</i> (Deichmann, 1936)	<i>P. aculeata</i> , n. sp.	<i>A. gleri</i> (Aurivillius, 1931)	<i>A. precipitata</i> , n. sp.
H: W of opercular lars; bw; coenenchymal scales	1.7–2.3 Granular; smooth; granu- lar	1.5–2.0 Smooth; smooth; smooth	1.6–2.2 All low granular (body wall sclerites may also be smooth)	1.8–3.9 Ridged; spinose; spinose	1.6–2.2 Ridged; granular; granu- lar
Tubercles present on un- dersides of sclerites	Yes	Yes	Yes	No	No
Distribution	off S. Carolina to Florida; 494–1065 m	off S. Carolina to Cuba; 310–878 m	Bahamas (northern Straits of Florida); 400–900 m	Straits of Florida to Yu- catan, Bahamas, Puerto Rico, Virgin Islands; 137–595 m	Off northeastern Yucatan Peninsula (164–476 m); Lesser Antilles, Straits of Florida (614–686 m)

16.—Bayer & Cairns (Verrill), 2004: pl. 26, fig. 1.

Plumarella pourtalesii var. *robusta* Deichmann, 1936:156–157, pl. 25, figs. 14–16, pl. 26, fig. 9.

Material examined.—Typical form: *Alb*-2416, 10 branches, USNM 10531; *Alb*-2662, 4 branches, USNM 14609; *Alb*-2663, 10 branches, USNM 14479; *Alb*-2667, 4 branches, USNM 49425; *Alb*-2668, 11 colonies, USNM 1019275; *Alb*-2669, over 50 colonies, USNM 14475; *Atl*-266-2, 6 colonies, USNM 1019276; *Atl*-266-7, 3 colonies, USNM 1021650; *Atl*-266-41, 7 colonies, USNM 1019277; *Bibb* 22, 2 branches, MCZ 4822 (reported by Deichmann 1936); *Bibb* 135, 2 branches, MCZ 4821 (reported by Deichmann 1936); *Cape Hatteras* SA6-5, 13 colonies, USNM 79782 (topotypic); *CI*-123, 9 colonies, USNM 1019278; *CI*-246, 26 branches, USNM 59491; *Clelia* 78, 1 colony, USNM 93910; *Clelia* 79A, 1 colony, USNM 93909; *Combat* 174, 1 colony, USNM 50799; *Eastward* 26017, 14 branches, USNM 59490; *Eastward* 26022, 2 branches, USNM 1019279; *Eastward* 26023, 10 branches (dry), USNM 1019280; *Eastward* 26028, 2 branches, USNM 1019281; *Eastward* 26052, 2 branches, USNM 1021652; *G*-170, 1 colony, USNM 1019305; *G*-177, 12 colonies, USNM 1019282; *G*-235, 1 branch, USNM 1019283; *G*-386, 3 colonies and SEM stub 250, USNM 53010; *G*-598, 1 colony, USNM 1019284; *G*-672, 1 colony, USNM 59498; *G*-785, 3 colonies, USNM 52994; *Gos*-2344, 10 branches, USNM 58448; *Gos*-2385, 10 colonies, USNM 56895; *Gos*-2387, 1 colony, USNM 57308; *Gos*-2413, 8 colonies, USNM 1019285; *Gos*-2414, 17 colonies, USNM 1019286; *Gos*-2461, 2 branches, USNM 1019287; *O*-1343, 3 branches, USNM 50183; *O*-1349, 3 branches, USNM 50443 (Bayer 1958); *O*-11703, 2 colonies, USNM 59501; *O*-11717, 1 branch, USNM 59507; *O*-11725, 5 colonies, USNM 1019288; *P*-105, 2 branches, USNM 52999; *SB*-453, 2 branches, USNM



Fig. 1. A, *Plumarella pourtalesii* typical, Alb-2662; B, *P. pourtalesii* var. *robusta*, Alb-2416; C, *P. aurea*, station unknown; D, *Acanthoprinnia pectinata*, Alb-2354. All scale bars = 1 cm.

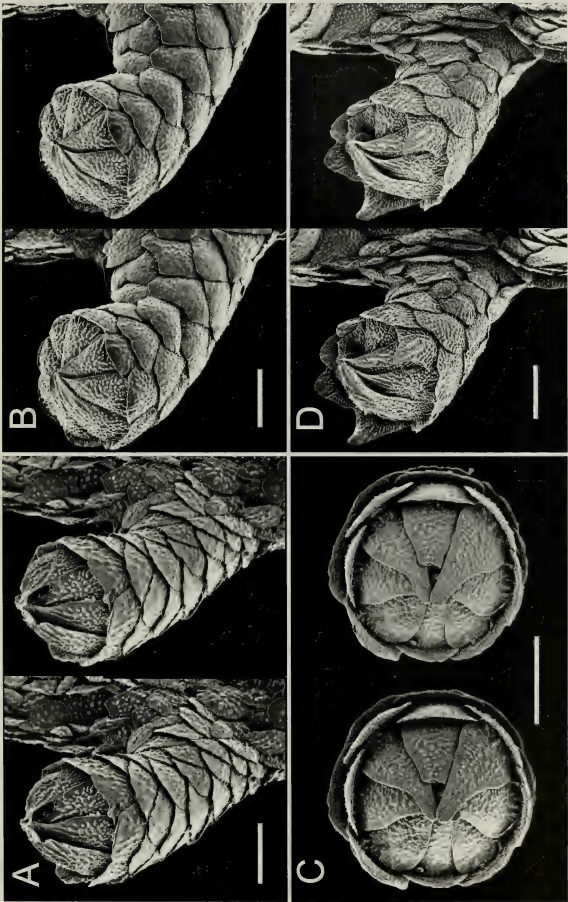


Fig. 2. A-B, *Plumatella pourtalesii* typical: A, syntype, MCZ 5749, stereo oblique view of a polyp; B, G-386, stereo oblique view of a polyp. C, *P. pourtalesii* var. *robusta*, Combat 368, stereo oblique view of a polyp; D, *P. pourtalesii* var. *obtusa*, G-1314, stereo oblique view of a polyp. All scale bars = 0.25 mm.

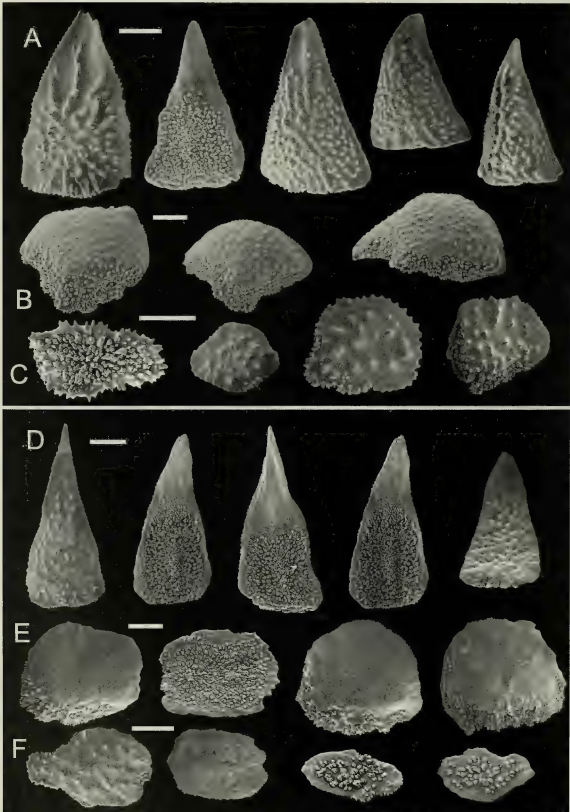


Fig. 3. A-C, *Plumarella pourtalesii* typical (A-B, G-386; C, syntype, MCZ 5749): A, upper and undersurfaces of 5 opercular scales; B, upper surfaces of 3 body wall scales; C, upper and undersurfaces of 4 coenenchymal scales. D-F, *Plumarella pellucida* (first opercular scale is from G-859, all other scales from the holotype): D, upper and undersurfaces of 5 opercular scales; E, upper and undersurfaces of 4 body wall scales; F, upper and undersurfaces of 4 coenenchymal scales. All scale bars = 0.10 mm.

51260; syntypes (MCZ, USNM, see below).

Forma *robusta*: *Alb*-2416, over 25 colonies and 1 unnumbered SEM stub, USNM 49430, 49433; *Alb*-2666, 2 colonies, USNM 49422; *Alb*-2668, 10 branches, USNM 14474; *Alb*-2669, 8 branches, USNM 1019289; *Anton Dohrn* 6392, 3 colonies, USNM 1019290; *Atl*-266-4, 1 colony, 1 branch, USNM 1019291; *Atl*-266-40, 15 branches, USNM 1019293; *Atl*-266-41, 1 branch, USNM 1019292; *Cape Hatteras* SA6-1, 5 colonies, USNM 79783; *CI*-140, 1 branch, USNM 59497; *Combat* 368, 14 colonies and SEM stub 253, USNM 50800; *Eastward* 26023, 1 dry branch, 4 alcohol branches, USNM 1019294; *G*-170, 1 branch, USNM 1019295; *G*-177, over 20 colonies and 1 unnumbered SEM stub, USNM 52995; *G*-247, 1 colony, USNM 53012; *G*-261, 3 colonies, USNM 1019296; *G*-598, 7 colonies, USNM 52997; *G*-835, 3 branches, USNM 52998; *Gos*-2413, 5 branches, USNM 1019297; *Gos*-2461, 8 colonies, USNM 1019298; *O*-11726, 1 branch, USNM 73756; *P*-197, 1 colony, USNM 53013; holotype (see below).

Forma *obtusa*: *Alb*-2416, 1 branch, USNM 1019299; *Alb*-2668, 8 branches, USNM 1019300; *Alvin* 77-761, 2 colonies, USNM 1019301; *Alvin* 1335, 2 colonies, USNM 73741; *Atl*-3780, 10 dry branches, MCZ 54321; *Cape Hatteras* SA6, 8 branches, USNM 79781; *CI*-140, 3 branches, USNM 59495; *CI*-246, 9 branches, USNM 1019302; *Eastward* 26022, 1 branch, USNM 76986; *Eastward* 26023, 1 branch, USNM 1019303; *G*-56, 1 colony and 1 unnumbered SEM stub, USNM 53005; *G*-169, 7 colonies, USNM 53008; *G*-235, 8 colonies and SEM stub 260, USNM 53007; *G*-241, 9 colonies, USNM 53004; *G*-246, 2 branches, USNM 53003; *G*-261, 10 colonies, USNM 53009; *G*-386, 3 branches, USNM 1019304; *G*-391, 6 colonies and SEM 252, USNM 1019305; *G*-598, 1 colony, USNM 1019306; *G*-664, 3 branches, USNM 53001; *G*-679, 4 colonies, USNM 53002; *G*-1012, 1 colony, USNM 53011;

G-1314, 9 colonies and SEM stub 251, USNM 53006; *Gilliss*, 25°50'N, 79°24'36"W, 603 m, 25 May 1973, 1 branch, USNM 79515; *Gos*-2387, 5 colonies, USNM 57306; *O*-1328, 1 colony, USNM 50528; *P*-209, 4 branches, USNM 53000.

Types and type localities.—Two colonies and several fragments of the typical form were mentioned by Verrill (1883) collected from *Blake* 318, all of which must be considered as syntypes. Deichmann (1936) attributed catalog number MCZ 4821 to the syntype series, but this number was preoccupied by Deichmann by specimens collected from "off Florida", thus the syntype series was later re-cataloged as MCZ 42887, and consists of three small branches. Four fragments and SEM stubs 249 and C1084 of one of these syntypes are also deposited at the USNM (5749). All syntypes are preserved in alcohol. Type Locality: *Blake* 318: 31°48'50"N, 77°51'50"W (Blake Plateau off South Carolina), 616 m.

The holotype of forma *robusta*, two small branches in alcohol, the largest 9 cm high, is deposited at the MCZ (4823). It also bears Verrill's personal number of 8032. It is also represented by an unnumbered SEM stub at the USNM. Type Locality: The type locality was stated to be "18 fms. off Alligator Reef, Florida" (Deichmann, 1936:157), but Deichmann correctly queried the extremely shallow depth of the collection. A newer label with this type indicates that it was collected at *Bibb* station 192 (24°48'05"N, 80°34'45"W: off Alligator Reef), at 216 m, this depth being more consistent with the known bathymetric range.

Diagnosis.—Distal edge of marginal scales rounded (scalloped) or straight; branching close pinnate, branchlets of moderate length and stiff; body wall scales granular, surface of operculars ridged; 11–13 polyps/cm (14–16 for forma *robusta* and *obtusa*).

Description.—Colonies are flabellate and pinnately branched (plumose), consisting of

a main branch, which gives rise to 1–4 primary branches (depending on the size of the colony), each main and primary branch giving rise to numerous stiff branchlets up to 55 mm in length, in an alternating sequence (alternate pinnate). Although flabellate, colonies may be uniplanar or slightly convex, such that the polyps are directed toward the convex side. A branchlet occurs on the main branch within 5 mm of the base of the colony; additional branchlets occur at regular intervals of 1.8–3.2 mm on the main and primary branches, producing a characteristic zig-zag pattern for the larger branches, the branchlets being straight and parallel to one another. The main stem is usually anchored by a dense, white, calcareous holdfast, which is often attached to the dead corallum of a deep-sea scleractinian. The axis is yellow-brown or gold and longitudinally striate; overall the colony is white in alcohol. The largest colony (*Combat* 174) is 33 cm in height, 13 cm in width, and 2.7 mm in basal diameter, but most colonies examined were considerably smaller.

Polyps are arranged on all branches (i.e., main, primary, and branchlets) biserially in the plane of the flabellum in an alternating fashion, but angled upward such as to produce a 30°–45° angle with the branch, as well as being slightly curved toward the anterior (convex) side of the flabellum. Two to six polyps occur on the internodes of the main and primary branches. Polyps are rarely more than 1 mm in height, slightly wider at the apex (0.5–0.6 mm) than the base, and fairly well spaced: polyps on the same side of a branchlet are separated by 1.0–1.2 mm. In general, 11–13 polyps occur/cm of branchlet length, this number sometimes lower in small colonies.

Each polyp is encased by 8 opercular and 8 rows of body wall scales. The abaxial rows of body wall scales consist of 5 or 6 scales, the adaxial rows usually one less (4–5 scales), the latter rows always shorter due to having less scales and being located on the shorter, concave, side of the upturned polyp. The marginal scales are up to 0.37

mm in width, bearing sparse, low granules (10 μ m in diameter) on their exterior surface and complex tubercles on undersurface (up to 13 μ m in diameter). Body wall scales proximal to the marginals are progressively smaller. Body wall scales overlap one another within each row as well as overlapping the edges of the scales in both adjacent rows. Body wall scales, including marginals, are somewhat crescent-shaped, wider than tall (H:W = 0.6–0.7), and slightly curved to accommodate the curvature of the polyp, the distalmost scales in each row (the marginals) having a straight or slightly rounded, finely serrate distal margin, projecting only about 10–20 μ m beyond the articulation with the base of the operculars, and, if rounded, producing a slightly scalloped calyx margin. The 8 opercular scales are similarly-shaped (H:W = 1.5–1.9), symmetrical, isosceles triangles, having an apical angle of 41°–51° but with rounded tips. The abaxial operculars are up to 0.42 mm in height, the adaxials about 0.30 mm in height. The upper surface of the each opercular is covered with small spines on the lower half and 3 or 4 longitudinal ridges apically. The lower two-thirds of the undersurface is covered with complex tubercles of the same size as those of the body wall scales; the distal region is smooth, not keeled. The lateral edges of each opercular is finely serrate like the distal edges of the body wall scales. The 8 opercular scales fold together forming a moderately tall, conical operculum.

Coenenchymal scales occur in one layer, are flat, and elliptical to elongate in shape, the largest scales being 0.40 mm in length. Like the other scales, they are sparsely granular above, tuberculate below, and bear finely serrate edges. Tentacular sclerites were not noted.

Comparisons.—See Table 1.

Distribution.—Typical form: Blake Plateau from North Carolina (34°45'N) through Straits of Florida (insular side) and north central part of Cuba; 196–882 m. Form *robusta*: Blake Plateau from off N. Car-

olina (34°15'N) through Straits of Florida to Florida Keys; 183–877 m. Forma *obtusata*: Blake Plateau from off Georgia (31°26'N) through Straits of Florida and Northwest Providence Channel; 183–743 m.

Remarks.—Deichmann (1936) described a variety of *P. pourtalesii* called *robustata*, which differs from the typical form in having a stouter corallum, thicker sclerites, a flatter operculum, and longitudinal ridges on the opercular scales. This form is well represented in our collection (listed separately above), and differs from the typical form (Table 1) in having a stouter, stiffer colony, and slightly larger and thicker polyps (1.0–1.2 mm tall, 0.65 mm in diameter) that are more closely spaced on the branch (distance between adjacent polyps on one side of a branch 0.5–0.8 mm), such that even though the polyps are slightly larger, there are more/cm, i.e., 14–16, the latter number achieved when polyps also bud from the anterior face of the branch. As Deichmann stated, in general, the operculum is flatter, even concave in some highly contracted polyps, but both forms have longitudinal ridges on the opercular scales. These several differences are fairly consistent but do not include any characters routinely used to differentiate species of *Plumarella* (see Kükenthal 1919). Furthermore, the distribution and bathymetric range of both taxa are virtually the same, 7 of the 22 records of *robustata* being from common stations. We thus concur with Deichmann in considering this form as just an environmental variation of the typical form.

Another common form of *P. pourtalesii*, represented in our collection by 27 lots, is otherwise similar to forma *robustata* but differs in that the marginal scales of at least some polyps of every colony have an angled or even pointed distal edge (Fig. 2D). The angle of the distal edge is often a sharp right angle extending about 0.1 mm, or less commonly may be a discrete spine up to 0.25 mm in length. There is great variation in the expression of this character. In some

colonies all marginal scales of all polyps will have a short angled distal edge, whereas in other colonies only those polyps toward the distal branch tips will be so modified, the marginal scales of the remaining polyps having a typically straight or rounded edge. Furthermore, individual polyps may have one or all eight marginal scales with an angled edge. The long-spined marginals are infrequent and when present only occur one to a polyp. All three forms sometimes occur at the same station, and their bathymetric and geographic ranges are quite similar. Because of the great variation of this single character that separates this taxon from forma *robustata* and the typical form, it is considered to be an environmental or genetic variation without taxonomic validity, but, in order to easily refer to this variation, the form name *obtusata* is applied to it, an allusion to the often obtuse angle formed by the distal edges of its marginal spines.

Plumarella pellucida, n. sp.

Figs. 3D–F, 4A–B, 10A

Material examined/types and type locality.—Holotype: G-647, 1 colony and SEM stubs C1079–1080, 1085–1086, USNM 52992. Paratypes: Alb-III 9-19, 1 colony, USNM 50573; Cape Hatteras SA6-5, 2 colonies, USNM 1019404; CI-266, 3 colonies, USNM 59506; G-647, 2 colonies, 3 branches, USNM 1019403; G-808, 1 colony, USNM 59499; G-859, 3 branches and 1 unnumbered SEM stub, USNM 52993; O-11705, 5 branches, USNM 1019405. Type Locality: 26°16'N, 79°43'W (Straits of Florida off Fort Lauderdale), 520–549 m.

Diagnosis.—Distal edge of marginal scales rounded or straight; branching closely pinnate, branchlets of moderate length and stiff; opercular scales granular but not ridged, other scales faintly granular, appearing almost smooth and translucent; abaxial and outer-lateral opercular scales quite long and curved; 10–12 polyps/cm.

Description.—Colonies are flabellate and

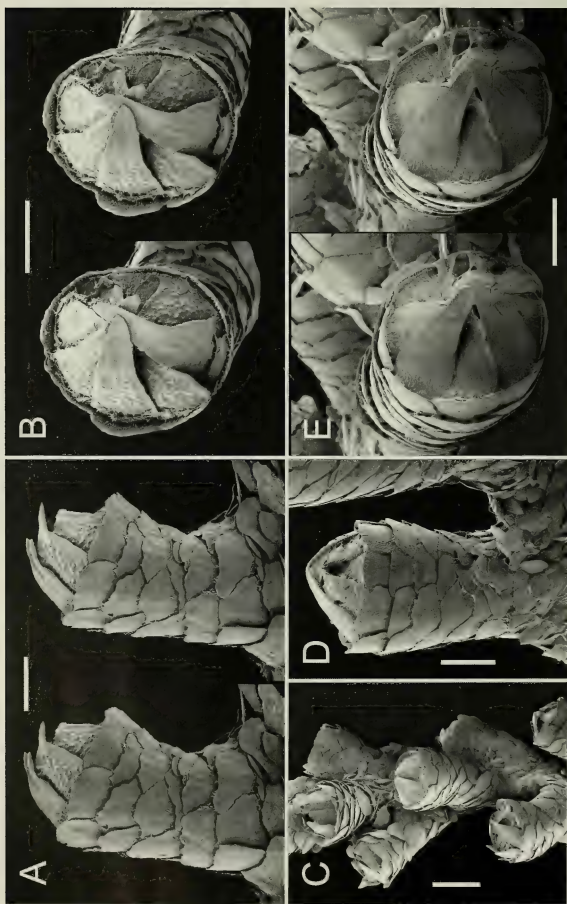


Fig. 4. A-B, *Plumarella pellucida*, holotype: stereo lateral and stereo opercular views of a polyp. C-E, *Plumarella laxiramosa*, holotype: lateral view of a branch and a polyp, and stereo opercular view. Scale bars for A, B, D, E = 0.25 mm; C = 0.50 mm.

closely pinnately branched, as in *P. pourtalesii*, the distance between successive branchlets 2.5–5.0 mm, and the entire flabellum is usually convexly shaped, the polyps curving toward the convex (anterior) face. Branchlets are up to 60 mm long and are fairly stiff. The main stem is anchored by a dense calcareous holdfast. The axis is yellow and faintly longitudinally striate; in alcohol the colony is light brown. The largest colony (holotype) is 17 cm in height, 16 cm in width, and 2.2 mm in basal stem diameter.

Polyps are quite regularly arranged in a biserial, alternating fashion on all branch edges, and are inclined distally. Polyps on the same side of a branchlet are well separated by 1.0–1.2 mm, resulting in 10–12 polyps/cm. Polyps are 1.1–1.2 mm in height and slightly flared distally (0.65 mm in diameter).

Each polyp is covered with 8 opercular and 8 rows of body wall scales, the abaxial body wall scales numbering about 6, the adaxial usually consisting of 5. The body wall scales, including the marginals, are similar in size and shape to those of *P. pourtalesii*; however, their exterior granulation is much reduced and the scales appear to be thinner, producing a smooth, almost translucent aspect. Like *P. pourtalesii*, the distal edges of the marginals are straight to slightly rounded, never spinose or angled. The 8 opercular scales are isosceles triangles (H:W = 1.7–2.4), having an apical angle of 20°–35°, ranging from sharply pointed to slightly rounded. The abaxial and outer-lateral operculars measure up to 0.54 mm in height, the adaxial and inner-lateral operculars only 0.37 mm in height. The distal third of the abaxial and outer-lateral operculars are attenuate, with slightly serrate edges; these scales are curved downward to follow the curvature of the polyp and almost reach the opposite side of the polyp, considerably overlapping the shorter adaxial and inner-lateral opercular scales. The opercular scales bear low sparse granules, lack distal ridges, and are tuberculate on the undersur-

face with no trace of a keel. In general, the opercular scales fold together in a conical operculum in a manner similar to that shown in Fig. 9f, the abaxial opercular having two exposed edges, the adaxial having none.

Coenenchymal scales occur in one imbricating layer, are flat, and elliptical to irregular in shape, the largest being about 0.41 mm in width. Their granulation is reduced similar to that on the opercular scales. Tentacular scales were not noted. All sclerite types, body wall, opercular and coenenchymal bear complex tubercles on their undersurfaces, the largest of which measures about 13 μ m in diameter.

Etymology.—The species name *pellucida* (Latin: *pellucidus*, transparent, translucent, clear) refers to the translucent nature of the body wall and coenenchymal scales when viewed in liquid, probably due to their thinness and sparse granulation, which allows a view of the outline of the branch axis and of 8 faint white longitudinal lines in the polyps corresponding to the mesenteries.

Comparisons.—*Plumarella pellucida* belongs to a closely related species complex characterized by having large, pinnately branched colonies and smooth to straight-edged (not spinose or pointed) marginal scales, this complex consisting of: *P. pourtalesii*, *P. laxiramosa*, and *P. pellucida*. It is probably most closely related to *P. pourtalesii*, but is distinguished by having non-ridged opercular scales, the adaxial and outer-laterals of which are quite long and curved; and smooth, almost translucent body wall and coenenchymal scales. It differs from *P. laxiramosa* in having closer pinnate branching; longer, more attenuate opercular scales that are granular; and fewer polyps/cm. (Table 1). All three species occur in roughly the same geographic and bathymetric range and often occur at the same stations.

Distribution.—North Carolina through Straits of Florida, Bahamas; 549–1160 m.

Plumarella laxiramosa, n. sp.

Figs. 4C–E, 5A–E, 10B

Material examined/types and type locality.—Holotype: *Cape Hatteras* SA6-1, 1 colony and SEM stubs C1081–1083, USNM 1019406. Paratypes: *Alb*-2416, 7 colonies, over 50 branches and 1 unnumbered SEM stub, USNM 50594 and 79458; *Atl*-266-41, 1 branch, USNM 1019407; *Cape Hatteras* SA6-1, 19 branches, USNM 79778; *Cape Hatteras* SA6-5, 8 colonies, USNM 79779; *Combat* 368, 1 branch, USNM 1019408; *Gos*-2387, 1 colony, USNM 1019409. Type Locality: 31°17'18"N, 79°00'39"W (Charleston Bump region, South Carolina), 572–575 m.

Diagnosis.—Distal edge of marginal scales rounded or straight; branching loosely pinnate, branchlets long and flabby; body wall, opercular, and coenenchymal scales smooth; 14–21 polyps/cm, polyps often occurring on anterior face.

Description.—Colonies are flabellate and pinnately branched, as in *P. pourtalesii*, but differ from that species in having more widely-spaced (loose pinnate) and thus fewer branchlets, each branchlet separated from their adjacent by 6–11 mm. Also, unlike *P. pourtalesii*, this species has flat, not curved, colonies, and its branchlets are longer (up to 80 mm) and less stiff, altogether producing a limp or languid colony tension. The main stem is anchored by a dense, white calcareous holdfast, which often attaches to the corallum of a dead scleractinian or stylasterid coral with an encrustation up to 1 cm in diameter. The axis is golden-yellow and faintly longitudinally striate; overall the colony is light brown in alcohol. The holotype is 18 cm in height, 17 cm in width, and has a main stem diameter of 2.7 mm, although the stem is broken from the substrate. The largest colony, which has an intact base (*Alb*-2416), is 24 cm in height.

Polyps are closely arranged on all branches biserially in the plane of the flabellum and in an alternating fashion; however, most larger colonies often have a third

row of polyps on the anterior side, which produces a very crowded arrangement of polyps that may number up to 21/cm. Up to 20 polyps may occur on the rather lengthy internodes of the main and primary branches. Polyps are 1.1–1.2 mm in height and are slightly flared distally (0.65 mm).

Each polyp is covered with 8 opercular and 8 orderly rows of body wall scales, the abaxial body wall scales numbering 6 or 7/row, the adaxial consisting of usually only 5. Body wall scales are roughly rectangular and slightly curved to fit around a segment of the polyp; the distalmost body wall scales (the marginals) are 0.30–0.34 mm in width and 0.20–0.25 mm in height, the scales becoming progressively smaller toward the branch. The distal edges of the marginals are finely serrate and straight to slightly rounded, never pointed or spinose. The undersurfaces of all scales are tuberculate (tubercles 12–26 μ m in diameter), whereas the upper surfaces of the body wall scales, as well as those of the opercular and coenenchymal scales, are virtually smooth. The 8 opercular scales are similarly-shaped (H:W = 1.75–2.20), symmetrical, isosceles triangles, having a blunt, rounded apical angle of about 30°. The abaxial operculars are up to 0.45 mm in height, the adaxials only slightly less tall (e.g., 0.37 mm). As mentioned above, the surface of the operculars is smooth and without ridges, whereas their undersurface is tuberculate. When contracted, the operculars form a closely fitted, overlapping, low operculum.

Coenenchymal scales occur in one imbricating layer, are flat, and elliptical to irregular in shape, the largest scales being about 0.25 mm in length. Tentacular scales were not noted.

Etymology.—The species name *laxiramosa* (Latin: *laxus*, loose, slack, and *ramosus*, branching) refers to the loose branching mode of the colonies as well as the limp tension of the branchlets.

Comparisons.—Among those western Atlantic species of *Plumarella* having smooth-edged marginal scales (Table 1), *P.*

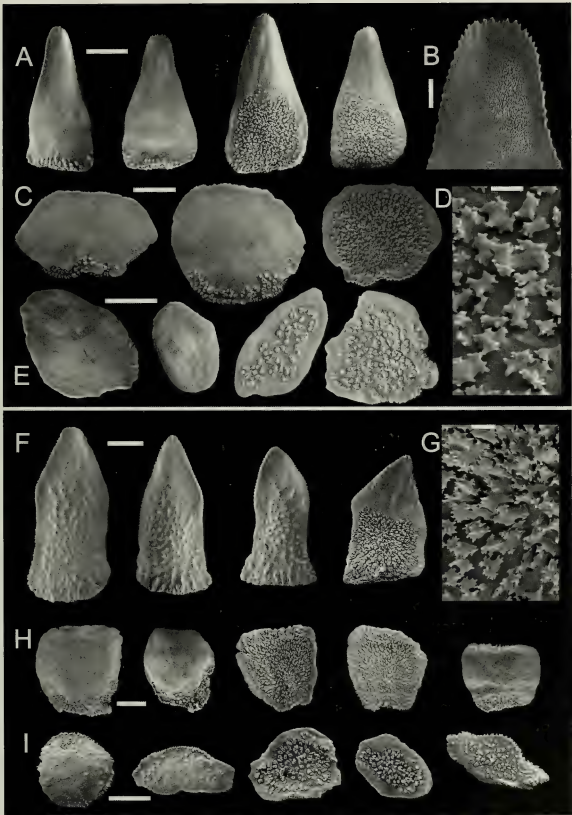


Fig. 5. A-E, *Plumarella laxiramosa*, holotype: A, upper and undersurfaces of 4 opercular scales; B, tip of undersurface of an opercular showing fine serration of edge; C, upper and undersurfaces of 3 body wall scales; D, tubercles on underside of a body wall scale; E, upper and undersurfaces of 4 coenenchymal scales. F-I, *Plumarella dichotoma*, holotype: F, upper and undersurfaces of 4 opercular scales; G, tubercles on underside of an opercular scale; H, upper and undersurfaces of 5 body wall scales; I, upper and undersurfaces of 5 coenenchymal scales. Scale bars for A, C, E-F, H-I = 0.10 mm; B = 25 μ m; D, G = 10 μ m.

laxiramosa is most easily distinguished by its growth form (loose pinnate) and by having a third, anterior row of branchlet polyps, which leads to a high number of polyps/cm. It is also distinguished by having no surface granulation on any scales.

Distribution.—Off North Carolina (to 34°15'N) and South Carolina; 348–625 m.

Plumarella dichotoma, n. sp.

Figs. 5F–I, 6A–C, 10C

Material examined/types and type locality.—Holotype, Gos-2387, 1 colony and SEM stubs C1087–1089, USNM 57307. Paratypes: *Alb*-2666, 10 colonies, USNM 49423; *Alb*-2667, 9 colonies, USNM 49431; *Alvin* 77-762, 1 colony, USNM 1019427; *Alvin* 1335, 1 dry colony, USNM 73739; *Anton Dohrn* 65-32, 3 dry branches, USNM 1019429; *Cape Hatteras* SA6-5, 5 colonies, USNM 79780; *Eastward* 26004, 2 colonies, USNM 1019430; *Eastward* 26023, 1 colony, USNM 1019431; *G*-169, 2 colonies, USNM 52990; *G*-170, 1 colony, USNM 52996; *Gos*-2344, 3 colonies, USNM 58447; *Gos*-2387, 10 colonies, USNM 1019428; *Gos*-2413, 7 colonies, USNM 1019432; *Gos*-2469, 1 colony, USNM 59021. Type Locality: 31°14'48"N, 78°59'W (off South Carolina), 530 m.

Diagnosis.—Distal edge of marginal scales straight or rounded; branching dichotomous, sometimes lyrate, branchlets relatively short and wiry; opercular and body wall scales smooth; 8–10 polyps/cm (polyps widely spaced), standing perpendicular to branches on large-diameter branchlets.

Description.—Colonies are flabellate and usually slightly curved, as in *P. pourtalesii*, but consistently dichotomously branched. The main stem is attached to a substrate by a thin calcareous encrustation and rises only 12–16 mm before it bifurcates, producing an axil angle of 65°–85°. Subsequent equal, dichotomous branching occurs at intervals of 5–12 mm, although some end branches are up to 40 mm in length and are the result

of 7–11 previous branching nodes. Terminal branchlets are wiry to limp in tension. Higher order axil angles are slightly smaller, i.e., 40°–45°, undamaged colonies usually being slightly broader than tall. In some large colonies the two outermost branches remain slightly larger than their inner branchlets (unequal dichotomous branching), as in the holotype, producing a lyrate form. The largest colony (the holotype) is 11 cm in height, 13 cm in width, and has a basal main stem diameter of 1.4 mm, although most colonies examined were considerably smaller. The axis is golden yellow and the colony appears white in alcohol.

As in all species of *Plumarella*, the polyps are biserially arranged in alternating fashion on the edges of all branches, angled slightly toward the anterior side of the flabellum, and standing perpendicular to large-diameter branches, but inclined distally in smaller-diameter distal branches. Polyps are widely spaced, adjacent polyps on the same side of a branch separated by as much as 2.0 mm. Polyps are fairly tall and slender, up to 1.3 mm in height and 0.65 mm in apical diameter.

The polyps are protected by 8 opercular and 8 rather disorganized rows of body wall scales, both ab- and adaxial rows containing 5 or 6 scales. Body wall scales are smooth, quickly decreasing in size from the marginal to the more proximal ones. The distal edges of the marginals are straight to slightly rounded and the scales themselves are square to slightly rectangular. The opercular scales are modified isosceles triangles (almost pentagonal), the two long sides of the triangle being parallel for much of the length, only the distal third having an apical angle of 45°–50°, culminating in a blunt tip. Abaxial opercular scales are up to 0.50 mm in height, adaxial, 0.35 mm; the H:W ranges from 1.7–2.3. Operculars have a granular upper surface and a tuberculate lower surface, devoid of a keel. They infold to form an operculum as illustrated in Fig 9f.

Coenenchymal scales are mildly granular

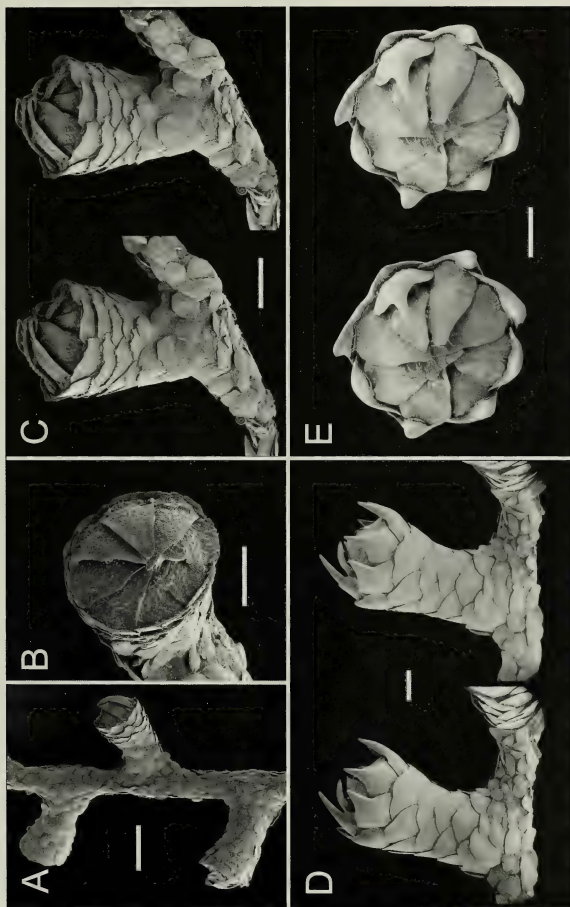


Fig. 6. A-C, *Plumarella dichotoma*, holotype: lateral view of a branch, opercular view, and stereo lateral view of polyp. D-E, *Plumarella aurea*, AH-266-40: stereo lateral view of a polyp and stereo view of operculum and surrounding spined marginals. Scale bars for A = 0.50 mm; B-E = 0.25 mm.

above, tuberculate below, and irregularly elliptical in shape, rarely over 0.25 mm in greater diameter.

Etymology.—The species name *dichotoma* (Greek: to be divided into two parts), is an allusion to the dichotomous branching of the colonies.

Comparisons.—Among the western Atlantic species of *Plumarella*, *P. dichotoma* is unique in having both dichotomous branching and smooth-edged marginal scales (Table 1). It is also distinctive in having such widely spaced polyps that are often oriented perpendicular to the branches.

Distribution.—Off southeast coast of United States from South Carolina to off Dry Tortugas, Florida; 494–1065 m.

Plumarella aurea (Deichmann, 1936)

Figs. 1C, 6D–E, 7A–D

Thouarella aurea Deichmann, 1936:165–166, pl. 25, figs. 12–13, pl. 26, fig. 11.—Bayer, 1954a:281 (listed).

Plumarella pourtalesii.—Deichmann, 1936:156 (in part: 2 of 4 specimens from *Bibb* 22, Bahia Honda).

Plumarella aurea.—Bayer, 1981:934, fig. 70 (new combination).—Bayer & Cairns (Verrill), 2004: pl. 25, 6a, pl. 83, 1a.

Material examined.—*Alb*-2666, 4 colonies, USNM 52984; *Alb*-2667, 5 colonies and 1 unnumbered SEM stub, USNM 52985; *Alb*-2668, 4 branches, USNM 1019312; *Alvin* 77-762, 3 colonies, USNM 1019313; *Atl*-3780, 15 dry colonies, MCZ; *Atl*-3782, 1 dry colony, MCZ 54327; *Atl*-266-40, 5 colonies and SEM stub 390, USNM 58443; *Atl*-266-41, 5 colonies, USNM 1019314; *Cape Hatteras SA* 6-5, 2 colonies, USNM 1019315; *Discoverer X*, 1 colony and SEM stub 391, USNM 58446; *Eastward* 26004, 1 colony, USNM 1019316; *Eastward* 26022, 2 branches, USNM 1019317; *Eastward* 26023, 4 dry branches and 1 in alcohol, USNM 1019318; *G*-672, 1 colony, USNM 52974; *G*-679, 1 colony, USNM 1019319; *G*-936, 1 branch, USNM 1019320; *Gos*-2385, 4 colonies and

SEM stub C1092, USNM 56892; *Gos*-2414, 6 colonies, USNM 1019321; *O*-11716, 1 colony, USNM 59500; *P*-105, 3 colonies, USNM 52976; *SB*-453, 1 colony, USNM 51265; syntypes (see below); specimens misidentified as *P. pourtalesii* by Deichmann (1936) from the type locality, *Bibb* 22 (MCZ 59442).

Types and type locality.—Five small branches (syntypes) preserved in alcohol are deposited at the MCZ (4801), which also bear Verrill's number 8042. An unnumbered SEM stub of one of these branches is also deposited at the USNM. Type Locality: 24°14'20"N, 80°59'40"W (off Bahia Honda, Straits of Florida off Florida Keys), 310 fathoms (=567 m). Although not stated in the original description, a label with the type specimens indicates they were collected at *Bibb* 22 (dredge 12), made on 4 May 1868.

Diagnosis.—Distal edge of most marginal scales prominently spinose; branching dichotomous; opercular, body wall, and coenenchymal scales smooth; polyps crowded, sometimes on anterior face, 14–22 polyps/cm.

Description.—Colonies are flabellate and dichotomously branched. The main stem is attached to the substrate by a thin calcareous expansion and rises only 5–8 mm before it bifurcates, producing an axil angle of about 55°; subsequent axial angles are 40°–45°. Branching is usually equal and dichotomous, occurring at intervals of 5–10 mm, but some terminal branches are up to 10 cm in length. Branches and colonies are quite flexible in tension, almost limp. The largest colony examined (*Gos*-2385) is 13 cm in height, 12 cm in width, and has a main stem diameter of 1.5 mm. The axis is golden-yellow and the colony appears white in alcohol.

Polyps are crowded, occurring biserially in alternating or opposite fashion on the branchlets and often with occasional polyps on the anterior side, resulting in 14–22 polyps/cm. Polyps are oriented perpendicular to the branches or tilted only slightly ante-

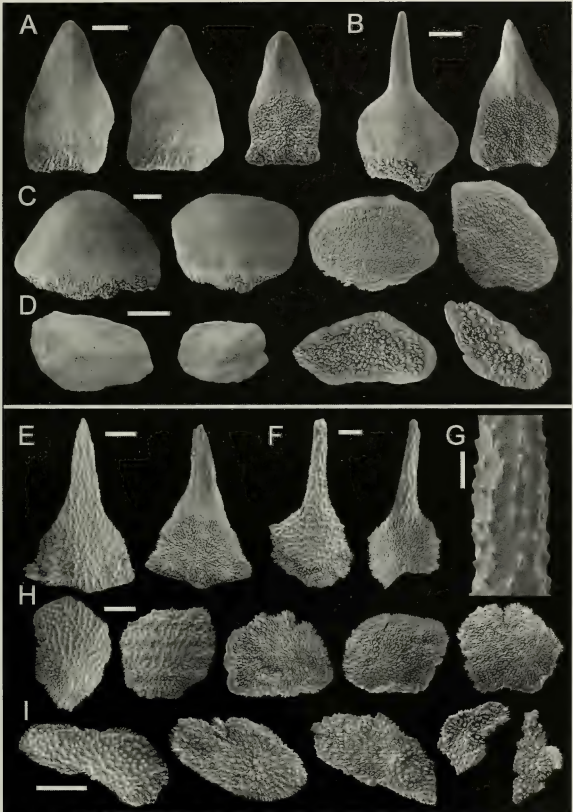


Fig. 7. A–D, *Pluromarella aurea*, Gos-2385: A, upper and undersurfaces of 3 opercular scales; B, upper and undersurfaces of 2 marginal scales; C, upper and undersurfaces of 4 body wall scales; D, upper and undersurfaces of 4 coenenchymal scales. E–I, *Pluromarella aculeata*, paratype from G-252: E, upper and undersurfaces of 2 opercular scales; F, upper and undersurfaces of 2 marginal scales; G, spination on marginal spine; H, upper and undersurfaces of 5 body wall scales; I, upper and undersurfaces of 5 coenenchymal scales. Scale bars for A–F, H–I = 0.10 mm; G = 25 μm.

riorly. They are usually squat, cylindrical, and robust, 0.8–1.2 mm in height (depending on contraction) but always 0.75–0.80 mm in apical diameter.

Each polyp is protected by 8 opercular and 8 well-defined rows of body wall scales, the abaxial rows having 6 or 7 scales, the adaxial, 5 or 6. The distal edges of the marginal body wall scales are usually strongly spinose, the 8 tooth-like spines forming a small crown encircling the operculum and often rising above it. Occasionally 1 or 2 of the marginals of a polyp lack spines or have reduced spines, but most polyps have 8 prominent, equal-sized spines. The marginal spines are sharp (apical angle 20°–25°), often constituting half the height of the marginal scale, a large spine being up to 0.25 mm in length and 0.08 mm in basal diameter, contributing to a H:W for this kind of scale of up to 1.3–1.5, the low value due to the wide base of the marginal scales. The marginal spines are circular in cross section and have finely serrate edges where they join the lower rectangular section of the scale (Fig. 7B). Opercular scales are fairly flat (not curved) and isosceles triangular in shape, the distal point being somewhat rounded, forming an angle of 33°–45°. Abaxial opercular scales are up to 0.55 mm in height, adaxial only 0.30 mm; the H:W ranges from 1.5–2.0. The upper surfaces of the body wall and opercular scales are smooth, the undersurfaces covered with complex tubercles that are up to 15–16 μm in diameter.

Coenenchymal scales are also smooth above, tuberculate below, and irregularly elliptical, elongate, or circular in shape; and up to 0.40 mm in greater diameter.

Comparisons.—Among the western Atlantic *Plumarella* having spinose marginal scales, *P. aurea* is most similar to *P. aculeata* (see that description and Table 1).

Distribution.—Blake Plateau from off South Carolina (32°10'N) through Straits of Florida to off Bahia Honda; Northwest Providence Channel, Bahamas; 310–878 m.

Plumarella aculeata, n. sp.

Figs. 7E–I, 8A–B, 9a–g, 10E

Material examined/types and type locality.—Holotype: G-707, USNM 52980, 1 dichotomous colony and SEM 248. Paratypes: Cape Florida X, 11 pinnate colonies, USNM 1019533; Eastward 26535, 15 pinnate branches, USNM 1019534; Eastward 26547, 2 dichotomous colonies, USNM 1019535; G-241, 1 pinnate branch, USNM 1019536; G-252, 2 pinnate branches and SEM stubs 255 and C1090, USNM 52979; G-633, 2 pinnate colonies, USNM 52983; G-692, 8 pinnate colonies, USNM 52986; G-695, 1 dichotomous colony, USNM 52978; G-707, 5 dichotomous and 1 lyrate colonies, USNM 52981–52982; G-1125, 3 pinnate colonies, USNM 52977; G-1312, 1 lyrate colony, USNM 52975; SB-440, 4 dry pinnate branches, USNM 51292. Type Locality: 26°27'N, 78°40'W (Northwest Providence Channel, Bahamas), 514–586 m.

Diagnosis.—Distal edges of 4–7 marginal scales prominently spinose, the spines corresponding to those opercular scales that have one or both of their edges overlapped by flanking opercular scales; branching variable, including dichotomous, close-pinnate, and lyrate; all scales covered with a low, often inconspicuous, granulation; 10–12 perpendicularly oriented polyps/cm.

Description.—Colonies are flabellate, slightly convex, and occur in three branching forms: dichotomous, lyrate, and close-pinnate. The most commonly collected form is close-pinnate, colonies up to 12 cm in height and 11 cm in width, with a basal branch diameter of 1.7 mm, and consisting of 4 or 5 distinct plumes. Internodes are only 3–5 mm apart, producing a series of closely spaced, parallel, wiry branches that rarely exceed 4 cm in length. Dichotomous colonies are usually smaller, the holotype only 6 cm tall, 7.5 cm in width, and having a basal stem diameter of 0.8 mm. The first bifurcation occurs 7–11 mm above the substrate; subsequent branching occurs every 3–10 mm, distal branchlet rarely more than

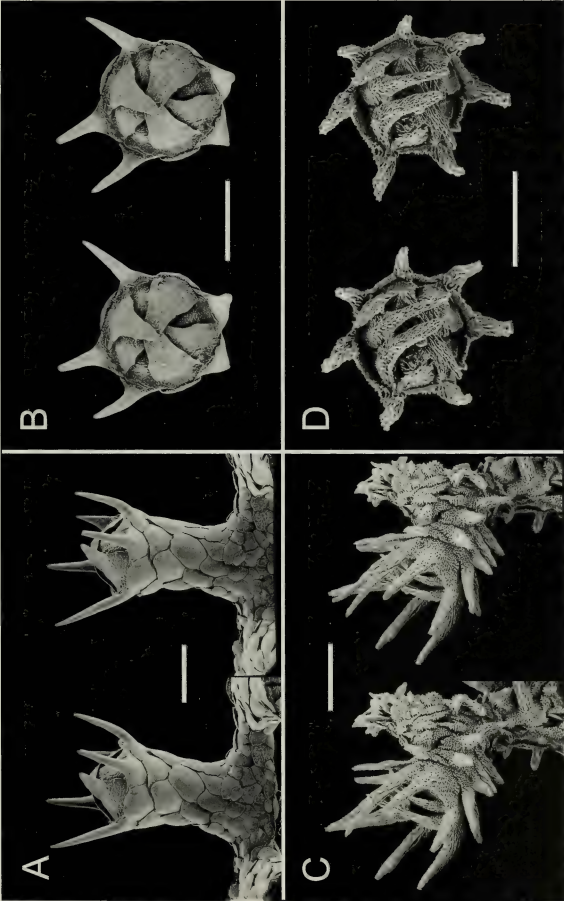


Fig. 8. A-B, *Plunarella aculeata*, holotype: stereo lateral view of an operculum showing characteristic arrangement (see Fig. 9b) of opercular spines. C-D, *Acanthoprimnoa goesi*: C, G-679, lateral stereo view of a polyp showing well-developed body wall spines; D, G-633, stereo view of operculum and surrounding marginal spines. All scale bars = 0.50 mm.

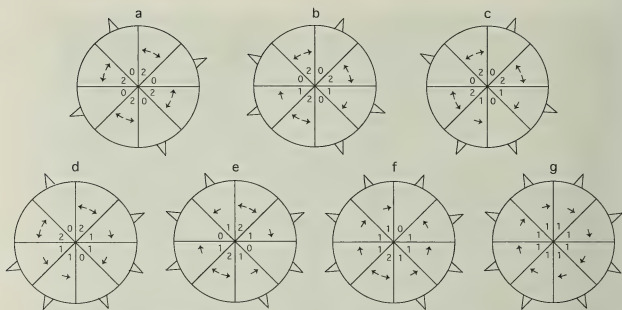


Fig. 9. Diagrammatic representation of seven arrangements (a-g) of marginal and opercular scales in *Plu-marella aculeata*, as viewed from above the operculum. The eight large triangles of each figure are the 8 operculars; the smaller triangles are the corresponding marginal scale spines. The numbers on the operculars indicate how many of its two edges overlap an adjacent opercular, the arrows also indicating which edge overlaps an adjacent opercular. Spines occur only on those marginal scales corresponding to operculars having one or both of its edges overlapped by an adjacent opercular; marginal corresponding to operculars that are overlapped by both adjacent operculars do not have a spine.

3 cm. The lyrate form is believed to be a variation of the dichotomous form. The axis is yellow-gold; polyps (in alcohol) are white.

Polyps are arranged biserially in the plane of the flabellum in an alternating fashion and are well spaced (1 mm apart), resulting in 10-12 polyps/cm. Polyps are oriented away from the convex side of the flabellum (toward the anterior side) and usually perpendicular to the branchlet. Polyps are distally flared, and including the elongate marginal spines, measure up to 1.8 mm in height and 0.7-0.8 mm in distal diameter.

Each polyp is protected by 8 operculars and 8 rows of body wall scales, both ab- and adaxial rows having the same number of scales (3 or 4) as the polyp is not curved toward the branch. Four to seven (usually 5 or 6) of the marginal scales bear extremely long, slender, sharp (apical angle 8° - 10°) spines, that are cylindrical in cross section. They are slightly curved over the polyp

face and often lack granulation, thus appearing translucent, or may be covered with aligned spinules (Fig. 7G). The spine portion of the marginal scales constitutes 60-65% of the length of the scale, resulting in a H:W of 1.8-2.8. The basal portion of the spined marginals is massive: rounded or shield-shaped. The number and position of marginal spines appears to be directly correlated to the corresponding opercular scales that have one or both of their edges overlapped by flanking opercular scales. Opercular scales that overlap both adjacent operculars do not have a corresponding spinose marginal, their distal margins being only slightly rounded. Because every polyp has 8 operculars and thus 16 opercular edges, and every edge must either overlap or be overlapped by an adjacent opercular, it is mathematically possible for 4 to 8 operculars to have one or two edges overlapped, resulting in a polyp with 4-8 marginal spines (Fig. 9). Polyps having only 4-7 marginal spines have been observed; the



Fig. 10. A, *Plumarella pellucida*, holotype; B, *P. laxiramosa*, holotype; C, *P. dichotoma*, holotype; D, *Candidella imbricata*, Gos-2384; E, *Plumarella aculeata*, holotype; F, *Acanthoprinnoa goesi*, Atl-3465, MCZ 3741. Scale bars for A, B, F = 5 cm; C-E = 2.5 cm.

hypothetical 8-spined polyp has not been seen. Body wall scales of the second and third tier are large, thick, rectangular, and have rounded upper edges; they are smooth or bear only low granules. The fourth tier of scales consists of small scales indistinguishable from the coenenchymal scales. The opercular scales are isosceles triangular in shape with a broad base and attenuate rounded tips that form an apical angle of 20° – 25° ; their edges are finely serrate and their upper surface smooth to inconspicuously granular. Operculars are up to 0.62 mm in height and have a narrow range of H:W of 1.6–2.2.

Coenenchymal scales are flat, irregular in shape, 0.20–0.40 mm in width or diameter, and have a conspicuously granular upper surface. The undersurface of all scales and the upper proximal sides of most where the scale is overlapped by an adjacent scale, are covered with complex tubercles up to 18 μ m in diameter.

Etymology.—The species name *aculeata* (Latin: *aculeatus*, sharp-pointed) is an allusion to the extremely long, sharp-pointed spines of the marginal scales.

Comparisons.—Six species of *Plumarella* are characterized by having spinose marginal spines (Kükenthal 1919); four of those six endemic to Japan. *Plumarella aculeatus* differs from these in having extremely elongate and sharp marginal spines that occur only on those marginal scales that correspond to opercular scales that have overlapped margins (Figs. 8B, 9).

Distribution.—Insular northern Straits of Florida; Northwest Providence Channel, Bahamas; 400–900 m.

Acanthoprímnoa, n. gen.

Type species.—*Plumarella goësi* Aurivillius, 1931, here designated.

Diagnosis.—Primnoidae with a well-defined operculum; polyps usually inclined apically, each completely surrounded by 8 rows of body wall scales; polyps arranged alternately and biserially; 8 marginal scales,

each with a spinose or finely serrate (pectinate) distal margin; no sclerites bear tubercles on their under surfaces; opercular scales not keeled; colonies uniplanar, usually pinnately branched (plumose), dichotomous, or lyrate. Brooding polyps are common.

Distribution.—Straits of Florida, Bahamas, Yucatan Peninsula, Lesser Antilles; Japan; 60–1125 m.

Remarks.—In his unpublished manuscript on the western Atlantic deep-water octocorals (Bayer & Cairns 2004), Verrill referred to the type species of this genus as *Acanthoprímnoa aspera*, a species later described by Aurivillius as *Plumarella goësi*. Because only Verrill's plates and not the text survived we do not know what criteria he used to distinguish his new genus. We separate this genus from the morphologically similar *Plumarella* by three criteria: the lack of tubercles on the undersurfaces of the sclerites, the distinctive pectinate distal edges of the body wall and opercular scales, and the coarsely granular coenenchymal scales. Two other species, previously placed in *Plumarella*, also share these characteristics and are transferred to *Acanthoprímnoa*: *A. sërta* (Kükenthal & Gorzawsky, 1908), n. comb. and *A. cristata* (Kükenthal & Gorzawsky, 1908), n. comb.

Etymology.—The genus name *Acanthoprímnoa* (Greek: *acantha*, a thorn + *primnoa*, a common suffix used in this family) is an allusion to the spiny nature of the polyps of the type species.

Acanthoprímnoa goësi (Aurivillius, 1931), n. comb.

Figs. 8C–D, 10F, 11A–I, 12A–B

?*Primnoa Pourtalesii*.—Hargitt & Rogers, 1901:281, fig. D.

Plumarella goësi Aurivillius, 1931:244–248, pl. 5, figs. 6a–b, text fig. 47, 3–5.—Bayer, 1957:388 (Cay Sal Bank).

Thouarella goësi Deichmann, 1936:164–165, pl. 25, figs. 2, 19–23, pl. 26, fig. 8.—Bayer, 1954a:281 (listed).

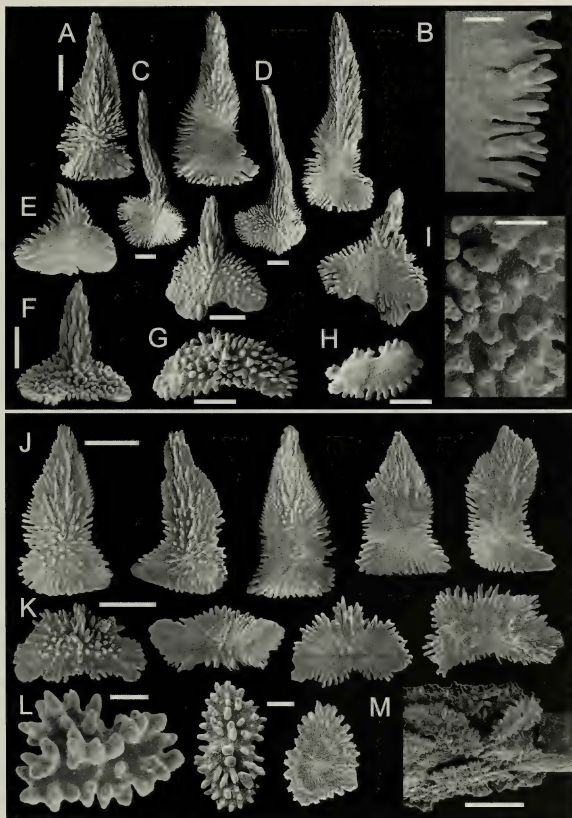


Fig. 11. A-I, *Acanthoprismoa goesi*, G-633: A, upper and undersurfaces of 3 opercular scales; B, pectinate edge of an opercular; C-D, under and upper surfaces of 2 marginal scales; E, upper and undersurfaces of 3 body wall scales; F-H, upper and undersurfaces of 3 coarsely granular coenenchymal scales, F having a central spine; I, granules on upper surface of a coenenchymal scale. J-M, *Acanthoprismoa pectinata*, holotype: J, upper and undersurfaces of 5 opercular scales; K, upper and undersurfaces of 4 butterfly-shaped body wall scales; L, upper and undersurfaces of 3 coarsely granular coenenchymal scales; M, coenenchymal scales on a branch. Scale bars for A, C-H, J-K, M = 0.10 mm; B, I, L = 25 μ m.

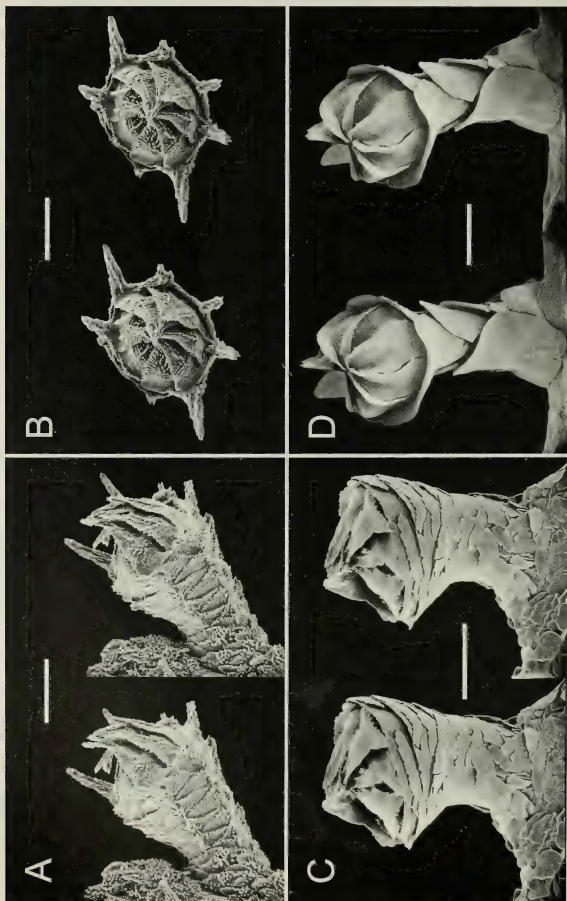


Fig. 12. A-B, *Acanthoprimnoa goesi*, G-897: stereo lateral view of a polyp and stereo view of operculum and surrounding marginal spines. C, *Acanthoprimnoa pectinata*, G-692, stereo lateral view of a polyp. D, *Candidella imbricata*, Eastward 26031, stereo lateral view of a polyp. Scale bars for A-C = 0.25 mm; D = 0.50 mm.

"*Acanthoprimnoa aspera*" Bayer & Cairns (Verrill), 2004: pl. 10, fig. 8, pl. 13, fig. 8a, pl. 27, figs. 5a–b, pl. 141, fig. 6.

Material examined.—*Alb*-2342, 10 dry pinnate colonies, USNM 10236; *Alb*-2343, 1 pinnate colony, USNM 10243; *Alb*-2346, 1 pinnate colony, USNM 10783; *Alvin* 846, 3 dry pinnate colonies, USNM 79517; *Alvin* 77-764, 4 pinnate colonies, USNM 96825; *Atl*-2999, 10 dry pinnate branches, MCZ 54324 and 3832; *Atl*-3402, 4 dry pinnate branches, MCZ 3703; *Atl*-3403, 7 dry pinnate branches, MCZ 54335; *Atl*-3438, 3 dry pinnate branches, MCZ 3751; *Atl*-3463, 7 dry pinnate colonies, MCZ 3604; *Atl*-3465, 54 dry pinnate colonies, MCZ 3744a, 3741, and 3737; *Atl*-3466, 17 dry pinnate colonies, MCZ 3603; *Atl*-3478, 20 dry pinnate colonies, MCZ 3605; *Atl*-3479, 17 dry pinnate colonies, MCZ-3608 and 3759; *Atl*-3480, 11 dry pinnate colonies, MCZ 3668 and 3762; *Atl*-3482, 32 dry pinnate colonies, MCZ 3654 and 3663; *Cape Florida* X, 8 pinnate colonies, USNM 73932; JS-43, 6 pinnate colonies and 1 unnumbered SEM stub, USNM 43801; JS-102, 1 dry pinnate colony, USNM 1011364 (topotypic); JS-103, 3 pinnate colonies, USNM 50951 (topotypic); *Eastward* 26537, 2 pinnate (USNM 98161) and 13 dichotomous colonies (USNM 98850); *Eastward* 26538, 10 pinnate branches, USNM 1019537; *Eastward* 26549, 1 pinnate colony (USNM 75064) and 24 dichotomous colonies (USNM 75065, 76987, and 79485); *Eastward* 26550, 53 pinnate colonies, USNM 94500; *Eastward* 26559, 8 dichotomous (USNM 98851) and 1 pinnate colony (USNM 98852); *Eastward* 31281, 15 pinnate colonies, USNM 94522; *G*-235, 3 pinnate colonies, USNM 98853; *G*-241, 16 pinnate colonies, USNM 52966; *G*-242, 1 pinnate colony, USNM 52968; *G*-251, 2 pinnate colonies, USNM 52969; *G*-252, 1 pinnate branch, USNM 98854; *G*-254, 1 pinnate colony, USNM 52962; *G*-387, 12 pinnate colonies, USNM 52970; *G*-533, 1 pinnate colony, USNM 52971; *G*-633, 13

pinnate colonies and SEM stubs 258 and C1091, USNM 52973 and 52983; *G*-679, 8 pinnate colonies and SEM stub 256, USNM 52963; *G*-680, 4 dichotomous colonies, USNM 1019538; *G*-696, 1 pinnate colony, USNM 52972; *G*-704, 1 pinnate colony, USNM 52965; *G*-706, 25 pinnate colonies, USNM 52967; *G*-707, 1 pinnate colony, USNM 98855; *G*-879, 2 dichotomous colonies, USNM 76988; *G*-897, 10 dichotomous colonies and SEM stub 257, USNM 52964; *P*-594, over 50 pinnate colonies, USNM 52961, and 4 dichotomous colonies, USNM 98856; *P*-596, 2 dichotomous colonies, USNM 52960; *P*-598, 1 pinnate colony, USNM 52957 and 1 dichotomous colony, USNM 98858; specimens reported by Deichmann (1936) and Bayer (1957); a syntype (USNM 44192).

Types and type locality.—Three specimens are mentioned in the original description, only one of which was figured; all three are considered to be syntypes. They are deposited at the Stockholm Museum (#28); a fragment of one of the colonies is also deposited at the USNM (44192). Type Locality: "Virgin Islands", 457–548 m.

Diagnosis.—Distal edges of 7 marginal scales (not one of the adaxial marginals) prominently spinose; branching dichotomous in shallow-water form and close pinnate in deeper-water form, branchlets flexible but not flaccid; opercular scales covered with numerous tiny spines, abaxial and outer-lateral body wall scales bear single, robust spines on distal margin; coenenchymal scales highly granular and sometimes bear a single tall spine; 13–15 polyps/cm; branch axis bronze; polyp brood chambers common.

Description.—Colonies are flabellate and occur in two branching forms. The deeper water form is larger (up to 30 cm in height and equally broad), with closely pinnate branching colonies consisting of 2 or 3 regular plumes. Pinnate branchlets begins within 5 mm of the base and are subsequently arranged in a regular parallel fashion, the internodes being only 2–3 mm in

length; unbranched terminal branchlets are flexible and rarely exceed 4 cm in length. These large colonies are attached by a calcareous holdfast that may reinforce the main stem as much as 15 mm above the base and attain a diameter of 4 mm. As with most species of *Plumarella*, the colony flabellum is slight convex, with the polyps directed slightly upward and toward the convex face. The shallow-water form is much smaller (rarely exceeding 4 cm in height) and is dichotomously branched, often resulting in a colony broader than tall. Internodes are 2–4 mm in length; terminal branchlets are rarely more than 15 mm and number only about 10–15; the basal axis is about 0.5 mm in diameter. In both forms the axis is a rich bronze color, which contrasts with the white (in alcohol) color of the polyps.

Polyps are arranged biserially in the plane of the flabellum in an alternating fashion and are well spaced approximately 0.6–0.8 mm apart, resulting in 13–15 polyps/cm. Polyps of the deep-water form are 0.8–1.2 mm in height (including the marginal spines) and about 0.5 mm in diameter; polyps of the shallow water form are smaller, usually less than 0.8 mm in height. As mentioned in the remarks section, some polyps of both forms have brood chambers that greatly swell the base of the polyp.

Each polyp is protected by 8 opercular and 8 rows of body wall scales, the abaxial row having 5 or 6 scales, the adaxial, 4 or 5. Seven of the 8 marginal body wall scales bear a prominent distal spine, the 8th (adaxial) marginal having a very reduced spine, allowing the abaxial opercular scales to overlap the polyp edge at that point of the circumference (Fig. 8D). The marginal scales have a flat, rectangular to ellipsoidal base up to 0.4 mm wide from which the elongate, sharp-tipped (apical angle 7° – 8°), often crooked spine emerges. The entire marginal scale may be up to 0.85 mm in height, the spinose part constituting 75–85% of its height and contributing to a rather high H:W of 1.7–3.2. The elongate spi-

nose part of each marginal scale is spinose itself, bearing prominent rows of smaller spines (25–30 μ m in length), which are arranged in rows on both the upper and lower surface of the spine. The smaller spines also cover the edges and upper surfaces of the base of the marginals, but the undersurfaces of the marginal base, covered by tubercles in all species of *Plumarella*, is smooth. The body wall scales of the abaxial and inner-lateral rows that lie proximal to the marginals also have apical spines, but these are quite variable in size, some quite large (up to half the height of the scale), others inconspicuous. The body wall scales of the adaxial and outer-lateral rows that lie proximal to the marginals have greatly reduced or no apical spines. The opercular scales are similar to the marginal scales in many ways but are isosceles triangular in shape, not having a rectangular base, and often have a notch on either side near the base. The abaxial operculars are quite elongate (up to 0.7 mm) and, when closed, often completely traverse the polyp. Their tips are pointed (apical angle 15° – 25°), with a H:W ranging from 1.8–3.9. As with the marginal spines they are covered with prominent spines on the upper and undersurfaces, except for the undersurface of the base, which is smooth. All three edges of the opercular scales are serrate, but in the region of the proximal notches the serrations are developed into elongate (up to 40 μ m long and 9 μ m in diameter), finely granular pillars that often bi- and trifurcate (Figs. 11A–B).

Coenenchymal scales are rather large (up to 0.5 mm) and have coarse granular edges and surfaces, the granules rounded and up to 12 μ m in diameter and often twice as tall. Some coenenchymal scales also bear a prominent, centrally located, perpendicular spine up to 0.3 mm in height and 0.1 mm in basal diameter. These spines are ornamented with smaller spines similar to those on the opercular and marginal scale spines. The undersurface of the coenenchymal scales is smooth.

Comparisons.—See *A. pectinata*.

Distribution.—Throughout the Straits of Florida to Arrowsmith Bank, Yucatan Channel; Northwest Providence Channel; Old Bahama Channel; Puerto Rico (Hargitt & Rogers 1901); Virgin Islands. In general, the dichotomous form occurs from 137–350 m and the pinnate form deeper, 320–595 m.

Remarks.—The only differences between the two forms, aside from their different range of capture depths, are that the deeper-water form has close pinnate branching, a larger colony, and larger polyps, whereas the shallow-water form has dichotomous branching, a smaller colony, and smaller polyp size. All other characters are quite similar, unique characters including the brooding polyps, spinose body wall and coenenchymal scales, and long, spiny operculars. Several stations contain both forms (see material examined), but in general the forms occur at different depth ranges. Some colonies are transitional in form, beginning as dichotomous but with a tendency toward pinnate branching at least in part of the upper colony. Such was the syntype illustrated by Aurivillius (1931: pl. 5, fig. 6a), although he unequivocally classified that colony as dichotomous.

About one-third of the colonies examined contained polyps with bulbous brood chambers in their base, this feature occurring in both the dichotomous and pinnate forms. Among the colonies containing polyps with brood chambers, approximately one in 50 polyps would be so modified, but oftentimes there would be 2 or 3 contiguous brooding polyps. There appears to be no seasonality regarding the presence of the brooding polyps.

Acanthoprinoa pectinata, n. sp.

Figs. 1D, 11J–M, 12C

Material examined/types and type locality.—Holotype: *G*-899, 1 colony and SEM stubs C1093–1095, USNM 1019539. Paratypes: *Alb*-2354, 20 colonies and 1 unnumbered SEM stub, USNM 43026 and 75112; *Alvin* 77-760, 5 dichotomous colonies,

USNM 1019540; *Atl*-3303, 3 dry pinnate colonies, MCZ 3627; *G*-692, 2 branches and SEM stub 254, USNM 52954; *G*-889, 4 colonies, USNM 52952; *G*-898, 1 pinnate colony, USNM 52956; *G*-899, 19 colonies, USNM 52955; *O*-4940, 2 colonies, USNM 52953; *P*-592, 20 colonies, USNM 52958; *P*-954, 1 colony, USNM 52959; *SB*-5190, 6 pinnate colonies, USNM 1019541. Type Locality: 20°57'N, 86°34'W (off Arrowsmith Bank, Yucatan, Mexico), 40–164 m.

Diagnosis.—Distal edge of marginal scales straight or only slightly spines; branching loosely pinnate, branchlets long and flaccid; opercular scales ridged and covered with numerous tiny spines; lateral edges of opercular and distal and proximal edges of body wall scales bear a series of comb-like spines; coenenchymal scales coarsely granular, but without a central boss; 11–13 polyps/cm; branch axis bronze; polyp brood chambers common.

Description.—Colonies are flabellate and loosely pinnate, each colony consisting of 2 or 3 plumes, although one colony (*P*-594) is lyrate in branching. The first branchlets occur very near the base of the colony, succeeding branchlets at a periodicity of every 4–5 mm (internode length), the branchlets up to 55 mm in length and flaccid in tension. The main stem is anchored by a dense, calcareous, white holdfast, although the holdfasts of only five of the colonies are intact. Like *A. goesi*, the axis is bronze in color, which contrasts with the white polyps. The holotype is 18 cm in height, 7 cm in width, but lacks a base; the largest specimen (*Atl*-3303) is 22 cm tall. The largest main stem of an attached colony (*G*-899) has a diameter of only 1.1 mm.

Polyps are arranged biserially on the branchlets and main stem (6–7 polyps/internode on main stem) in an alternating fashion 0.8–1.1 mm apart, resulting in 11–13 polyps/cm. Polyps are relatively small, only 0.8–0.9 mm in height and 0.40–0.45 mm in diameter. Colonies from all stations recorded contain some polyps with brood

chambers, which greatly swell the base of those polyps.

Each polyp is protected by 8 opercular and 8 rows of body wall scales, the abaxial row consisting of 8–10 scales, the adaxial, 7–9. All body wall scales, including the marginals, are slightly curved to accommodate the curvature of the polyp, and considerably wider than tall, such that a relatively high number occurs in the wall of a relatively short polyp. The upper surface of the body wall scales bears many small spines, especially toward the center of the scale, and their distal and proximal margins bear a series of fine, comb-like (pectinate) projections measuring up to 32 μm in length. Only rarely will the marginal body wall scale have a larger, projecting spine, the largest up to 0.25 mm in length and constituting about half the height of the scale. The opercular scales are isosceles triangular in shape (H:W = 1.6–2.2), and strongly curved in order to cover the top of the rounded polyp. Operculars are up to 0.38 mm in height and have an apical angle of 35°–45°. They are sculptured as in *A. goesi*.

Coenenchymal scales are relatively small (0.09–0.21 mm in width) and circular to irregular in shape. As in *A. goesi*, they are densely covered on their upper surface with prominent, blunt granules measuring up to 15 μm in height and 10–12 μm in diameter, but smooth on the undersurface.

Etymology.—The species name *pectinata* (Latin: *pectinatus*, comblike) refers to the comb-like serration of the edges of the opercular and body wall scales.

Comparisons.—*Acanthoprinoa pectinata* resembles *A. goesi* in the morphology of its opercular spines, color of the branch axis, coarsely granular coenenchymal scales, and the common presence of brood polyps. Further, *A. pectinata* differs (Table 1) in lacking distally spinose body wall scales (instead having pectinate distal and proximal margins), lacking a central boss on the coenenchymal scales, having more scales/body wall row, having much shorter

operculars, and in having a looser pinnate branching mode. *A. pectinata* is most similar to the Japanese *A. cristata*, but lacks the longitudinal ridges on the body wall scales.

Distribution.—Off northeastern Yucatan Peninsula and northwestern Cuba (164–476 m); Straits of Florida; Mona Passage and off Montserrat, Lesser Antilles (614–686 m).

Remarks.—All but two colonies of *A. pectinata* occur in relatively shallow water (164–476 m) off the Yucatan Peninsula, but the colonies from P-954 (off Montserrat, Lesser Antilles) and Alvin 77-760 (Straits of Florida) occur in deeper water (614–686 m) and are the only colonies to have non-pinnately (dichotomous, lyrate) branching colonies.

Genus *Candidella* Bayer, 1954

Primnoa.—Johnson, 1862:245 (in part).

Stenella Gray, 1870:48 (junior primary homonym of *Stenella* Gray, 1866, a cetacean).—Wright & Studer, 1889:56 (in part).—Kükenthal, 1919:443–445 (in part); 1924:303 (in part).—Aurivillius, 1931:289–290 (in part).

Narella.—Studer, 1878:643 (in part).

Stenella (Primnoa).—Roule, 1896:304.

Stenella (Stenella).—Versluys, 1906:38–39.

Candidella Bayer, 1954b:296 (nom. nov.); 1981:937.—Tixier-Durivault, 1987:171.

Candidella (Candidella).—Bayer, 1956: F222.

Type species.—*Primnoa imbricata* Johnson, 1862, by monotypy.

Diagnosis.—Primnoidea with a well-defined operculum; polyps stand perpendicular to branch (not bent); polyp body wall completely surrounded by 2–4 rows of sclerites; polyps arranged in whorls; only four marginal scales; undersurfaces of all sclerites tuberculate, opercular scales strongly keeled; colonies dichotomously branched in one plane.

Distribution.—North Atlantic, Ascension, central and western Pacific; 183–2139 m.

Remarks.—Four species are known in

this genus: *C. imbricata* (Johnson, 1862); *C. johnsoni* (Wright & Studer, 1889), Ascension; *C. gigantea* (Wright & Studer, 1889), Fiji; and *C. helminthophora* (Nutting, 1908), Hawaiian Islands. After its original description, the monographers Kükenthal, Studer, and Aurivillius took a broad view of the genus *Stenella*, including similar species but some differing in having 5 or 8 marginal scales, these species later being transferred to *Parastenella*, *Pterostenella*, and *Dasystenella*. Versluys (1906) was the first to relegate what is now known as *Candidella* to a monophyletic group, the nominate subgenus of *Stenella*. After renaming the genus *Candidella* (Bayer, 1954b), because the name *Stenella* was a junior homonym, Bayer (1956) also recognized it as a monophyletic subgenus: *Candidella* (*Candidella*), subsequently elevating it to generic rank in 1981. Characters used to distinguish species include the arrangement of polyps, colony branching, and polyp size (Kükenthal 1924).

Candidella imbricata (Johnson, 1862)

Figs. 10D, 12D, 13A–G, 14A–D

Primnoa imbricata Johnson, 1862:245, pl. 31, figs. 2, 2a (Madeira); 1863:299 (verbatim).

Stenella imbricata.—Gray, 1870:48–49, 2 figs. (listed, new comb.).—Wright & Studer, 1889:56, 281 (listed).—Kükenthal, 1919:448–449 (*Blake* from Cuba, first record for western Atlantic); 1924:305–306 (diagnosis, key).—Thomson, 1927:32–33, pl. 2, fig. 9, pl. 3, fig. 9, pl. 5, figs. 5–6 (Azores, Morocco).—Aurivillius, 1931:290 (mentioned).—Deichmann, 1936:167–168, pl. 26, fig. 5 (West Indies).—Bayer, 1954a:281 (listed for Gulf of Mexico); 1964:532 (Straits of Florida).

Narella imbricata.—Studer, 1878:643 (listed, new comb.).

?*Stenella* (*Primnoa*) *johnsoni*.—Roule, 1896:304 (Gulf of Gascogne).

Stenella (*Primnoa*) *imbricata*.—Roule, 1896:304 (comparison to *C. johnsoni*).

Stenella (*Stenella*) *imbricata*.—Versluys, 1906:42–43, 44, fig. 46 (redescription of type, key to spp.).

Candidella imbricata.—Bayer, 1954b:296 (new comb.).—Tixier-Durivault & d'Hondt, 1974:1412–1413.—Grasshoff, 1981:222, map 1 (mid-Atlantic Ridge sw of Azores); 1982a:738, maps 4, 20; 1982b:948–949, figs. 20–21.—Grasshoff & Zibrowius, 1983:119–120, 122, pl. 2, fig. 7 (mid-Atlantic Ridge), pl. 3, fig. 14 (Biscay Bay).—Carpine & Grasshoff, 1985:6 (frontispiece), 33 (Musée Océanographique de Monaco catalog numbers).—Pasternak, 1985:29 (Rockaway Seamount).—Pettibone, 1991:705, 707 (polychaete commensal).

Candidella (*Candidella*) *imbricata*.—Bayer, 1956:F222, fig. 159–4b.

Candidella johnsoni.—Bayer, 1981:934, fig. 74.

Stenella “*florida*” Bayer & Cairns (Verrill), 2004: pl. 13, figs. 1, 1a, pl. 25, fig. 13a–b, pl. 82, figs. 2, 2a, pl. 83, fig. 6, 6a.

Material examined.—*Alb*-2753, 3 branch fragments, USNM 44126; *Alvin* 762, 6 branches, USNM 80939, 80940, and 1017255; *Alvin* 1335, 2 fragments (one dry), USNM 73744 and 73745; *Alvin* 3885–5, 1 complete colony, USNM 1019238; *Alvin* 3903-101–2, 1 branch, USNM 1019273; *Atl*-266-47, branch fragments, USNM 60337; *Atl*-280-9, 3 branches and SEM stub 273, USNM 57552; *CI*-63, 1 colony, USNM 60223; *CI*-140, 1 branch, USNM 60341; *Eastward* 26019, 6 colonies, USNM 60338; *Eastward* 26022, 2 colonies, USNM 60340; *Eastward* 26023, dry branch fragments, USNM 1011365; *Eastward* 26031, 3 colonies (some dry) and SEM stubs 274 and C1071–1076, 1078, USNM 57553 and 60339; *G*-169, 6 colonies, USNM 52778; *G*-170, 2 colonies and 1 unnumbered SEM stub, USNM 52779; *G*-177, 2 colonies, USNM 52780; *G*-386, 14 colonies and numerous branches, USNM 52784; *G*-660, 1 branch, USNM 52781; *G*-661, 1 branch, USNM 52782; *G*-936, 2

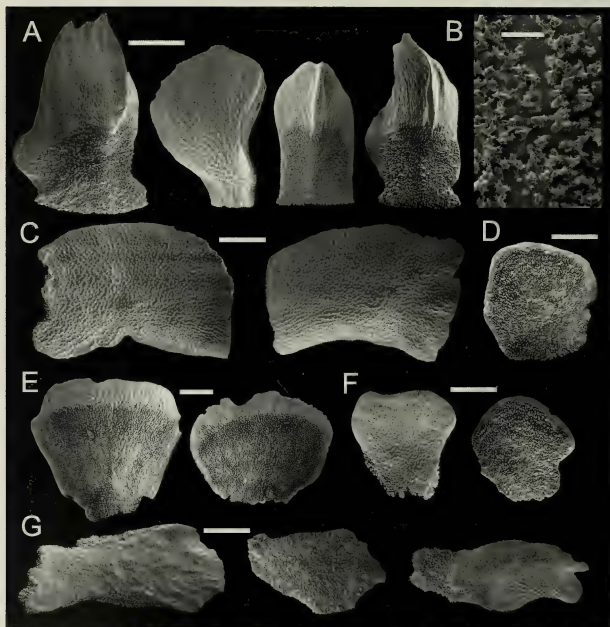


Fig. 13. A-G, *Candidella imbricata*, Gos-26031: A, upper and undersurfaces of 4 opercular scales; B, tuberculate undersurface of an opercular; C, upper surface of 2 basal body wall scales; D, F, upper and undersurfaces of 3 medial body wall scales; E, undersurface of 2 marginal scales; G, upper and undersurfaces of 3 coenenchymal scales. Scale bars for A, C-G = 0.25 mm; B = 25 μ m.

branches, USNM 52783; G-965, 1 colony, USNM 52787; Gos-2383, 1 colony, USNM 57309; Gos-2384, 1 colony, USNM 57310; Gyre CO4, 1 colony (dry), USNM 89124; P-197, 2 colonies, USNM 52785; P-881, 2 colonies, USNM 52786; P-892, 2 colonies, USNM 52911; P-1146, 1 branch, USNM 52912; off Bermuda, 1200 m, 1 colony, USNM 75104.

Types and type locality.—The holotype

is deposited at the BM (1863.1.31.1). Type locality: Madeira, depth unknown.

Description.—Colonies consist of a robust vertical main stem up to 9 mm in basal diameter, which supports a uniplanar fan achieved by dichotomous branching. The main stem is anchored by a dense, white, encrusting, calcareous holdfast, which often encrusts other calcareous Coelenterata, such as the scleractinians *Enallopsammia pro-*

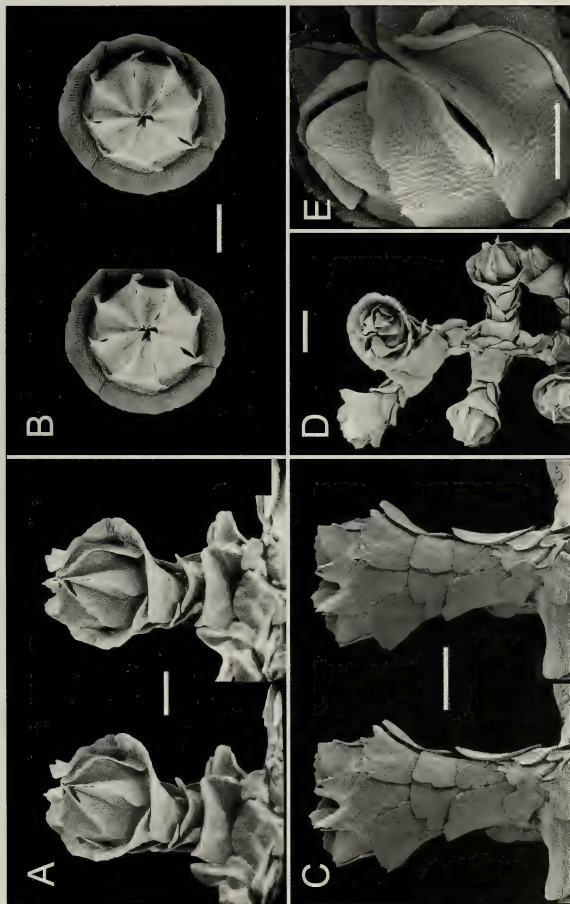


Fig. 14. *Candidella imbricata*: A-B, D, Atl-280-9; A, stereo lateral view of a polyp; B, stereo opercular view, also showing the four marginal scales; D, branch tip; C, E, Easward 26031; C, stereo view of the adaxial side of a polyp; E, close up of some opercular scales. Scale bars for A-C = 0.50 mm; D = 1.0 mm; E = 0.25 mm.

funda, *Lophelia prolifera*, *Javania cailetti*, the stylasterid *Stylaster erubescens*, and various bryozoans. The calcareous deposits may reinforce the basal stem as much as 2 cm upwards from the base. The holdfast and basal reinforcement are composed of 100% aragonite, consistent with the findings of Bayer & Macintyre (2001) for the congeneric *C. helminthophora*. The axis is yellow-gold in color and longitudinally striate; overall the colony is white. The largest known colony (the holotype) is reputed to be 21.6 cm in height and 27.9 cm in width. Branching is dichotomous at intervals of 3–12 mm, but unequal, resulting in asymmetrical branching; there is little to no branch anastomosis.

Polyps are arranged in whorls of 3 or 4 polyps (rarely as pairs); if in a whorl of 3, 2 polyps are usually directed in the plane of the fan in opposite directions, the third polyp standing perpendicular to the plane of the fan and thus at 90° to the other 2, the polyp projecting perpendicular to the fan defining the anterior face of the fan; few polyps originate from the posterior face of the fan. When 4 polyps constitute a whorl, the angular separation between polyps is not 90°, but about 60°, polyps avoiding the posterior face. Polyp whorls are closely spaced, about every 1.2–2.0 mm, 5–6 occurring per cm, polyps present even on the calcified region of the basal stem and holdfast. Most polyps are 2.1–2.5 mm in height and slightly clavate (1.3–1.4 mm in distal diameter), encased by the distal margin of the flared marginal scales, but some geographic outliers have larger polyps (see Remarks). Polyps are fairly rigid, projecting perpendicularly from the branches; however, those in the plane of the fan are sometimes slightly curved toward the anterior face.

Polyps are protected by 4 marginal scales, 2–4 medial scales, 4–8 basal scales, and 8 operculars. The marginal scales are dimorphic in size and shape, consisting of 2 adjacent larger (0.9 mm in height, 1.1 mm in width), highly curved scales that define

the abaxial side of the polyp and 2 adjacent smaller (0.65 mm in height, 0.62 mm in width), slightly curved adaxial scales, which overlap with the edges of the larger marginals. Three opercular scales correspond to each of the larger marginals, whereas about 1.5 operculars correspond to the smaller marginals, the number of operculars adding to more than 8 because of the overlap of marginal scales. The marginals are flared outward distally, rising about 0.15 mm above the junction with the opercular scales, but not enclosing the operculum. Medial body wall scales are roughly rectangular and flat, with sides measuring 0.45–0.65 mm in length; their lateral edges overlap one another. Sometimes it appears that only 2 medial scales are present, these occurring on the adaxial side. Basal scales are dimorphic in size, consisting of 2 large, square to rectangular scales up to 0.65–0.70 mm in side length, and outwardly concave, as though squeezing the base of the polyp into a narrow opening. When polyps become abraded from the branches, these large scales often remain to mark the original position of the polyp. Between the 2 large basal scales, on the adaxial side, are 1 or 2 pairs of much smaller basal scales that are overlapped and overshadowed by the larger basals. The 8 operculars are elongate triangular, having a H:W of 1.6–2.0, pointed distally, highly convex above, and prominently keeled below. They form a tight conical operculum over the polyp, rising well above the marginal scales. One of the 8 operculars is slightly larger (e.g., 0.8 mm tall, 0.5 mm wide) than the others and is positioned opposite the smallest opercular (e.g., 0.6 mm tall, 0.3 mm wide), these two operculars defining the sagittal axis of the polyp. The remaining 6 operculars are of similar size, constituting 3 pairs mirrored across the sagittal axis. The 2 sagittal operculars are symmetrical, in that their keels are in a medial position, whereas the other 6 operculars are asymmetrical, their keels being offset toward the abaxial side (the side toward the large sagittal opercular),

producing a longer and slightly upturned edge of their adaxial side. Each upturned adaxial opercular edge overlaps the abaxial edges of the adjacent operculars, the edges of the small sagittal opercular being overlapped by both adjacent operculars and the large sagittal opercular overlapping both adjacent operculars (compare to Fig. 9f).

Coenenchymal scales are large (up to 1.0 mm in length), occur in one layer, are polygonal in shape, and are usually slightly concave above. As mentioned below, they sometime orient perpendicular to the branch in order to contribute to the formation of the worm tube. The upper surfaces of all sclerites are finely and uniformly granular, the granules 11–13 μm in diameter; their undersurfaces are covered with complex tubercles 15–17 μm in diameter. Tentacular sclerites were not noted.

Comparisons.—There is only one other species of *Candidella* known from the Atlantic, *C. johnsoni* (Wright & Studer, 1889), described from Ascension. As summarized by Versluys (1906), that species differs in having a very low operculum, marginal scales that are equal in size, and polyps that occur in pairs and singly. Although these two species are probably distinct, the only subsequent report of *C. johnsoni* is by Roule (1896) from the Gulf of Gascogne, which is probably *C. imbricata*, as he implied that his *C. johnsoni* might be a deep-water variety of *C. imbricata*.

Candidella imbricata is morphologically more similar to the central Pacific *C. helminthophora* (Nutting, 1908), both species having dimorphic marginal scales and a similarly shaped polyp. However, *C. helminthophora* differs in having two rings of medial body wall scales, a larger colony with longer internodes (up to 4 cm), larger polyps, and more flexible branches.

Distribution.—Western Atlantic: New England Seamounts (San Pablo, Rockaway, Kelvin, Muir), Bermuda, eastern coast of Florida, Bahamas, Greater and Lesser Antilles, northern Gulf of Mexico; 514–2063 m. A rather large distributional gap exists

between the New England Seamounts and the coast of Florida. Eastern Atlantic: commonly collected in the Bay of Biscay, off Morocco, Canary Islands, Madeira, Azores, and the mid-Atlantic Ridge southwest of the Azores; 815–2139 m (see Grasshoff 1982b for map).

Remarks.—Colonies of even small size will usually host the commensal polynoid polychaete *Gorgoniapolynoe caeciliae* (Fauvel, 1913), larger colonies often hosting 5 or 6 worms. The polychaete has essentially the same known distribution as *C. imbricata*, despite the fact that it occurs in at least two other gorgonians (Pettibone 1991). The gorgonian appears to be induced to form a tube that is slightly elliptical in cross section, the greater diameter being approximately 2.3–2.5 mm and the length up to 25 mm, the tube always occurring on the anterior side of the fan; the length of the polychaete is about 11 mm. The tubes are formed predominantly of greatly enlarged and outwardly curved basal scales from two adjacent polyps. These basal scales, normally only 0.7 mm in height, increase in size up to 1.6 mm in height and up to 2.9 mm in width. The curvature is such that basal scales from two adjacent polyps in the same whorl meet and sometimes fuse along the dorsal midline of the tube, whereas the proximal and distal edges of these enlarged basal scales meet and sometimes fuse with those of adjacent whorls, altogether forming a somewhat porous tube that is open at both ends. Occasionally, small coenenchymal scales that project perpendicular to the branch will fill in the spaces between basal scales of adjacent whorls. Although an obvious advantage is gained for the worm in this association, no advantage can be conjectured for the gorgonian.

Several specimens, collected at the margins of the known distribution, show some variation in morphology. The single specimen known from the northern Gulf of Mexico (USNM 89124) has a very low operculum, like that of *C. johnsoni*, but otherwise is similar to *C. imbricata*. The colo-

nies from Bermuda (USNM 75104) and San Pablo Seamount (USNM 57552) have unusually large polyps, 4.0 and 3.2 mm, respectively, but are otherwise similar to *C. imbricata*.

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APPENDIX: Station Data

Station	Latitude (°N)	Longitude (°W)	Depth (m)	Date
<i>U.S.F.C.S Albatross</i>				
2342	23°10'39"	82°20'21"	384	19 Jan 1885
2343	23°11'35"	82°19'25"	510	19 Jan 1885
2346	23°10'39"	82°20'21"	366	20 Jan 1885
2354	20°59'30"	86°23'45"	238	22 Jan 1885
2416	31°26'	79°07'	505	1 Apr 1885
2662	29°24'30"	79°43'	794	4 May 1886
2663	29°39'	79°49'	770	4 May 1886
2666	29°47'30"	79°49'	494	5 May 1886
2667	30°53'	79°42'30"	499	5 May 1886
2668	30°58'30"	79°38'30"	538	5 May 1886
2669	31°09'	79°33'30"	644	5 May 1886
2753	13°34'	61°03'	514	4 Dec 1885
III9-19	off Beaufort, N. Carolina		?	27 May 1949
<i>Alvin</i> (submersible)				
77-760	27°04.9'	79°20.1'	613-654	Jun 1977
77-761	27°04'	79°18.8'	600	Jun 1977
77-762	27°03.3'	79°20.0'	600	Jun 1977
77-764	27°55.8'	79°09'	410	Jun 1977
846	26°26'	77°52'	525	3 Nov 1978
1335	27°05'	79°40'	608	21 Feb 1984
3885-5	33°46.17'	62°33.9'	1821	4 Jun 2003
3903-101-2	38°47.33'	64°07.95'	2063	15 Jul 2003
<i>Anton Dohrn</i>				
6392	30°49'	79°49'	400	?
65-32	Tortugas		1064	30 Jul 1932
<i>R/V Atlantis (Atl)</i>				
266-02	31°58'	77°18.5'	813	25 Jun 1961
266-04	31°56'	77°26'	768	26 Jun 1961
266-07	31°53'	77°23'	750	28 Jun 1961
266-40	30°53'	78°47'	804	13 Jul 1961
266-41	30°59'	78°14'	877	15 Jul 1961
266-47	30°53'	78°47'	819	19 Jul 1961
280-09	38°51'18"	60°29'00"	1902	17 Jun 1962
2999	23°10'	81°29'	265-512	17 Mar 1938
3303	23°05'	82°33'	476	23 Mar 1939
3402	22°36'	78°21'	421	28 Apr 1939
3403	22°36'	78°22'	384	28 Apr 1939
3438	23°05'	79°37'	485	2 May 1939
3463	23°09'	81°26'	421	9 May 1939
3465	23°09'	81°27'	320	9 May 1939
3466	23°09'	81°27'	366	9 May 1939
3478	23°09'	81°27'30"	240	11 May 1939
3479	23°10'	81°26'	384	11 May 1939
3480	23°10'	81°28'	366	11 May 1939
3482	23°09'	81°27'	348	11 May 1939
3780	30°27'	79°52'	458-485	24 Feb 1940
3782	30°10'	78°44'	795-804	24 Feb 1940
<i>U. S. C. S. S. Bibb</i>				
19	23°03'	83°10'30"	567	4 May 1868
22	24°14'20"	80°59'40"	567	4 May 1868
135	24°20'30"	81°58'30"	229	17 Feb 1869

APPENDIX: Continued

Station	Latitude (°N)	Longitude (°W)	Depth (m)	Date
<i>Johnson-Smithsonian Deep-Sea Expedition (JS)</i>				
43	18°04'	67°48'	439-549	11 Feb 1933
102	18°51'	64°33'	90-500	4 Mar 1933
103	18°51'	64°33'	274-732	4 Mar 1933
<i>R/V Cape Florida</i>				
X	27°31'	79°15'	350-400	Jul 1984
<i>R/V Cape Hatteras</i>				
SA6	31°18'08"	79°00'08"	545-549	17 Nov 1985
SA6-1	31°17'18"	79°00'39"	572-575	17 Nov 1985
SA6-5	31°49'40"	78°19'16"	625	18 Nov 1985
<i>R/V Columbus Iselin (CI)</i>				
63	28°06'	77°08'	1023-1153	21 Sep 1980
123	24°12'06"	77°18'	1435	24 Sep 1973
140	26°24'	79°36'	738	28 Sep 1973
246	26°23'	79°37'	743-761	29 Oct 1974
266	24°18.5'	77°11.7'	?	3 Nov 1974
<i>Clelia (submersible)</i>				
78	32°43'38"	78°05'38"	175-196	5 Jul 1993
79A	32°43'38"	79°05'50"	210	7 Jul 1993
<i>M/V Combat</i>				
174	34°45'	75°28'	320	14 Nov 1956
368	34°15'	75°23'	348	16 Jun 1957
<i>Discoverer</i>				
X	32°10'	78°07'18"	446	5 Oct 1967
<i>R/V Eastward</i>				
26004	28°08'	79°33'	785-830	Nov 1974
26017	26°38'30"	79°32'30"	775	Nov 1974
26019	27°16'48"	79°25'	655-685	Nov 1974
26022	27°28'30"	79°25'18"	655-685	Nov 1974
26023	27°32'	79°22'	690	Nov 1974
26028	27°09.5'	79°25'	635-700	Nov 1974
26031	27°00'	79°24'18"	645-690	Nov 1974
26052	25°42.7'	79°47.5'	660-770	Nov 1974
26535	27°17.6'	79°15.6'	480	29 Mar 1975
26537	27°14'	79°15'	520	29 Mar 1975
26538	27°12'	79°13.7'	420	29 Mar 1975
26547	27°18'	79°17'	520	Mar 1975
26549	27°17'30"	79°12'30"	370	30 Mar 1975
26550	27°16'24"	79°14'18"	440	30 Mar 1975
26559	26°30.3'	79°14.7'	?	31 Mar 1975
31281	26°53'54"	79°07'18"	320	1977
<i>R/V Gerda (G)</i>				
56	25°31'	79°20'	458	28 Aug 1962
169	27°01'	79°21.5'	229-275	29 Jun 1963
170	27°06'	79°32'	659-677	29 Jun 1963
177	27°17'	79°34'	686	30 Jun 1963
235	25°44'	79°22'	531	30 Jun 1963

APPENDIX: Continued

Station	Latitude (°N)	Longitude (°W)	Depth (m)	Date
241	25°26'	79°18'	494-502	30 Jan 1964
242	25°36'	79°21'	485-530	30 Jan 1964
246	26°57'	79°12.5'	512	5 Feb 1964
247	27°07'	79°21'	567	5 Feb 1964
251	27°25'	78°41'	293-311	5 Feb 1964
252	27°29.5'	78°37.5'	485-496	5 Feb 1964
254	27°34.5'	78°49'	488-516	6 Feb 1964
261	27°20'	79°22'	494-511	7 Feb 1964
386	27°09'	78°18'	604	19 Sep 1964
387	27°17'	79°15'	412	19 Sep 1964
391	27°20'	79°12'	?	19 Sep 1964
533	26°27'	78°43'	383-403	4 Mar 1965
598	24°47'	80°26'	183	15 Apr 1965
633	25°59'	79°19'	479-458	30 Jun 1965
647	26°16'	79°43'	520-549	15 Jul 1965
660	26°59'	79°21'	631	17 Jul 1965
661	27°07'	79°32'	695-718	17 Jul 1965
664	27°35'	79°22'	567	17 Jul 1965
672	27°53'	79°03'	796	18 Jul 1965
679	25°56'	78°09'	595-711	20 Jul 1965
680	25°56'	78°05'	571-657	20 Jul 1965
692	26°34'	78°25'	329-421	21 Jul 1965
695	26°28'	78°37'	535-575	22 Jul 1965
696	26°28'	78°43'	458-467	22 Jul 1965
704	26°29'	78°40'	275-366	22 Jul 1965
706	26°27'	78°43'	489-522	22 Jul 1965
707	26°27'	78°40'	514-586	22 Jul 1965
785	24°39'	80°40'	205-210	16 Aug 1966
808	26°38'	79°33'	751	13 Sep 1966
835	24°22'	81°11'	187-198	11 Jul 1967
859	23°54'	81°57'	1160-1190	21 Aug 1967
879	21°00'	86°25'	210	9 Sep 1967
889	20°55'	86°28'	175-220	10 Sep 1967
897	20°59'	86°24'	210-290	10 Sep 1967
898	21°04'	86°19'	340-360	10 Sep 1967
899	20°57'	86°34'	40-164	10 Sep 1967
936	26°35'	79°20'	600	1 Oct 1967
965	23°45'	81°49'	1394-1399	1 Feb 1968
1012	23°35'	79°33'	509-531	14 Jun 1968
1125	26°45'	79°05'	900-950	17 Jun 1968
1312	26°38'	79°02'	505-527	31 Mar 1971
1314	26°52'	79°11'	532	?
<i>R/V Gosnold (Gos)</i>				
2344	30°29'	77°29.5'	882	?
2383	30°56'24"	78°34'18"	869	27 Aug 1965
2384	30°54'24"	78°44'00"	820	27 Aug 1965
2385	30°57'12"	78°54'36"	379	27 Aug 1965
2387	31°14'48"	78°59'00"	530	27 Aug 1965
2413	30°14.5'	79°44.7'	585-622	2 Sep 1965
2414	30°16'	79°55.1'	494	3 Sep 1965
2461	28°14.4'	79°30.5'	850	15 Sep 1965
2469	29°43'12"	79°51'48"	640	16 Sep 1965

APPENDIX: Continued

Station	Latitude (°N)	Longitude (°W)	Depth (m)	Date
<i>M/V, R/V Oregon and Oregon II (O)</i>				
1328	24°33'	83°34'	366	Jul 1955
1343	22°59'	79°17'	457	Jul 1955
1349	24°03'	80°30'	274	18 Jul 1955
4940	20°30'	86°14'	310-330	12 Jun 1964
11703	30°28'	79°51'	494	19 Jan 1972
11705	30°26'	79°44'	640	19 Jan 1972
11716	30°52'	79°39'	576	21 Jan 1972
11717	30°52'	79°34'	658	21 Jan 1972
11725	31°44'	79°02'	543	22 Jan 1972
11726	31°42'	78°53'	512	12 Jan 1972
<i>R/V Gyre</i>				
CO4	27°28'06"	89°43'36"	1358-1518	13 Apr 1984
<i>R/V Pillsbury (P)</i>				
105	30°28'	79°42'	388-403	27 Jul 1964
197	27°59'	79°20'	567-586	11 Aug 1964
209	26°59'	79°16'	550	12 Aug 1964
592	21°00'	86°23'	180	15 Mar 1968
594	21°00.5'	86°23.0'	330	15 May 1968
596	24°42'	80°32'	137	15 May 1968
598	21°07'	86°21'	155-205	15 May 1968
881	13°20.8'	61°02.5'	576-823	6 Jul 1969
892	14°17'	60°45'12"	1236-1313	6 Jul 1969
954	16°55'	62°43'	686-1125	16 Jul 1969
1146	20°08'	73°27'	1110-1189	14 Jun 1970
<i>M/V, R/V Silver Bay (SB)</i>				
440	27°21'	79°15'	439-503	8 Jun 1958
453	29°38'	78°26'	879	12 Jun 1958
5190	18°24'	68°05'	366	17 Oct 1963

A new species of the sea anemone *Megalactis* (Cnidaria: Anthozoa: Actiniaria: Actinodendridae) from Taiwan and designation of a neotype for the type species of the genus

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Abstract.—*Megalactis comatus*, new species, from Taiwan is the third species in this genus of sea anemones with highly branched tentacles. The others are *M. hemprichii* Ehrenberg, 1834, from the Red Sea, and *M. griffithsi* Saville-Kent, 1893, from the Great Barrier Reef. Size of nematocysts from acrospheres and column clearly separate *M. comatus* from the other species of *Megalactis*. One of us (A.A.) observed asexual blastulae in *M. comatus*. This is the first record of asexual reproduction in the genus. Because type specimens of *M. hemprichii* have not been found and the original description cannot be used to distinguish this species from other species of *Megalactis*, we designate a neotype for the type species of the genus, *M. hemprichii* Ehrenberg, 1834. All the specimens of actinodendrids examined lacked basilar muscles; this calls into question the placement of family Actinodendridae among thenarian sea anemones.

The family Actinodendridae is a group of three genera of exclusively tropical Indo-Pacific sea anemones: *Actinodendron* Blainville, 1830, *Megalactis* Ehrenberg, 1834, and *Actinostephanus* Kwietniewski, 1897. An actinodendrid has the oral disc drawn out into a number of branched tentacles that make it resemble a tree (Blainville 1830, 1834; Quoy & Gaimard 1833; Haddon 1898; Carlgren 1949). The last branches of tentacles terminate in acrospheres that appear as white swellings of tissue; they are packed with nematocysts and spirocysts. Because the actinodendrids have been documented to sting humans badly (Saville-Kent 1893, Halstead 1970), knowledge of these animals is significant not only for taxonomy and phylogeny, but also for medicine and toxicology.

Actinodendridae was considered by Carlgren (1900, 1949) to belong to the supra-familial group Thenaria. Basilar muscles,

which are structures “running along both sides of the base of the mesentery, close to the pedal disc” (Carlgren 1949, p. 8), were used by Carlgren (1899, 1900, 1942, 1949) to define two major groups in sea anemones, Athenaria “Nyantheae without basilar muscles” (Carlgren 1949, p. 21) and Thenaria “Nyantheae with basilar muscles” (Carlgren 1949, p. 41). We did not find basilar muscles in specimens of actinodendrids studied, which makes placement of Actinodendridae among Thenaria questionable.

The morphology of the tentacles of these sea anemones varies with environment, behavior, and conditions of preservation. Although the number of species described in Actinodendridae is small, the lack of terminology for describing branched structures and the enormous variety that can be found makes identification of species difficult. In this paper we describe one species and redescribe two others of *Megalactis*,

and standardize terminology for the branched tentacles of Actinodendridae.

Actinodendrids are found in shallow water in sheltered places with sandy or muddy bottoms. Members of the genus *Megalactis* reportedly attach the pedal disc to hard substrata in sand or mud into which the anemones burrow (Saville-Kent 1893, Fishelson 1970). The new species of *Megalactis* described here lives in thickets of the scleractinian coral *Acropora* in Taiwan; this might be the same species as that reported by den Hartog (1997) as an unidentified actinodendrid living attached to coral branches in Indonesia.

The description of *Megalactis hemprichii* Ehrenberg, 1834, the type species of the genus, was diagnostic in the early 19th century. Mentioning only that a sea anemone had bipinnately branched tentacles was sufficient to distinguish *M. hemprichii* from all sea anemones known at that time. With the current state of knowledge, the original description of *M. hemprichii* does not distinguish it from other species of *Megalactis*: bipinnate disposition of the branches is generic rather than specific. Type specimens of *M. hemprichii* Ehrenberg, 1834 have not been found (Klunzinger 1877, Fautin 2004 Hexacorallians of the World: <http://hercules.kgs.ku.edu/hexacoral/anemone2/index.cfm>). We designate a neotype for *M. hemprichii* in accordance with Article 75.3 of the International Code of Zoological Nomenclature (International Commission of Zoological Nomenclature 1999); no new species can be described within *Megalactis* without having a basis of comparison with the type species of the genus.

In the course of this research, one of us (A.A.) found unusual gametogenic structures in male specimens: nodes filled with spermatid packets that have a three-dimensional structure more voluminous than the thickened band typical for gametogenic tissue in members of Actiniaria. Male and small individuals of *M. comatus* had blastulae inferred to be of asexual origin among the mesenteries. This is the first record of

asexual reproduction in a member of Actinodendridae. The only female found contained no gametogenic nodes or blastulae among its mesenteries.

Materials and Methods

Specimens of the new species of *Megalactis* were investigated alive by diving and as preserved material; museum specimens of other species of *Megalactis* and *Actinodendron* were investigated for internal morphology and histology (Table 1); results from this study are based on examination of more than 400 museum lots and photographic documents of actinodendrids.

Animals were recorded in situ on Hi8 videotape using a CanonES6000A video camera in an Amphibico underwater housing. Live material was collected underwater by hand using gloves for protection against stinging. Geographic coordinates were read with an Eagle 12-channel GPS receiver at the point of collection. The animals were kept in aquaria with running seawater for two days; no food was given. Photographs were made in the aquarium using a Nikon Coolpix 950 digital camera. Archived videotapes and photographs are in the collection of the Division of Invertebrate Zoology, University of Kansas Natural History Museum (KUNHM). Specimens were relaxed with magnesium sulfate in seawater, then preserved in 10% seawater formalin. After at least two months, they were transferred to 10% freshwater formalin.

Undischarged cnidae from preserved animals were examined at 1000 \times in squash preparations using a light microscope equipped with differential interference optics. Squash preparations were made from acrospheres, the oral face of the main branches of the tentacles, the proximal, middle, and distal column, the actinopharynx, and the mesenterial filaments. Sigma Scan Pro version 4.01.003 measurement software was used to measure the length and the width of undischarged capsules projected onto a Summa Sketch digitizing tab-

let (Summagraphics). Sampling nematocysts was done following the recommendations of Williams (1996).

For histology, tissue was embedded in Paraplast, sectioned at 9 μ m, and stained with Heidenhain's Azan or hematoxylin and eosin (Presnell & Schreiber 1997). Serial sections for three-dimensional reconstruction were obtained from mesenterial structures, column, and two entire juvenile individuals. Images were obtained using a Nikon Coolpix 995 digital camera connected to an Olympus microscope through an Optem eyepiece digital coupler. Serial images were aligned manually using layers in Adobe Photoshop. Three-dimensional reconstruction was done using the software Vaytek VoxBlast Version 3.0 Light (<http://www.vaytek.com/>).

In the following discussion, as is conventional in sea anemones, the proximal direction is toward the pedal disc and distal is the opposite. Tentacles are arranged in four cycles. Branches of the tentacles are ordered by how close they are to the oral disc: a branch arising from the oral disc is considered to be of the first order; a branch that ramifies from a branch of the first order is of the second order, etc. (Fig. 1).

Abbreviations: CAS, California Academy of Sciences, San Francisco, CA, USA; KUNHM, University of Kansas Natural History Museum, Lawrence, KS, USA; NNM, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; NMNS, National Museum of Natural Sciences, Taichung, Taiwan; TAUI, Zoological Museum, Tel-Aviv University, Tel-Aviv, Israel.

Taxonomic Account

Order Actiniaria

Family Actinodendridae Haddon, 1898

Diagnosis (modified from Carlgren 1949; see remarks below).—Limbus not well defined. No marginal sphincter muscle. Fosse absent. Up to 48 branched tentacles cyclically arranged. Terminal branches of tentacles with acrospheres. Two or more well de-

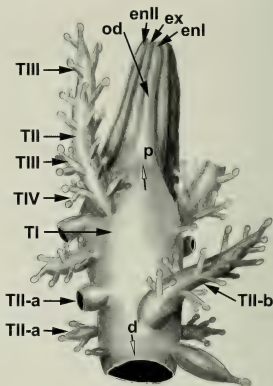


Fig. 1. Ramifications in a tentacle of the first cycle; view looking down a tentacle, i.e., proximally, to the oral disc. The arrow labeled "d" indicates the distal direction, that labeled "p" indicates the proximal direction. Abbreviations: enI, endocoele of the first cycle; enII, endocoele of the second cycle; ex, exocoele; od, oral disc; TI, first order branch; TII-a, lateral secondary order branch; TII-b, oral face secondary order branch; TIII, third order branch; TIV, fourth order branch.

veloped siphonoglyphs. Twenty-four pairs of mesenteries, all or almost all perfect and, apart from the directives, fertile. Retractor muscles diffuse, broad, band-like. Cnidom: spirocysts, basitrichs.

Remarks.—Carlgren (1949, p. 67) indicated a "well developed disc" and "pairs of mesenteries up to 48" for Actinodendridae. Pedal disc size varies greatly: that of some specimens is wide, but that of others is narrow with a limbus that is hard to recognize. None of the specimens studied had more than 24 pairs of mesenteries. Carlgren (1949) asserted that parietobasilar and basilar muscles are distinct in actinodendrids, but we found them to be absent in all genera of the family.

Genera.—*Actinodendron* Blainville,

1830, type genus; *Megalactis* Ehrenberg, 1834; *Actinostephanus* Kwietniewski, 1897.

Genus *Megalactis* Ehrenberg, 1834

Diagnosis (modified from Carlgren, 1949; see remarks below).—Actinodendridae with ramified tentacles having second-order branches arranged bipinnately. Last order branches with capitate acrospheres.

Remarks.—Carlgren (1949, p. 68) stated that *Megalactis* has "the oral face of the arms [branches of the first order] free from tentacles." All specimens of *Megalactis* we studied had two to three second-order branches on the oral face of branches of the first order. Carlgren (1949, p. 68) stated in his diagnosis for *Megalactis* that "the ultimate branches of the tentacles are simple and pointed." One of us (A.A.) found specimens of *Megalactis* that have capitate terminal tentacles.

Species.—*Megalactis hemprichii* Ehrenberg, 1834, type species by monotypy, Ras Kafil, Red Sea; *Megalactis griffithsi* Saville-Kent, 1893, Warrior Reef, Torres Strait, Great Barrier Reef, 9°30'S, 143°06'E. Coordinates from Gazetteer of Australia, 2001 (<http://www.ga.gov.au/>).

Megalactis hemprichii Ehrenberg, 1834

Megalactis Hemprichii Ehrenberg, 1834: 263 (original description).

Megalactis Hemprichii Ehrenberg: Milne Edwards & Haime, 1851:11.

Actinaria Hemprichii Ehrb.: Klunzinger, 1877:90–91.

Megalactis Hemprichii Ehr.: Andres, 1883: 308–309.

Megalactis Hemprichii E.: Carlgren, 1899: 14.

Megalactis Hemprichii Klunzinger: Delage & Hérouard, 1901:539.

Megalactis hemprichii Ehrenberg, 1834: Carlgren, 1949:68.

Megalactis hemprichi Ehrenberg: Fishelson, 1970:109.

non *Megalactis hemprichii* Ehrenberg, 1834: Cutress & Arneson, 1987:53–62.

Description.—Dimensions: column diameter 14–26 mm distally and 14–15 mm in the middle; pedal disc diameter 5–9 mm; column length 23–41 mm; oral disc diameter 21–23 mm; tentacles of the first cycle 45–51 mm long; tentacles of the fourth cycle 10–11 mm long.

Color: Of live specimens unknown. Preserved specimens beige to pale yellow.

Column: Pyramidal to elongate with narrow pedal disc; limbus hardly recognizable (Fig. 2A). Column smooth and mesenterial insertions clearly visible through column in relaxed specimens. In contracted specimens, column with circumferential folds (Fig. 2A).

Oral disc and tentacles: Oral disc narrow. In preserved specimens, mesenterial insertions on oral disc visible as dark lines; radial bumps near mouth mainly on exocoelic intervals (Fig. 2D). Forty-eight tentacles arrayed in four cycles (6 + 6 + 12 + 24). Tentacles of first, second, and third cycles ramified in branches of up to three orders. Proximal secondary branches of first, second, and third tentacle cycles short (Fig. 2B).

Branches regularly oriented. Secondary branches pinnately disposed in one row on each side of a branch of the first order (Fig. 2E). Up to two long and broad secondary branches on aboral side of primary branches of tentacles belonging to first, second, and third cycles (Fig. 2E). Up to 45 secondary branches on tentacles of first and second cycle; up to 25 secondary branches on tentacles of third cycles; up to 11 secondary branches on tentacles of fourth cycle. Branches of last order relatively long. Large, round acrospheres.

Internal structure: Actinopharynx short with two deep siphonoglyphs. Twenty-four pairs of mesenteries in three cycles (6 + 6 + 12); first two cycles usually perfect. Oral stomata large; marginal stomata very small. Retractor muscles diffuse and strong. Fila-

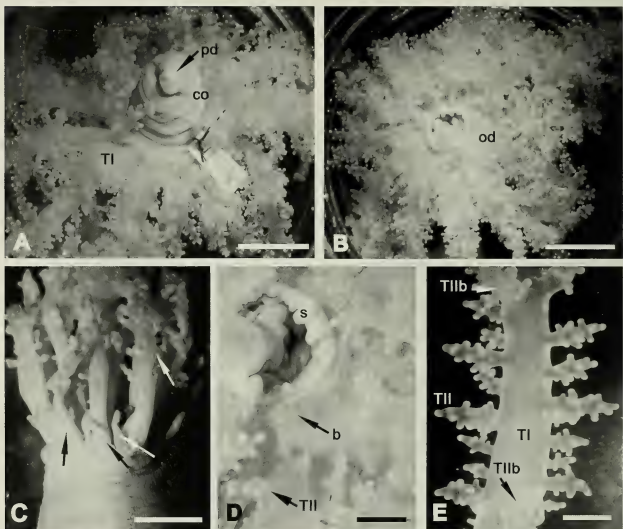


Fig. 2. *Megalactis hemprichii*, external morphology (TAUI 21560). A, Aboral view of entire animal. B, Crown of tentacles, oral view of entire animal. C, Regenerated tentacles (TAUI 7812). Arrows indicate tentacles with missing secondary branches. D, Detail of oral disc and mouth. E, First order branch. Abbreviations: b, radial bumps on exocoelic intervals; co, column; od, oral disc; pd, pedal disc; s, siphonoglyph; TI, branch of the first order; TII, short proximal secondary branch; TII-a, lateral secondary order branch; TII-b, oral face secondary order branch. Scale bars: A, B = 15 mm; C = 10 mm; D, E = 5 mm.

ments absent on mesenteries proximally. Parietobasilar and basilar muscles not seen. Gonochoric. The only specimen sectioned was female (Fig. 3).

Cnidae: Basitrichs densest in acrospheres. Cnidom: spirocysts and basitrichs (Fig. 4). Measurements in Table 2.

Type specimen and locality.—Neotype TAUI 31623, Red Sea, Gulf of Aqaba, Eilat, 29°30'N, 34°55'E. Coordinates from GEONet Names Server of National Imagery and Mapping Agency (<http://www.nima.mil>).

Voucher specimens.—Table 1.

Megalactis comatus, new species

Figs. 4–10

Description.—Dimensions: Diameter of column 2–38 mm distally and 5–21 mm in the middle, of pedal disc 2–8 mm; column length 8–26 mm; tentacles of the first cycle 9–11 mm long; tentacles of the fourth cycle 2–3 mm long; oral disc diameter 13–25 mm; tentacle crown diameter 50–100 mm.

Color: In live specimens, oral disc and tentacle color ranges from dark brown to pale orange or pink. Tentacles translucent, without pattern (Fig. 5). Oral disc with ra-

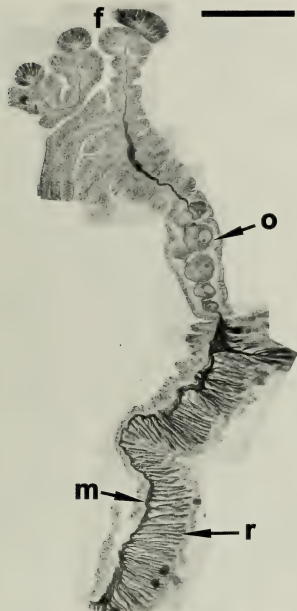


Fig. 3. *Megalactis hemprichii*, histology (KUNHM 001948). Abbreviations: f, filament; m, mesoglea; o, ova; r, retractor. Scale bar = 1 mm.

dial rows of white spots aligned along exocoelic spaces; radial spots may spread laterally onto adjacent endocoelic spaces (Fig. 5F). Insertions of mesenteries on oral disc visible as lighter lines (Fig. 5F). Column beige to white; distal column translucent tinged with brown or pale orange. Female gametogenic tissue purple and male gametogenic tissue white (Oscar Chen, currently at Institute of Oceanography, National Taiwan University, pers. comm.). Preserved

specimens beige, column paler than oral disc or crown.

Column: Pyramidal to elongate with a narrow pedal disc; limbus hardly recognizable (Fig. 5C). Pedal disc and proximal column adhesive with strong ripples of ectodermal tissue in preserved specimens. Circumferential folds resulting from contraction of the column between pedal region and distal-most third of column (Fig. 5C). Distal-most third of column thinner and smoother than proximal column. Mesenterial insertions clearly visible through column.

Oral disc and tentacles: Oral disc narrow. Mesenterial insertions on oral disc visible as light lines in live specimens. Radial bumps close to mouth mainly on exocoelic intervals.

Appearance of tentacle crown shaggy because of numerous branches not regularly oriented (Fig. 5A, E). Forty-eight tentacles arrayed in four cycles (6 + 6 + 12 + 24). Tentacles of first, second, and third cycles ramified in branches of up to four orders. Proximal secondary branches of first, second, and third tentacle cycles long.

Secondary branches pinnately disposed in one row on each side of a primary branch (Fig. 5D). On contracted tentacles, pinnate arrangement unclear; secondary branches appear to be arranged in two or more lateral rows on each side of a primary branch. Some large secondary branches occur on aboral side of primary branches of tentacles belonging to first, second, and third cycles. Secondary branches variable in length. Up to 48 secondary branches on each tentacle of first and second cycle; up to 40 secondary branches on each tentacle of third cycle; up to 12 on each tentacle of fourth cycle. Branches of last order relatively long, terminate in small round to pointed acrospheres.

Internal structure and histology: Actinopharynx short, with two deep siphonoglyphs (two specimens had three; Fig. 6), each connected to a pair of directive mesenteries. Twenty-four pairs of mesenteries

Table 1.—Specimens of *Megalactis* and *Actinodendron* examined. ? = missing data.

Species	Locality	Depth (m)	Collection date	Catalog number	Collector	Lot size	Status								
<i>Megalactis comatus</i>	Pacific Ocean, Taiwan, Hengchun Peninsula, Nanwan, power plant water intake basin, 21°57.27'N 120°45.22'E	3	27 June 2000	KUNHM 001663	AA & Oscar Cheng	1	holotype								
				KUNHM 001665		1	paratype								
				NMNS 4158-001		1	paratype								
				CASIZ 161680		1	paratype								
				RMNH 32194		1	paratype								
				KUNHM 001664		1	voucher								
				KUNHM 001666		1	voucher								
				KUNHM 001667		1	voucher								
				KUNHM 001668		1	voucher								
				KUNHM 001669		1	voucher								
<i>Megalactis hemprichii</i>	Pacific Ocean; Taiwan; Kenting; Houpihwa	2-3	28 May 2002	KUNHM 001252		15	vouchers								
				KUNHM 001657	Fan Tung Yung and Tsai Wan Hsu	17	vouchers								
				KUNHM 001611	Keryea Soong	6	vouchers								
				KUNHM 001612		1	voucher								
				KUNHM 001613		1	voucher								
				TAUI CO 31623	Guy Ayalon	1	neotype								
				TAUI CO 21560	?	1	voucher								
				KUNHM 001948	?	1	voucher								
				TAUI CO 7812	L. Fishelson?	1	voucher								
				KUNHM 001159	Jean Koven	1	voucher								
<i>Megalactis griffithsi</i>	Pacific, Papua New Guinea, Lion Isl., 9°31'60"S, 147°16'0"E	6	23 June 2000	KUNHM 001162	AA & DGF	1	voucher								
				<i>Actinodendron plumosum</i>	Pacific, New Caledonia, Baies des Citronnes Station 109, HZ19	?	29 July 1980	MNH 1562	P. Laboute	1	voucher				
								<i>Actinodendron glomeratum</i>	inferred Philippines	?	?	USNM 1025089	?	1	voucher

Table 2.—Size of nematocysts: average of measurements for a sample in which more than 40 nematocysts were measured are indicated in parentheses; n = number of nematocysts measured, N = ratio between number of individuals containing a type of nematocyst and number of individuals investigated. Basitrich 1 is illustrated in Fig. 4A; basitrich 2 in Fig. 4D, E; basitrich 3 in Fig. 4B, C; basitrich 4 in Fig. 4H.

Species Tissue	Cnidaria type	<i>Megalacis comatus</i>			<i>M. hemprichii</i>		
		n	N	Range length × range width (μm)	n	N	Range length × range width (μm)
Acrospheres	Basitrich 1	2973	10/10	34.56–78.83 × 2.47–4.98 (58.0 × 3.8)	93	2/2	53.5–76.8 × 2.8–4.7 (67.8 × 3.5)
	Basitrich 3	36	6/6	42.44–70.69 × 3.93–10.41	2	2/2	76.3–81.7 × 4.8–5.4
	Spirocyst	60	6/6	18–31.22 × 2.28–3.80	20	2/2	18.8–25 × 2–2.8
	Basitrich 2	82	5/5	16.77–25.21 × 1.61–3.83	20	2/2	16.6–23.2 × 2.4–3.2
	Basitrich 1	147	5/5	27.58–55.62 × 2.4–5.4	104	2/2	27.0–44.2 × 2.3–3.8
Oral face tentacle Actinopharynx	Basitrich 2	0	0/5		54	2/2	17.6–26.3 × 2.2–3.5
	Basitrich 3	5	1/5	31.26–33.1 × 4.17–7.59	0	0/2	
	Basitrich 1	300	7/7	32.31–63.63 × 2.6–5.12	116	2/2	33.8–72.8 × 2.6–4.2
	Basitrich 2	63	5/7	17.91–31.97 × 2.24–4.35	54	2/2	18.8–26.1 × 2.2–3.2
	Basitrich 3	12	3/7	37.67–59.22 × 4.57–8.14	1	1/1	54.0 × 5.2
Filaments	Basitrich 4	0	0/7		1	1/1	over 150 × 15
	Spirocyst	41	4/7	23.24–39.54 × 2.63–4.05	10	1/1	18.4–27.0 × 1.9–3.8
	Basitrich 2	203	7/7	15.23–48.16 × 2.41–5.07	37	2/2	17.0–27.45 × 2.2–4.0
	Basitrich 2	435	10/10	23.07–42.96 × 2.63–5.54 (34.8 × 3.7)	103	2/2	21.9–30.0 × 2.5–4.51 (26.4 × 3.2)
	Basitrich 3	10	3/10	29.91–40.34 × 4.39–9.50	0	0/2	
Proximal column	Basitrich 2	127	5/5	15.96–40.24 × 2.6–4.52	23	2/2	22.2–30.3 × 2.6–4.4

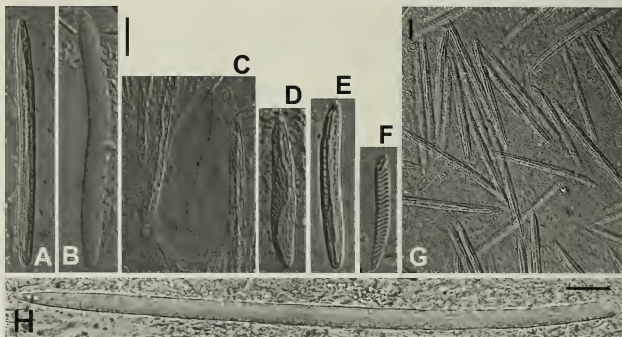


Fig. 4. Cnidae. Basitrichs of acrospheres (A, B), and middle column (C, D, E). Spirocyst (F). Image of a squash preparation from an acrosphere showing numerous basitrichs (G). Long basitrich (H) from filaments of *M. hemprichii* (TAUI 21560). Scale bars = 10 μ m.

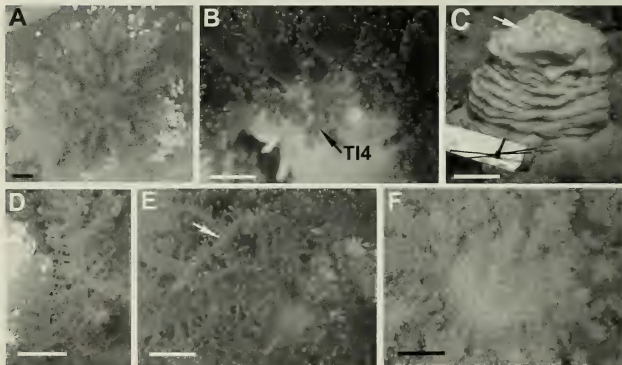


Fig. 5. *Megalactis comatus*, external morphology. A, Crown of tentacles, oral view of entire animal. B, Tentacles of the fourth cycle oriented toward substrate. C, Column in a preserved specimen. Arrow indicates deep ripples in the pedal disc region. D, Secondary branches in bipinnate arrangement. E, Long proximal secondary branches (arrow). F, Oral disc. Scale bars = 10 mm.

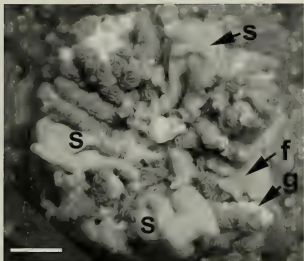


Fig. 6. *Megalactis comatus*, internal anatomy of a specimen with three siphonoglyphs (KUNHM 1664); transverse view. Abbreviations: f, filaments; g, gametogenic tissue; s, siphonoglyphs. Scale bar = 5 mm.

in three cycles (6 + 6 + 12); first two cycles usually perfect. Stomata not seen. Retractor muscles diffuse and strong (Fig. 7A–C). Filaments absent on mesenteries proximally. Parietobasilar and basilar muscles not seen.

Goanochoric: Mesenteries in male specimens have nodes filled with spermatic packets. Each spermatic node formed through plications of mesentery along oral-aboral axis; node digitiform, closed on one side of mesentery and open on the other (Fig. 8). The only female specimen found had ova in arrangement typical of Actiniaria.

Cnidae: Largest and densest basitrichs in acrospheres (Fig. 4G). Cnidom: spirocysts and basitrichs (Fig. 4). Measurements in Table 2.

Type specimens and locality.—Holotype KUNHM 1663, Pacific Ocean, Taiwan, Hanchun Peninsula, Nanwan, power plant water intake basin, 21°57.27'N 120°45.22'E. See Table 1 for paratype and voucher specimens.

Etymology.—The epithet *comatus*, which means “with long hair, shaggy” in Latin (Brown 1978), refers to the hairy and irregular aspect of the tentacle crown in this species.

Natural history.—Animals live in symbiosis with zooxanthellae. We found specimens of *M. comatus* in water a few centimeters to 4 m deep. Each specimen of *M. comatus* attaches to a coral skeleton with its pedal disc and proximal part of the column. The color, similar to that of brown and red algae, and shaggy aspect of the tentacle crown make specimens difficult to find even when abundant.

The water intake basin of the nuclear power plant from which the type specimens were collected was 18 years old at the time. It was inhabited by a large number of specimens of *M. comatus* and other species of sea anemones tentatively identified as *Bolocerooides mcmurrichi* (Kwietniewski, 1898), *Thalassianthus* sp., and a species of family Actiniidae. The initially large population of *M. comatus* had decreased in the previous decade (Dr. Keryea Soong, National Sun Yat-sen University, Kaohsiung, Taiwan, and Oscar Chen, pers. comm.), and has been replaced by the actiniid.

One of us (A.A.) found in nature specimens of *M. comatus* that appeared to be undergoing transverse fission; several specimens had their columns strongly constricted. One specimen, KUNHM 1667, lacks a pedal disc, having a circular opening into the gastrovascular cavity (Fig. 9A, B); specimens KUNHM 1670 and KUNHM 1251 are sacciform, lack tentacles, and have a small opening rather than an oral disc (Fig. 9C), or have small undeveloped tentacles (Fig. 9D). Specimens of *M. comatus* are easy to collect, so it is not likely that the pedal or oral disc of a specimen was torn off during collection as can happen in other sea anemones that attach or are deeply buried in the substrate. Further observations in aquaria should be made to confirm transverse fission.

Some sectioned individuals of *M. comatus*, including males and infertile individuals, had blastulae among their mesenteries (Fig. 10). These larvae contained syncitial blastoderm (solid blastula or stereoblastula in Fautin et al. 1992) and were similar to

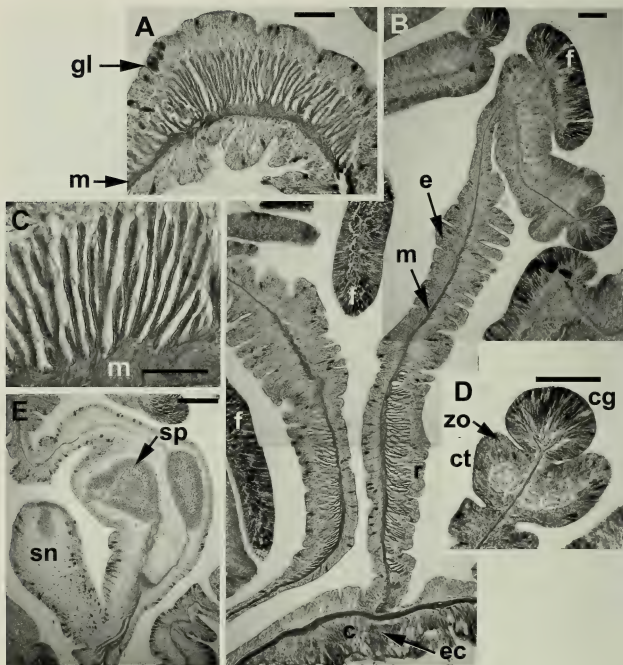


Fig. 7. *Megalactis comatus*, histology. A, Retractor muscle. B, Mesenteries. C, Detail of retractor muscle. D, Detail of mesenterial filament. E, Male gonads with the beginning of spermatic node. Abbreviations: c, column; cg, cnido-glandular tract; ct, ciliated tract; e, endoderm; ec, ectoderm; f, filament; gl, glandular cells; m, mesoglea; sn, spermatic node; sp, spermatic packet; zo, zooxanthellae. Scale bars: A, B, D, E = 100 μm ; C = 50 μm .

those depicted in Yanagi et al. (1999). A.A. also found larvae in an individual lacking tentacles presumably because of transverse fission. Some larvae showed incipient blastopores, indicating an early gastrula stage (Fig. 10B, C). In some larvae, the outer layer contained nematocysts at regular inter-

vals (Fig. 10D, E). Juvenile stages were not found in histological sections.

Discussion

Systematics.—Type specimens of *Megalactis hemprichii* have not been found

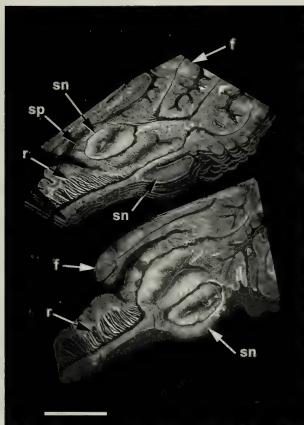


Fig. 8. Three-dimensional reconstruction of spermatic nodes in mesenteries of *M. comatus* from 20 serial slices each 9 μm thick. Abbreviations: f, filament; r, retractor muscle; sp, spermatic packet; sn, spermatic node. Scale bar = 0.5 mm.

(Klunzinger 1877, Fautin 2004 Hexacorallians of the World: <http://hercules.kgs.ku.edu/hexacorall/anemone2/index.cfm>). To typify the genus, we designate a neotype for *M. hemprichii*. Specimens of *M. hemprichii* from the type locality of Ras Kafil in the Red Sea bordering Sinai (now part of Egypt) were unavailable and collection in this region is not feasible. We designate as neotype specimen TAU1 31623 from the Gulf of Aqaba in the Red Sea, a locality "as near as practicable from the original type locality" (Art. 75.3.6, International Commission of Zoological Nomenclature 1999).

Because of poor descriptions and complex morphology of the tentacles, species of *Megalactis* are difficult to distinguish from each other. Ehrenberg's (1834) description of *M. hemprichii* includes a very brief Latin

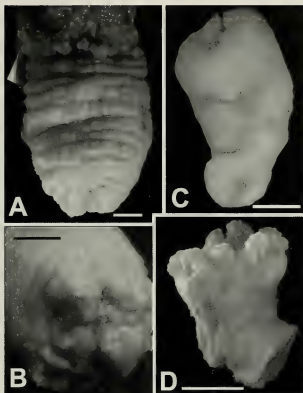


Fig. 9. *Megalactis comatus*, transverse fission. A, B, Column without pedal disc KUNHM 1667. C, Specimen without oral disc (KUNHM 1670). D, Specimen with short tentacles (KUNHM 1668). Scale bars = 5 mm.

description and no illustration. The only illustration for *M. hemprichii* in Klunzinger (1877) is based on drawings left by Ehrenberg. Subsequent references to *M. hemprichii* are translations of the original description (Milne-Edwards 1857, Andres 1883, Delage & Hérouard 1901) and a distribution record (Fishelson 1970). The specimen identified as *M. hemprichii* depicted in figure 2A of Cutress & Arneson (1987) has secondary branches not bipinnately disposed, and therefore is probably a specimen of *Actinodendron*.

Differences and similarities between the species of *Megalactis* are presented in Table 3. Type specimens of all the species described by Saville-Kent (1893), if they existed, have not been located (Fautin 2004 Hexacorallians of the World: <http://hercules.kgs.ku.edu/hexacorall/anemone2/index.cfm>). The photograph and description of the color pattern of the oral disc in *M. griffithsi*

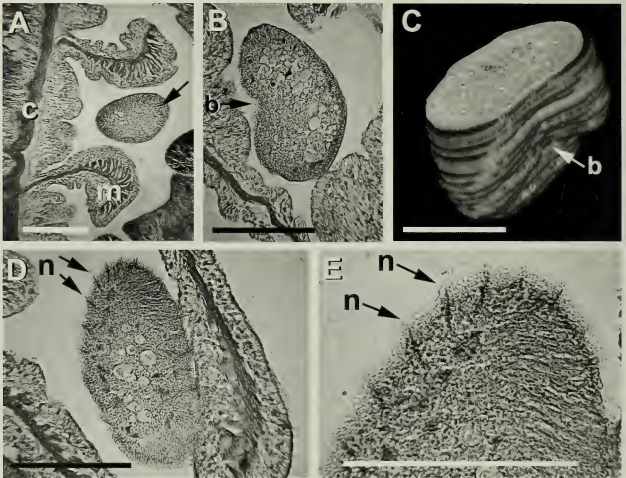


Fig. 10. *Megalactis comatus*, asexual larvae. A. Larva (arrow) among mesenteries. B. Late blastula (arrow). C. Three-dimensional reconstruction of a larva from 17 serial slides each 9 μm thick. D, E. Larva with nematocysts. Abbreviations: b, blastopore; c, column wall; m, mesentery; n, nematocyst. Scale bars = 0.25 mm.

Saville-Kent, 1893, can be used to identify specimens and distinguish this species from *M. comatus*.

Haddon (1898) used the shape of acrospheres to distinguish *M. griffithsi* from *M. hemprichii*: clubbed for *M. hemprichii* and pointed for *M. griffithsi*. The shape of acrospheres cannot be used as a diagnostic character in either living or preserved specimens of *Megalactis* because it is influenced by behavior and preservation. It is common to find a museum specimen that has acrospheres of both shapes.

Nematocysts from the acrospheres and middle column differ in size between specimens of *M. comatus* and *M. griffithsi*. The ratio between length and width of nematocysts shows a clear difference between the two species (Fig. 11). Three specimens of

M. hemprichii from the Red Sea have a similar gross morphology to specimens of *M. griffithsi* but the nematocysts of the acrospheres have size values close to those of *M. comatus*. The nematocysts in the middle column of *M. comatus* are larger than those in *M. hemprichii*.

The number of tentacles for all species of *Megalactis* is given as 10+10 for *M. hemprichii* by Ehrenberg (1834), Milne-Edwards (1857), Andres (1883), Delage & Hérouard (1901), and Klunzinger (1877) and 6+6+12 for *M. griffithsi* by Saville-Kent (1893) and Haddon (1898). We agree with Haddon (1898) that the number of tentacles indicated by Ehrenberg (1834) for *M. hemprichii* might be an individual peculiarity. One of the three specimens of *M. hemprichii* studied (TAUI 7812) had only 41

Table 3.—Diagnostic characters of species of *Megalactis*. ? = missing data.

Species/character	<i>M. comatus</i>	<i>M. griffithsi</i>	<i>M. hemprichii</i> original description	<i>M. hemprichii</i> neotype
Tentacle crown aspect	Irregular, shaggy	Regular	Regular	Regular
Secondary branches	Elongated, usually constricted proximally	Relatively short, constricted proximally	?, may be constricted proximally	Relatively short, usually constricted proximally
Number secondary branches	Up to 48	Up to 35	?	Up to 45
Proximal secondary branches	Long to very long	Short	?	Short
Distal secondary branches	Present	Present	?	Present
Oral disc pattern of live specimens	Rows of white spots	Complex pattern of radiating lines and alternating dark and white regions	?	No pattern
Color of live specimens	Oral disc and tentacles pink to brown; column white, beige	Oral disc and tentacles brown or green; column beige	Oral disc brick red and gray; tentacles pale pink; column white	Light brown

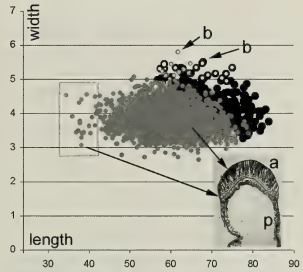


Fig. 11. Length in μm of basitrichs from acrospheres of *M. comatus* (gray dots) and *M. griffithsi* (black dots). In the region delimited by the rectangle are measurements of nematocysts from the region where acrosphere (a) meets peduncle (p); open circles represent basitrichs type 2 (see Fig. 4B).

tentacles, all of which showed signs of regeneration—lacking secondary branches, or having branches not bipinnately arranged (Fig. 2C). It is possible that *M. hemprichii* has predators that feed on its tentacles. We infer that in both previously described species of *Megalactis*, the fourth cycle of tentacles was overlooked, being probably considered secondary branches on the adjacent tentacles. In situ, members of *Actinodendridae* usually orient the tentacles of the fourth cycle towards the substrate. All specimens of actinodendrids studied, including those belonging to *Megalactis*, had a typical tentacle arrangement in multiples of six ($6 + 6 + 12 + 24$).

Because we did not find basilar muscles in specimens of *Actinodendron plumosum* Haddon, 1898, *A. glomeratum* Haddon, 1898, *Megalactis griffithsii* Saville-Kent, 1893, and *M. comatus*, the position of family *Actinodendridae* among *Thenaria* as defined by Carlgren (1899, 1900, 1942, 1949) is questionable. It is possible that basilar muscles are reduced in size or have been lost in the family *Actinodendridae*; basilar muscles are reduced or absent in many burrowing sea anemones (Carlgren 1949, Daly

et al. 2002). Basilar muscles are absent in the thenarian family Aliciidae. Another explanation may be that the basilar muscles were not present in the ancestral lineage of Actinodendridae and this family does not belong to Thenaria.

Spermatic nodes.—We report for the first time spermatic nodes in Actiniaria. Hyman (1940, p. 583) stated that generally the gametogenic tissues in actinarians “occur as thickened bands on the septa behind the septal filaments.” Atypical organization of gametogenic tissue is reported in the hexacorallian groups Actiniaria (Excoffon & Zamponi 1999), Zoanthidea (Ryland 2000), and Scleractinia (Harrison & Wallace 1990). The most similar structure to spermatic nodes in *M. comatus* are the “gonadal nodes” reported by Ryland (2000) that are lens-shaped folds in the perfect mesenteries of females of the zoanthid *Parazoanthus anguicomus* and of a male of *P. axinellae*. Spermatophores were described by Excoffon & Zamponi (1999) in the sea anemone *Sagartia troglodytes*. The spermatic nodes in *M. comatus* are not stalked like the spermatophores in *S. troglodytes* but have a three-dimensional structure more developed than a simple fold of the mesentery like the “gonadal nodes” reported by Ryland (2000). Excoffon & Zamponi (1999) reported that spermatozoa in *S. troglodytes* were released from spermatophores through the stalk, the region by which the spermatophores are attached to the mesenteries, and the mesogleal wall of the spermatophores is continuous with that of adjacent mesentery. Thus, like spermatic nodes, spermatophores must develop from folds of mesenteries through evagination. We agree with Ryland (2000) that one function of the “gonadal nodes” is to increase the number of “gonadal packets” with no increase in length of body.

Asexual larvae.—The origin of larvae found in the coelenteron of some sea anemones is uncertain (Fautin 2002). Chia & Rostron (1970) assumed that the larvae inside *Actinia equina* (Linnaeus, 1758) were

sexually produced, but Carter & Thorp (1979) found this to be unlikely because the phenotypes were identical between a brood and the adult host. In fungiid corals, any tissue fragment in the coelenteron is able to transform into a larva (Kramarsky-Winter & Loya 1996). Because one of us (A. A.) found blastulae in immature and male individuals of *M. comatus*, they are considered to be of asexual origin.

Acknowledgments

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**A new genus and new species of crab of the family Xanthidae
MacLeay, 1838 (Crustacea: Decapoda: Brachyura) from the
southwestern Gulf of Mexico**

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Abstract.—A new genus and new species belonging to the Euxanthinae subfamily, *Batodaeus adanad*, are described from the southwestern part of the Gulf of Mexico. Whereas the new genus is similar to *Monodaeus* Guinot, 1967 in the carapace ornamentation and shape of pereopods, it differs in the structure of the abdomen and male telson, sternoabdominal cavity, and shape and ornamentation of the first gonopod.

Resumen.—Se describe un nuevo género y una nueva especie perteneciente a la subfamilia Euxanthinae, para el suroeste del Golfo de México. Este género nuevo es similar a *Monodaeus* Guinot, 1967, en la ornamentación del caparazón y forma de los pereopodos; sin embargo, difiere de éste en la forma y tamaño del abdomen, telson y cavidad esterno-abdominal, así como en la estructura de los apéndices sexuales.

In the course of deep-water biodiversity surveys in the Cayo Arcas and west side of Triangulos in the southwestern part of the Gulf of Mexico, specimens of an unusual species of xanthid crab were obtained. Although superficially similar to species of *Monodaeus* Guinot, 1967, they possess several atypical features that suggest otherwise. They are here described as a new genus and new species.

Material and Methods

Specimens were collected in 1998 during surveys investigating the marine fauna in the deep southwestern Gulf of Mexico, cruise BATO (Biota de los Arrecifes, de la Plataforma y Talud continental en el noroeste del Banco de Campeche), carried out on board the R/V *Justo Sierra* by the Instituto de Ciencias del Mar y Limnología, UNAM. The samples were caught using a semicommercial otter trawl.

The material was deposited in the reference collection of the Instituto de Biología,

UNAM (CNCR). Measurements listed are in millimeters (mm): total carapace length (CL) and carapace width (CW).

Batodaeus, new genus

Diagnosis.—Carapace subhexagonal, broader than long; dorsal surface convex and granulated. Regions in male well demarcated especially in the anterior half, front strongly deflexed; inner orbital teeth conspicuous; thoracic sternum relatively narrow. Anterolateral margins armed with 4 teeth (excluding outer orbital tooth), subequal in size to posterolateral margins; posterior margin of epistome triangular, median part depressed, with distinct median fissure, and a pair of shallow but clearly visible lateral notches; preorbital and postorbital lobes conspicuous, granulated. Incomplete endostomial ridges present. Basal antennal segment long, subcylindrical, almost touching front, not filling space between front and inner orbital teeth; a small gap between basal antennal segment and suborbital mar-

gin. Third maxillipeds not filling buccal cavity; merus with deep, rounded depression near mesial margin. A longitudinal tuberculated ridge just below suture separating subhepatic and subterygostomial regions. Pereopods 2–5 long, slender, with conspicuous spines on upper margin of merus and carpus. Sternoabdominal cavity relatively narrow and deep; thoracic sternite 4 with median part slightly raised, with short longitudinal furrow. Abdomen long, completely covering sternoabdominal cavity. Second abdominal segment in each sex not reaching coxae of fifth pereopod, leaving a small portion of sternite 8 visible. Sternite 7 covering part of penis groove on sternite 8. First gonopod slender, slightly incurved; a row of spines on mesial margin. Second gonopod very short, sigmoid, terminal process curved with short setae on distal end.

Type species.—*Batodaesus adanad*, new species, by present designation.

Gender.—Masculine.

Etymology.—The name is a combination of Bato, the name of the cruise during which it was collected, and “daeus” to indicate its similarity with the genus *Monodaesus*.

Remarks.—The taxonomic position of *Batodaesus* is uncertain. Although the specimens studied here share some characteristics with the subfamily Actaeninae in having sternite 4 with a longitudinal furrow and the male abdomen with locking mechanism on sternite 5, they also share some features with the Xanthinae in having the carapace with four teeth and with thoracic sternite 4 being rather long (see Serène, 1984). In fact, *Batodaesus* more closely resembles the euxanthinid genus *Monodaesus* Guinot, 1967 in the following characters: regions of the carapace well demarcated; hepatic region inflated; presence of four anterolateral teeth; surface of carapace with several strong granules; basal antennal segment just touching the front; anterior border of buccal cavity with a conspicuous crest; third maxillipeds not completely closing buccal cav-

ity and merus with prominent distolateral angle; and thoracic sternite 4 with a median longitudinal furrow. However, the carapace of *Batodaesus* is more convex and the regions are less well demarcated and with acute spines, particularly on the hepatic region; the posterolateral margins are subequal in length to the anterolateral; the front is more advanced, with a deep sulcus; the preorbital lobe is conspicuous; the sternoabdominal cavity is relatively deeper and narrower; thoracic sternite 4 has a shallow but distinct longitudinal median furrow; the abdomen is relatively narrow and longer; and the first male gonopod is long, slender and slightly incurved with few spines, not setose or stout as in *Monodaesus*.

The bathymetric and geographic distribution of these two genera is also different. *Monodaesus* (type species *Xantho couchii* Bell, 1851) at present contains eight species: *M. arnaudi* Guinot & Macpherson, 1988; *M. couchii* (Bell, 1851); *M. cristulatus* Guinot & Macpherson, 1988; *M. guinotae* Forest, 1972; *M. pettersoni* Garth, 1985; *M. rectifrons* (Crosnier, 1967); *M. rouxi* (Capart, 1851); and *M. tuberculidens* (Rathbun, 1911). They all occur in the Western Indian Ocean, the Eastern Atlantic, the Mediterranean Sea and the Eastern Pacific, from 20 to 500 meters. *Batodaesus adanad*, however, was collected in the Western Atlantic at depths from 160 to 250 m.

In comparison with *Medaeops* Guinot, 1967 (only known from the Indo-West Pacific), *Batodaesus* has a carapace which has the regions less inflated, the merus of third maxilliped with a prominent distolateral angle; the pereopods are more slender and longer, the thoracic sternum is not flat; and the first male gonopod lacks setae. It differs from the superficially similar Indo-West Pacific genus *Alainodaesus* Davie, 1992 in having a carapace which is subhexagonal, not ovoid; a straight frontal margin; a rounded telson (triangular in *Alainodaesus*) and an almost straight first male gonopod.

Batodaesus, for the moment, is tentatively

placed in the Euxanthinae, as it seems to fit there considering the primary character of the subfamily stated by Serène (1984): the form of the anterolateral margin which has the anterior part gradually sloping downwards via subhepatic region to meet the infraorbital margin. The similarity to *Mono-daesus* confirms that it can be placed as Euxanthinae, even though the subfamily is now poorly defined.

***Batodaesus adanad*, new species**

Figs. 1–4

Material examined.—Holotype: 1 ♂ CNCR (21023), 16.6 mm × 23.2 mm; Sta. 9, 22°17.19'N, 91°43.08'W (Banco de Campeche, off Cayo Arenas), 251 m, 23 May 1999. Allotype: 1 ♀ CNCR (22509), 11.8 mm × 16.6 mm, Sta. 9, 22°17.19'N, 91°43.08'W (Banco de Campeche, off Cayo Arenas), 251 m, 23 May 1999. Paratype: 1 ♀ CNCR (21024), 12.1 mm × 17.6 mm, off Sta. 8, 22°13.72'N, 91°46.64'W (Banco de Campeche, off Cayo Arenas), 162 m, 23 May 1999.

Description.—Carapace (Fig. 1A) subhexagonal, about 1.4 to 1.5 times broader than long; dorsal surface convex, granulated, granules coarse, more abundant on anterolateral and posterolateral margins, with sparse short setae on frontal, hepatic and protogastric regions. Regions in male well demarcated, especially in the anterior half; orbital region with small, acute spines; hepatic region inflated, with 3–4 rows of spines; a depression between cardiac and gastric region; meso and urogastric regions less granulated; front straight, strongly deflexed; margin dentate, at most $\frac{3}{4}$ as long as CW, separated from protogastric region by a long transverse furrow. Deep notch between frontal and preorbital lobes, the latter strongly granulated. Anterolateral margins armed with 4 teeth (excluding the outer orbital), first small, with margins granulated, second and third longest, subequal in size, spinose and directed anteriorly, fourth bigger than first, with borders and base gran-

ulated. Posterolateral and posterior margins of carapace almost straight, granulated. Pterygostomian region (Figs. 2A, 4C) densely granulated, with a longitudinal, spinose crest just below suture that divides subhepatic and pterygostomian regions; pterygostomian ridges present, marked with small tubercles.

Orbits $\frac{3}{4}$ as wide as front, separated from it by a deep, long notch, borders conspicuously dentate; 2 large sutures on supraorbital region; preorbital and postorbital lobes dentate. An acute granulated tooth on infraorbital angle. Eyestalks completely fitting in orbits when retracted, with 4 sharp spinules and stiff setae.

Antennules (Figs. 2A, 4C) with basal segment considerably inflated, and with a longitudinal crest of small granules; penultimate and ultimate segments slender.

Basal antennal segment subcylindrical, with 4 sharp spinules; second to fourth segments mobile, longer than broad; flagellum long.

Ischium of third maxilliped (Fig. 2B) longer than broad; outer surface with median longitudinal furrow. Merus subquadrate, outer surface coarsely granulated, mesial margin dentate, setose; distolateral angle ending in a semiacute lobe, directed anteriorly. Palp marginally setose. Exopod reaching to tip of distolateral angle of merus.

Left cheliped shorter than right and more spinose (Figs. 4A–B); merus granulose, upper and lower margins delimited by a row of strong, acute, inward spines; outer surface of carpus spinose, inner margin armed proximally with strong acute spine curving inwards, junction between carpus and chelae fringed with setae, inner surface densely granulated. Palm of long chela with 3 upper rows of acute spines directed inwards, diminishing in number and size towards lower margin, inner surface slightly punctate. Dactylus about as long as palm; fingers leaving small gap when closed, each terminating in inwardly curved corneous claw; movable

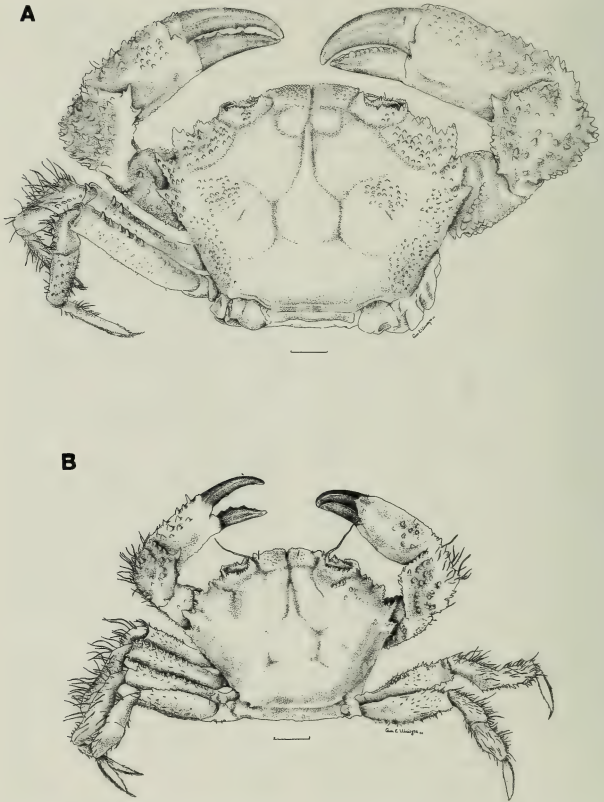


Fig. 1. *Batodaeus adanad*, new genus, new species. A, Holotype male 16.6 mm \times 23.2 mm (CNCR 21023); B, Allotype female 11.8 mm \times 16.6 mm (CNCR 22509), dorsal view.

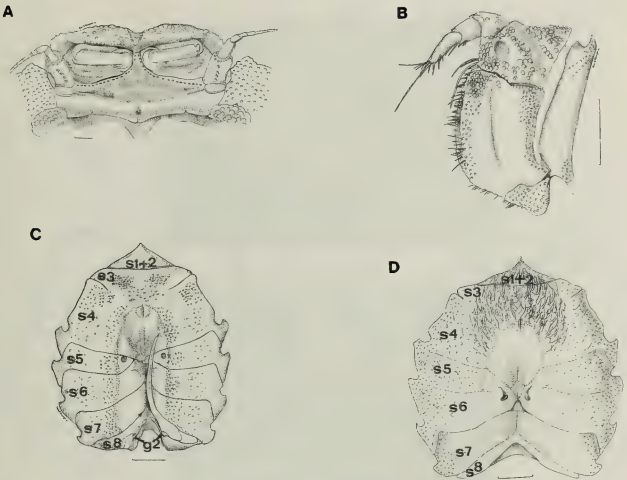


Fig. 2. *Batodaesus adanad*. A–C, holotype male. A, antennal, pterygostomial, suborbital, and epistomal regions; B, third left maxilliped, outer view; C, sternoabdominal cavity. D, allotype female, sternoabdominal cavity. Abbreviations: g2, gonopod 2; s1–8, sternites 1–8.

part with upper margin armed with small acute spines, cutting edges with blunt teeth.

Pereopods 2–5, slender, subequal in length; pereopod 4 slightly long, and pereopod 2 slightly short; all segments with lateral and mesial faces spinose, covered by dense, thin setae. Dactylus slightly longer than propodus, terminating in corneous claw. Propodus with long thin setae on upper border, outer surface punctate. Upper border of carpus with 4–6 small spines. Merus with 12 spines on upper border, which diminish in size proximally, directed anteriorly.

Thoracic sternum in male (Fig. 2C) relatively narrow, densely granulated; sternal sutures 1–2 indistinct, 2–3 complete, 3–4 incomplete and confined to lateral regions;

4–5 and 5–6 interrupted medially; 6–7 and 7–8 complete. Sternite 4 with slightly raised median part, with short longitudinal furrow. Locking mechanism on sternite 5 just below suture 4–5. Sternoabdominal cavity deep and relatively narrow.

Male abdomen (Fig. 3A) with short marginal setae on segments 1–6 and telson. First segment long, slender. Second as long as first, broadest, not reaching coxa of fifth pereopod, with small portion of sternite 8 visible (Fig. 3B). Third to fifth segments fused, punctate, longer than broad. Sixth segment as long as broad. Posterior margin of telson rounded. Male sexual openings coxal.

First gonopod (Fig. 3C, D) long, reaching beyond suture separating sternites 4 and

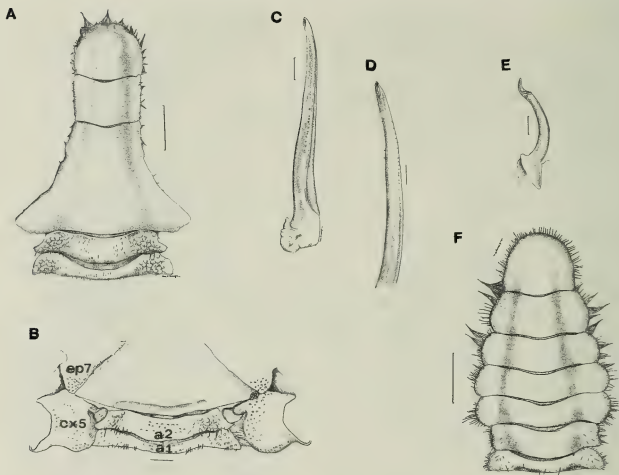


Fig. 3. *Batodaeus adanad*. A-E, holotype male. A, abdominal segments; B, abdominal segments 1-3, coxa 5 and sternite 8; C, gonopod 1; D, tip of gonopod 1; E, gonopod 2. F, allotype female, abdominal segments. Abbreviations: a1-2, abdominal segments 1 and 2; cx 5, coxa 5; ep7, episternite 7.

5, when in situ, slender and with distal part slightly incurved. Second gonopod (Fig. 3E) very short, curved, tip sharp, recurved.

Females with regions of carapace less demarcated (Fig. 1B); front straight, less deflexed; right cheliped longer than left, palm with less conspicuous spines, pereopods more setose, without spines on upper border of merus, carpus with spines more acute. Thoracic sternum (Fig. 2D) with longitudinal furrow on sternite 4 less marked; abdominal cavity less deep and broad; in longest specimen, locking mechanism on sternite 5 not visible. Abdomen (Fig. 3F), with first and second segments as in male, leaving visible a small portion of sternite 8; segments 3-6 free and subequal in size; posterior part of telson rounded. Pleopods long,

slender, extending past edge of telson; gonopores small, ovate.

Color in life.—Cream, with tip of chelae fingers dark.

Etymology.—This species name is formed from an arbitrary combination of the two first letters of each of our sons' names: Adolfo, Andrés, and Adrián, and is used as a noun in apposition.

Distribution.—Western Atlantic; southwestern Gulf of Mexico; Banco de Campeche.

Remarks.—The shape and ornamentation of carapace and pereopods of *B. adanad* are superficially similar to the species of *Monodaeus*, notably *M. rouxi*. Also, the pterygostomial region is densely granulated and the incomplete endostomial ridges of *B.*

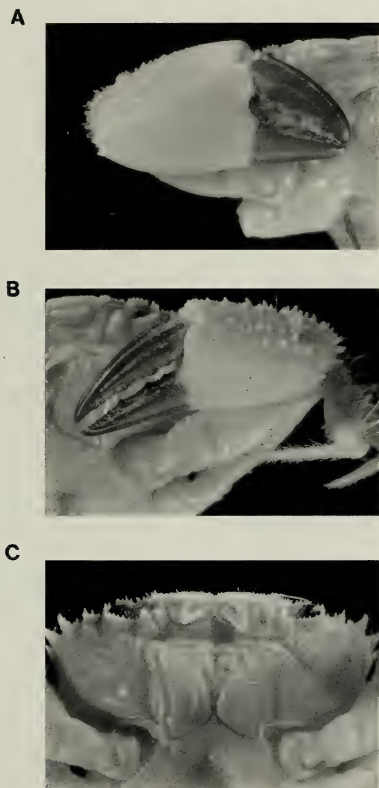


Fig. 4. *Batodaeus adanad*, holotype male. A, right chela; B, left chela; C, ventral view of anterior part of carapace.

adanad are similar to those seen in *M. tuberculidens* and *M. couchii*. The morphology of the merus of the third maxilliped of *B. adanad* also resembles those of *M. guinotae* and *M. tuberculidens*.

However, *Batodaeus adanad* is easily separated from all *Monodaeus* species in that the former has the posterolateral margin almost as long as the anterolateral, the chelipeds are less stout, spinose, and are covered by strong tubercles; the sternoabdominal cavity is deeper and with a less marked longitudinal furrow on sternite 4. The abdomen of *Batodaeus* is long, completely covering the sternoabdominal cavity, whereas in *Monodaeus* species the abdomen does not completely cover the sternoabdominal cavity, leaving a longitudinal furrow on sternite 4 exposed; the pereopods 2–5 without a granulated crest on the superior border of merus; and the telson of male is rounded. In addition, the morphology of the first gonopod in *B. adanad* differs from that in any known *Monodaeus* species.

The new species differs from *Medaeops edwardsi* Guinot, 1967, *M. neglectus* (Balss, 1922), and *M. granulatus* (Haswell, 1882) in that all these species have a less convex carapace, with the regions hardly projecting; their pereopods are shorter and broader; and the fingers of their chelipeds are granulated. The first gonopod, thoracic sternum, and sternoabdominal cavity, too, are also different in morphology.

Batodaeus adanad can be easily separated from *Alainodaeus akiaki* Davie, 1992 and *A. rimatara* Davie, 1992 in that those species have a carapace that is transversally ovoid; the front is less deflexed; the chelipeds are more robust; the first male gonopod is stout with slightly twisted tip; and the second male gonopod is moderately longer.

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A new anchialine shrimp of the genus *Procaris* (Crustacea: Decapoda: Procarididae) from the Yucatan Peninsula

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Abstract.—A fourth species of the anchialine shrimp genus *Procaris* is described from Cozumel Island, Quintana Roo, México. The combination of character states observed for the abdomen, antennal scale/stylocerite, second antennular segment, carapace, eyes, rostrum, and telson is unique in the genus. The new species appears to be morphologically most closely related to *P. ascensionis* from Ascension Island. Cladistic analysis of differentiating character states supports a sister group relationship between *P. ascensionis* and the Mexican species, in two out of three most parsimonious hypotheses. In addition, the Bermudan *P. chacei* and Hawaiian *P. hawaiiiana* are positioned as sister taxa in all minimal length trees. While the discovery of a new *Procaris* species adds to our biogeographical knowledge of the genus, it has pointed to the possibility that the Atlantic taxa may be a paraphyletic assemblage.

Shrimps of the family Procarididae are restricted to anchialine habitats, and occupy an unclear position within the Decapoda relative to the Caridea (Christoffersen 1988, 1990; Felgenhauer & Abele 1983; Kensley & Williams 1986; Schram 1986). The Procarididae contains two genera, *Procaris* and *Vetericaris* Kensley & Williams, 1986. *Procaris* has perhaps the most interesting distribution of any anchialine decapod: *P. ascensionis* Chace & Manning, 1972 is restricted to Ascension Island in the mid-south Atlantic, *P. chacei* Hart & Manning, 1986 is endemic to Bermuda, and *P. hawaiiiana* Holthuis, 1973 is found on the Hawaiian archipelago. [A photograph of an undescribed “Procarid sp.” from Christmas Island in the Indian Ocean has been published (Jones & Morgan 2002), although the habitus of the pictured specimen looks more atyid than procaridid.]

What is even more remarkable is the conservative morphology of *Procaris* species, considering the disjunct biogeography of

the taxa, as the three species differ in only a few characters (Hart & Manning 1986). *Vetericaris* is monotypic with the Hawaiian *V. chaceorum* Kensley & Williams, 1986 separated from any *Procaris* species by a plethora of character states. Despite the distinctiveness of *Procaris* and *Vetericaris*, the monophyly of the family has not been questioned. A recently described family for a genus of abyssal shrimp, the Galatheacarididae Vereshchaka, 1997, overlaps with the Procarididae in several key (albeit plesiomorphic) character states, indicating that the hypothesized connection between anchialine and abyssal caridean taxa of Hart et al. (1985) may not be entirely without merit. Interrelationships aside, an open question is how many additional anchialine and submerged cavernicolous carideans await discovery that could, potentially, complete the known biogeographical gaps.

Here we describe a fourth species of *Procaris*, from the Yucatan Peninsula. The discovery of this new species adds consider-

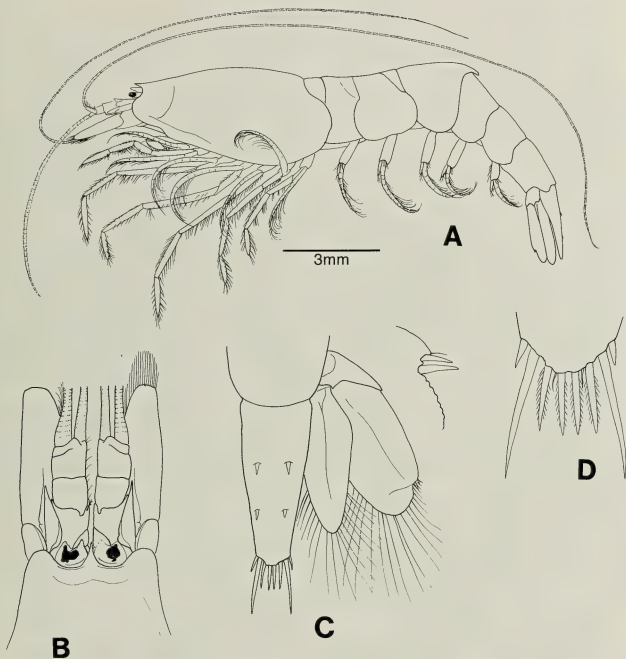


Fig. 1. *Procaris mexicana*, n. sp. A, habitus, lateral view; B, anterior region; C, telson and uropods; D, apex of telson.

ably to our biogeographic knowledge of the genus. The new *Procaris* material was collected by Drs. Dennis Williams and Jeff Bozanic who during the years 1988, 1989, and 1995 collected them from the cenotes of Quintana Roo, México. CL numbers refer to carapace length; USNM numbers denote catalog numbers in the National Museum of Natural History, Smithsonian Institution.

Procarididae Chace & Manning, 1972

Procaris mexicana, new species

Figs. 1–3, Table 1

Procaris sp. Kensley, 1988:688.

Material.—Holotype (USNM 1068789): México, Cueva Quebrada, Chankanaab Park, Cozumel, Quintana Roo, 25 September 1987, coll. Dennis Williams, CL 8 mm. Paratypes: USNM 1068790, 1 specimen, CL

6.5 mm, same locality as holotype, coll. Dennis Williams, 23 Sep 1987; USNM 1068791, 3 specimens (1 damaged), CL 5.1 mm, 5.5 mm, and 5.9 mm, Cueva Quebrada, depth of 25–30 feet, coll. Jeff Bozanic, 5 April 1988; USNM 1068792, 4 specimens, all CL 6 mm, Cueva Quebrada, coll. Dennis Williams, Feb. 1993; USNM 1068793, 1 specimen, CL 8 mm, Lagoon Cave, Cozumel, Quintana Roo, México, coll. Jeff Bozanic, 3 Apr. 1988.

Description.—Integument fragile and thin. Rostrum acutely triangular and lacking teeth, only reaching medial concavity of eyes. Carapace devoid of spines; anterior margin distinctly convex and slightly emarginate below distinct cervical sulcus; prominent anteroventral sulcus positioned parallel to ventral margin, and meeting ventral end of cervical sulcus; posterodorsal margin markedly concave.

Eyestalk produced into two lobes, the medial lobe sharply triangular and extending beyond the more bluntly triangular lateral lobe; eye lacking facets and with irregular mass of pigment.

Antennular peduncle does not reach distal one-third of antennal scale, broad; stylocerite tapering distally to acute apex, almost reaching distal margin of second antennular article; segments subequal in length; anterior margin of basal article with distinct V-shaped dorsomedial cleft.

Antennal scale lacking distolateral tooth, distal margin convex, length approximately 2.5 times the width; distal margin of scale reached by antennal peduncle.

Mandible pronouncedly developed, with three-segmented palp, molar and incisor processes forming one piece; incisor process subtrapezoidal, lacking distinct marginal teeth except for the two angular regions, scooplike. Paragnath sinuous, surrounding incompletely mandibular bases, distal end pointed, broadest around midlength. Endites of first maxilla well-developed, broad; palp simple. Second maxilla with two endites, distal endite with deep incision, palp pronounced and broader proximally, tapering

slightly distally, scaphognathite small in comparison to the endites and palp. Maxilliped 1 with near tongue-shaped endite, well-developed palp; long, simple epipod; caridean lobe prominent. Maxilliped 2 endopod with seven segments of roughly similar width throughout; exopod long, straplike; epipod simple, reduced. Maxilliped 3 with seven-segmented endopod, distal half of merus broader than all other parts of the appendage; exopod long, subequal to endopod length; epipod simple, small.

Pereiopods 1–5 similar in organization, flexor margins lined with simple setae; dactyli approximately 0.12–0.13 times length of propodi, with strong, curved spines. All five pereiopod pairs with straplike exopod; pereiopods 1–4 with distinct simple epipod, and pleurobranch and seto-branch; pereiopod 5 lacking epipod, pleurobranch, and seto-branch.

Third abdominal somite with dorsal cap not reaching middle of fourth somite; posteroventral margin of the six anterior somites broadly rounded. Abdominal sternites 1–5 with median tubercle between coxae of pleopods; sternite 6 with bulbous tubercle posteriorly directed between uropod bases. Telson approximately 1.4 times length of somite 6, not including posterior spines, armed with two pairs of dorsal spines; posterior margin armed with four pairs of spines, lateral spines shortest, two mesial pairs roughly half the length of sublateral spines.

All pleopods similar in organization; endopods short and weakly developed; appendices internae and masculinae absent from all pleopods.

Distribution.—Known only from anchialine habitats of Cozumel, Quintana Roo, Yucatan Peninsula, México.

Remarks.—All *Procaris* species are remarkably similar in morphology, differing slightly but specifically in a set of characters (Table 1; Hart & Manning 1986). This is significant given the immense distances separating all four taxa, especially *P. hawaiiiana* vis-à-vis the three Atlantic species. On the basis of biogeography, one might expect the



Fig. 2. *Procaris mexicana*: A, pleopod 4; B and C, mandible; D, second maxilliped; E, paragnaths; F, first maxilliped; G, pleopod 1; H, first maxilla; I, second maxilla; J, third maxilliped; K, pleopod 3; L, pleopod 2; M, pleopod 5.

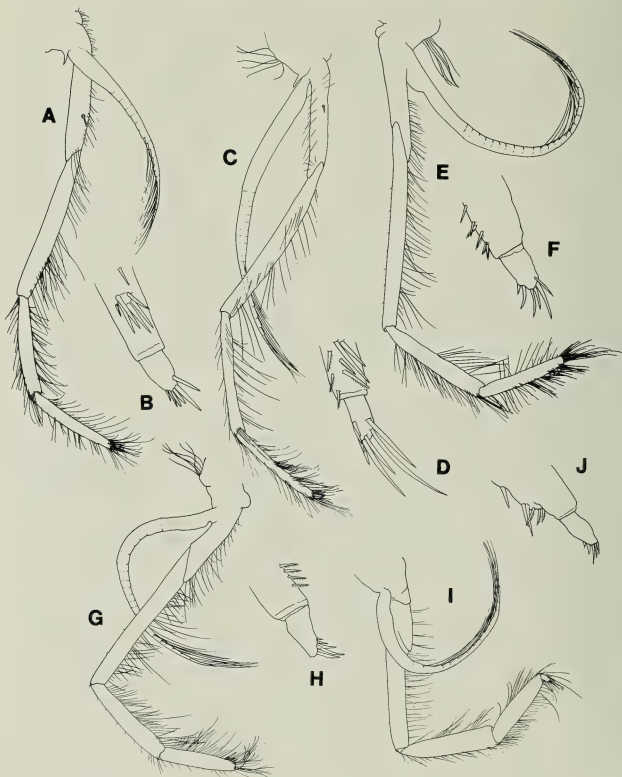


Fig. 3. *Procaris mexicana*: A, pleopod 1; B, same, dactyl; C, pereopod 2; D, same, dactyl; E, pereopod 3; F, same, dactyl; G, pereopod 4; H, same, dactyl; I, pereopod 5; J, same, dactyl.

Table 1.—Character state differences among the four species of *Procaris*. Plesiomorphic states = 0; apomorphies = 1, 2, and 3.

	<i>Vetericaris</i>	<i>P. ascensionis</i>	<i>P. charci</i>	<i>P. hawaiiiana</i>	<i>P. mexicana</i>
1. Rostrum	not reaching medial concavity of eye (0)	reaches medial concavity (1)	overreaches medial concavity (2); reaches medial lobe	overreaches medial concavity (2); overreaches eyes lobes equal (1)	reaches medial concavity (1)
2. Eyes	median lobe longer (0)	median lobe longer (0)	lateral lobe equal to or longer than median lobe (1); lateral lobe longer	lobes equal (1)	median lobe longer (0)
3. Stylocerite	overreaching antennal segment 2 (0)	overreaching antennal segment 2 (0)	to end of antennal segment 2 or less (1); not reaching end of antennal segment 2	to end of antennal segment 2 (1)	almost to end of antennal segment 2 (1)
4. Antennal scale tooth	present (0)	absent (1)	present (0)	present (0)	absent (1)
5. Cervical sulcus	absent (0)	distinct (2)	weak (1)	weak (1)	distinct (2)
6. Third abdominal somite cap	absent (0)	to middle of fourth somite (2)	to middle of fourth somite (2)	beyond middle of fourth somite (3)	not reaching middle of fourth somite (3)
7. Posteroventral margin of fifth somite	narrowly rounded (0)	angular (2)	angular (2)	broadly rounded (1)	broadly rounded (1)
8. Length ratio: sixth abdominal somite to telson	~1.5 (0)	~1.75 (3)	~1.25 (2)	~1.4 (1)	~1.4 (1)

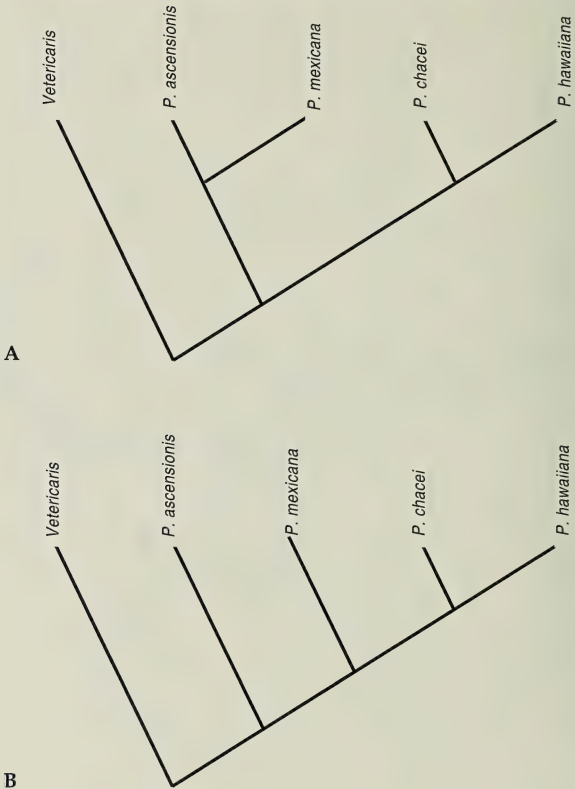


Fig. 4. Most parsimonious cladograms obtained with the data matrix in Table 2. A, single shortest length tree found with characters 1-7 ordered; B, one of two alternative minimal step topologies identified with all characters unordered (the other tree identical to A).

three Atlantic species to form a clade, with the Indo-Pacific *P. hawaiiiana* as the sister group of the lineage. However, a comparison of the character states presented in Table 1 affords no clear-cut separation between Atlantic and Pacific congeners. Each *Procaris* species instead appears to be a mosaic of character states found in the other taxa; species differences are due then to specific character state combinations as opposed to the presence of apomorphies. To test the possibility that *P. ascensionis*, *P. chacei*, and *P. mexicana* may be more closely related to each other than to *P. hawaiiiana*, a data matrix was prepared for parsimony analysis (Table 2), and *Vetericaris* was used as the outgroup for character state polarization (Table 1). The purpose of the cladistic test was twofold: to identify a parsimonious hierarchy of *Procaris* taxa, and to compare this hierarchy with biogeography.

When characters 1–7 were treated as ordered transformation series, one tree was obtained by Exhaustive Search using PAUP 3.1 software (Swofford 1993), with a length of 18 steps, consistency index (CI) value of 0.833, and a retention index (RI) number of 0.571 (Fig. 4A). This first hypothesis indicates that *P. ascensionis* and *P. mexicana* are sister species, with *P. chacei* and *P. hawaiiiana* forming a species pair. Placing the cladogram into the context of time and space, the split between Atlantic and Pacific *Procaris* species would have occurred after the emergence of two Atlantic clades: *P. ascensionis* and *P. mexicana* on the one hand, and the proto-*P. chacei*/*P. hawaiiiana* ancestor.

A second exhaustive search was performed though this time all characters were parameterized as unordered series. Two trees most parsimonious were found with lengths of 17 steps, CI = 0.882, and RI = 0.667. The topology of one of the cladograms is identical in structure to the one in Fig. 4A. The second hypothesis is also a resolved hierarchy, though with *P. ascensionis* branching off first, followed by *P. mexicana*, and

Table 2.—Data matrix used in the parsimony analysis. See Table 1 for explanation of character states.

Character	12345678
<i>Vetericaris</i>	00000000
<i>P. ascensionis</i>	10012223
<i>P. chacei</i>	21101222
<i>P. hawaiiiana</i>	21101311
<i>P. mexicana</i>	10112111

with *P. chacei* and *P. hawaiiiana* positioned as sister taxa (Fig. 4B).

Cladistic analysis of *Procaris* interrelationships indicates three things. First, *P. chacei* and *P. hawaiiiana* are more closely related to each other on morphological grounds than either is to any other *Procaris* species. Second, relationships between *P. ascensionis* and *P. mexicana* are ambiguous. Parsimony searches conducted with ordered and unordered characters support a sister group relationship between the two (Fig. 4A). Yet the hypothesis that *P. ascensionis* is basal to the remaining *Procaris* species (Fig. 4B) cannot be dismissed. Finally, the Atlantic species appear not to form a clade; i.e., they are a paraphyletic assemblage minus the inclusion of *P. hawaiiiana*.

One serious caveat of the parsimony study is the paucity of characters (eight) relative to the number of taxa (five). This reflects the extremely conservative morphology of *Procaris* species. Another caveat is the coding of character states (Table 1). Character states were coded to maximize hierarchical resolution given a limited number of characters. For instance, the rostrum character was divided into three character states: not reaching medial concavity of eyes (plesiomorphic); reaching medial concavity (apomorphic); overreaching medial concavity (also apomorphic). The way this character was coded for *Procaris* species, *P. chacei* and *P. hawaiiiana* have the same state. Yet the rostrum only reaches the median lobe in *P. chacei* although it overreaches the eyes in *P. hawaiiiana*. The same critique applies to character 2. Nevertheless, if characters are recoded to reflect all the differences seen,

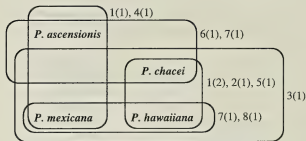


Fig. 5. Venn diagram of apomorphy-based groupings. Numbers to the right of a box denotes derived character states supporting a particular set of taxa.

the tree obtained is identical to that shown in Fig. 4A (unpublished results).

Figure 5 shows a Venn diagram of apomorphy-based relationships in *Procaris*, underscoring the polythetic nature of species differences.

Hart & Manning (1986) suggested that the remarkable similarity of *Procaris* species may be explained by the reduction of variability by natural selection. The "reduced variability" hypothesis appears rather weak considering that anchialine caridean taxa occurring with *Procaris* often exhibit considerable variability, morphs, and species-specific apomorphies (e.g., Kensley & Williams 1986, Smith & Williams 1981). It may be that the distribution of *Procaris* is much more extensive than currently known, with gene flow over great distances occurring via semi-continuous populations distributed among shallow submerged "crevicular" habitats (Hart et al. 1985, Maciolek 1983).

Acknowledgments

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Macrobrachium patheinense, a new species of freshwater prawn (Crustacea: Decapoda: Palaemonidae) from Myanmar

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Abstract.—A new species of freshwater palaemonid prawn, *Macrobrachium patheinense*, is described from Mayan Creek near Pathein City, Ayeyawaddy Division, Myanmar. The new species is most closely related to *M. mirabile* (Kemp, 1917), *M. palaemonoides* Holthuis, 1950, *M. superbum* (Heller, 1862) and *M. inflatum* Liang & Yan, 1985, but can be differentiated by the rostrum shape and dentition, telson shape, and the second pereopod chela proportions.

Like other South East Asian countries, Myanmar has a wealth of freshwater streams, lakes, ponds and rivers, but unlike its adjacent countries, the freshwater crustaceans have been poorly studied. Important relevant investigations on freshwater decapods have been undertaken in India, Thailand, China, Malaysia, Philippines, and Indonesia (Cai & Dai 1999, Cai & Ng 2001, Chace & Bruce 1993, Holthuis 1978, Jali-hal et al. 1988, Liang & Yan 1985, Shokita & Takeda 1989, Tiwari 1947, Wowor & Choy 2001, Yeo et al. 1999, and others).

It was not until 1918 that the first significant carcinological study of Myanmar's fauna was conducted, and since then only 12 species of the shrimp genus *Macrobrachium* Bate, 1868 have been recorded (see Jali-hal et al. 1988, Jayachandran 2001, Kemp 1918, Tiwari 1952). A major study by Cai & Ng (2002) reviewed the taxonomy of the Myanmar palaemonid freshwater prawns, reporting one new species and five new records of *Macrobrachium* for the country.

Myanmar's unique geographic position means that it has close connections with India, China, and the rest of the Indo-Malaysian region to the east and south. Thus, there is a strong likelihood that further investigation will lead to more new taxonomic and zoogeographic discoveries. In Myan-

mar, freshwater shrimps and prawns are important components of inland fisheries, and further taxonomic and ecological studies must be made an urgent priority in order to ensure sustainable management and conservation of stocks.

Specimens were collected from Mayan Creek near Thayet Kone village, about five miles west of Pathein City, Ayeyawaddy Division, on 6 September 2001. All specimens were preserved in formalin for shipping to Japan and examined at the Laboratory of Aquatic Resource Science, Faculty of Fisheries, Kagoshima University. Among the collected specimens, 38 individuals of a *Macrobrachium* species possessed similar distinctive characteristics that could not be attributed to any known species, and are thus here described as a new species.

The holotype and 33 paratypes are deposited in the Laboratory of Aquatic Resource Science, Faculty of Fisheries, Kagoshima University, Kagoshima, Japan (KUMB). Additional paratypes are also deposited in the Kitakyushu Museum of Natural History, Kitakyushu, Japan (KMNM), and the Zoological Reference Collection (ZRC), Raffles Museum, National University of Singapore.

Numbers in parentheses in "Materials examined" indicate the post-orbital cara-

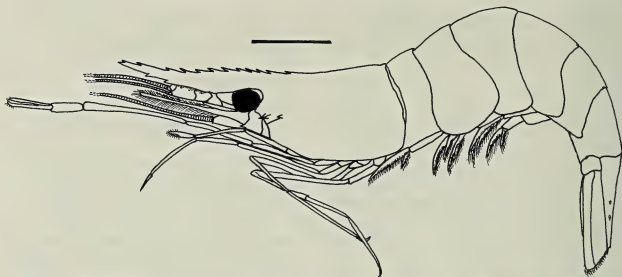


Fig. 1. *Macrobrachium patheinense*. Lateral view of holotype, KUMBCr 1101; male (8.9 mm). Scale equals 5 mm.

pace length in millimeters. Abbreviations used include: M, male; F, female.

Family Palaemonidae Rafinesque, 1815

Genus *Macrobrachium* Bate, 1868

Macrobrachium patheinense, new species
Figs. 1–2

Materials examined.—Mayan Creek, Thayet Kone village, Pathein City, Ayeyawaddy Division, 6 Sep 2001: holotype, M (8.96), KUMBCr 1101, paratype, 2M (9.16, 8.85), KMNH IvR 400.100, KMNH IvR 400.101, 2M (7.21, 8.75), ZRC 2003.0324, 33M (9.25, 9.14, 9.11, 8.47, 8.19, 8.50, 8.65, 8.85, 8.61, 8.33, 8.68, 8.48, 9.08, 9.12, 8.48, 8.31, 8.67, 8.65, 9.67, 8.98, 8.64, 8.10, 8.83, 7.97, 8.61, 8.16, 8.24, 7.92, 8.63, 9.10, 9.07, 7.91, 8.55), KUMBCr 1102–1134.

Diagnosis.—Carapace smooth, with antennal and hepatic spine. Rostrum slender, long; dental formula 2+10/5. Mandible with 3-segmented palp. Scaphocerite broad, with slightly concave outer margin. First pereiopod slender, reaching to end of scaphocerite. Second pereiopod equal, extremely slender; carpus 2 times as long as merus, finger 1.8 times as long as palm, without teeth on cutting edge. Telson with 2 pairs of dorsolateral spinules; posterior

margin ending in median tooth; 2 spines and 2 plumose setae on each side, inner spines well developed, outer spine very short, plumose setae shorter than inner spines.

Description.—Rostrum (Figs. 1, 2a) long, slender, reaching beyond end of antennular peduncle almost to end of scaphocerite, tip curving slightly upwards, upper margin with 12 teeth (mode 13, range 11–17), of which 2 teeth (mode 2, range 2–3) are placed behind orbit; first tooth smaller than second, placed further from second than third; upper margin of rostrum with single row of setae between teeth; lower margin with 5 ventral teeth (mode 4, range 3–8), first tooth level with seventh and eighth teeth; ventral portion with single row of setae. Carapace (Fig. 1) has strong antennal spine below lower orbital angle, produced anteriorly to broadly rounded lobe; hepatic spine smaller than antennal spine, placed below and some distance behind antennal spine; branchiostegal groove present.

Abdomen smooth, glabrous, with broadly rounded first to third pleurites; fourth and fifth pleurites produced posteriorly, sixth abdominal somite about 1.5 times as long as fifth. Telson (Figs. 2b, c) 1.4 times length of sixth abdominal somite, with 2 pairs of

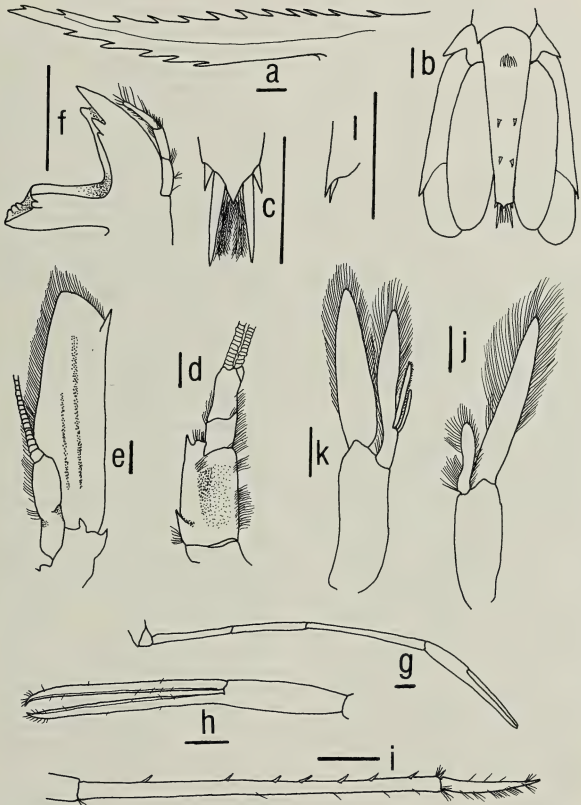


Fig. 2. *Macrobrachium patheinense*. Holotype, KUMBcr 1101; male (8.9 mm). a, lateral view of rostrum; b, dorsal view of telson; c, tip of telson; d, antennule; e, antenna; f, mandible; g, second pereiopod; h, chela of second pereiopod; i, dactylus and propodus of third pereiopod; j, first pleopod; k, second pleopod; l, uropodal diaeresis. Scales equal 1 mm.

dorsolateral spinules; posterior margin ending in a median tooth, flanked on each side by 2 spines and 2 plumose setae; inner spine well developed, 4 times as long as median tooth, outer spine very short, 2 plumose setae slightly shorter than inner spine.

Eyes well-developed, with cornea as long as stalk.

Basal segment of antennular peduncle (Fig. 2d) broad, stylocerite very short, distinctly pointed, not reaching middle of basal segment; anterolateral spine of basal segment reaching about middle of second segment; second segment as long as third segment; anterior margin of basal segment strongly curved. Scaphocerite (Fig. 2e) 3.2 times as long as broad, not reaching tip of rostrum; outer margin slightly concave, ending in a tooth, not reaching end of lamella. Mandible (Fig. 2f) with outer, lateral, 3-segmented palp. Other mouth parts typical for genus.

First pereopod slender, reaching end of scaphocerite (Fig. 1); fingers slightly longer than palm, with numerous setae; carpus about twice as long as chela, broadest distally, narrowing proximally; merus shorter than carpus; ischium about half as long as merus. Second pereopods (Figs. 2g, h) equal in size and shape, extremely slender, carpus reaching beyond scaphocerite by half its length; chela gradually narrowing proximally, finger very long, slender, about 1.8 times as long as palm (mean 1.7, range 1.4–1.9), same width throughout length, cutting edge entire, tip curves inwards; carpus as long as chela, unarmed, with distal portion broadest; merus about half as long as carpus (mean 0.7, range 0.5–0.9) but equal with ischium. Pereiopods 3–5 slender, subequal in size; third pereopods overreaching scaphocerite by length of entire dactylus; dactylus (Fig. 2i) slender, concave on ventral, with numerous setae on dorsal surface, measuring about $\frac{1}{2}$ of propodus length; propodus with eight spinules on ventral surface, about twice as long as carpus; merus nearly as long as propodus; ischium about same length as carpus; fourth

pereopods shorter than fifth but longer than third.

Exopod of first pleopod (Fig. 2j) oval-shaped, with small endopod, inner margin concave. Second to sixth pleopods nearly equal with endopods and exopods; endopod with a slender appendix interna. Second pleopod (Fig. 2k) with appendix masculina, placed between appendix interna and endopod; appendix masculina longer, stronger than appendix interna, bearing several stiff setae. Uropods reaching beyond end of telson; exopods ovate, outer margin straight, inner margin convex, uropodal diaeresis (Fig. 2l) with a spine slightly longer than outer angle; endopods broadly ovate, smaller than exopods.

Color.—Grayish white when live.

Etymology.—The specific name is adapted from the type locality (Pathein) where the specimens were collected.

Distribution.—*Macrobrachium patheinense* inhabits freshwater and slightly brackish water habitats, known so far only from the type locality.

Remarks.—*Macrobrachium patheinense* is similar to the *Palaemon*-like *Macrobrachium* species, that have slender and delicate pereopods, especially *M. mirabile* (Kemp, 1917), *M. palaemonoides* Holthuis, 1950, *M. superbum* (Heller, 1862) and *M. inflatum* Liang & Yan, 1985. *Macrobrachium patheinense* is, however, distinguishable from *M. mirabile* by the shape of the rostrum and telson. The rostrum of *M. patheinense* is slender and longer than the scaphocerite, while that of *M. mirabile* is shorter than the scaphocerite, and has a high dorsal crest (Kemp 1917). The telson of the former has two pairs of plumose setae slightly shorter than the inner spine, but that of the latter has only one pair of plumose setae longer than the inner spine. The new species is also distinguished from *M. palaemonoides* by shapes of the rostrum and telson, and the proportions of chelae of the second pereopods. The rostrum of *M. patheinense* is armed with teeth along the entire upper margin, but that of *M. palae-*

monoides has an unarmed area on its distal half (Holthuis 1950, Kamita 1974). The telson terminates in a short median tooth in *M. patheinense*, but this tooth is longer in *M. palaemonoides* (Kamita 1974). The movable finger of the second pereiopod is 1.4–1.9 (mean 1.7) times as long as the palm in *M. patheinense*, but 1.3–1.4 times as long as the palm in *M. palaemonoides* (Chace & Bruce 1993, Holthuis 1950). The new species can easily be distinguished from *M. superbum* by the shape of the rostrum and the second pereiopod chela proportions. The rostrum doesn't reach beyond the distal end of the scaphocerite in *M. superbum* (Cai & Dai 1999, Holthuis 1950), but distinctly further in *M. patheinense*. In addition, the upper margin of the rostrum is generally straight in *M. superbum*, but distally upcurved in *M. patheinense*. The movable finger of second pereiopod is 1.2–1.5 times as long as the palm in *M. superbum*, but 1.4–1.9 (mean 1.7) times in *M. patheinense*. The rostral shape and formula of *M. patheinense* is most similar to those of *M. inflatum*, but the second pereiopods and telson of both species are different. The movable finger of the second pereiopod of *M. inflatum* is subequal to the length of the palm (0.9–1.0 from the figures of Cai & Dai (1999) and Liang & Yan (1985)), but that of *M. patheinense* is much longer than the palm (1.4–1.9, mean 1.7). The telson of *M. inflatum* bears three pairs of plumose setae, these setae being longer than the inner spine on the posterior margin, but *M. patheinense* has only two pairs of plumose setae that are slightly shorter than the inner spine.

The unique chela of *M. patheinense* resembles that of *Leandrites stenopus* Holthuis, 1950, and *Pseudopalaemon bouvieri* Sollaud, 1911, however the presence of a mandibular palp in *M. patheinense* confirms its placement in *Macrobrachium* and distinguishes it from all *Leandrites* and *Pseudopalaemon* species (Holthuis, 1993).

Thus, the new species appears to occupy an interesting phylogenetic position and should be included in future studies inves-

tigating generic relationships within the family Palaemonidae.

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A new species of *Enhydrosoma* Boeck, 1872 (Copepoda: Harpacticoida: Cletodidae) from the Eastern Tropical Pacific

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Abstract.—Some enhydrosomids were found while sorting samples taken from the Urías system during a short-term study on the effects of organic enrichment on the abundance and diversity of benthic copepods. Upon careful examination, these specimens proved to belong to a new species, *Enhydrosoma brevipodum*, of the species-group defined by the lack of sexual dimorphism on the male P3 and can be separated by the reduced exopod of female P5. *Enhydrosoma brevipodum*, whose full description is herein provided, constitutes the fourth record of the genus from the Pacific Mexican coast.

The genus *Enhydrosoma* Boeck, 1872 is a group of harpacticoid copepods commonly found in shallow brackish and marine coastal systems worldwide. Some *Enhydrosoma* specimens were found in sediment samples from two shallow brackish systems in central (Ensenada del Pabellón lagoon) and southern (Urías system) Sinaloa during the course of two short-term studies about the effects of organic enrichment on the distribution and abundance of meiofauna (see Gómez-Noguera & Hendrickx 1997) and on the diversity of benthic harpacticoids. Some of these specimens belong to three species recently described by Gómez (2003), whereas some specimens constitute the Pacific counterpart of *Enhydrosoma lacunae* Jakubisiak, 1933 (Gómez 2003), originally described from Cuba and redescribed by Fiers (1996) from the Yucatan Peninsula. While sorting samples taken from Urías system, some specimens of a different species of *Enhydrosoma* were found. These specimens proved to belong to a new species mainly characterized by the reduced exopod of female P5. A detailed description of this species is herein provided.

Materials and Methods

Quantitative sediment cores were taken for the analysis of the effects of organic enrichment on benthic copepods along a polluted estuary (Urías system) in southern Sinaloa (north-western Mexico) during 2001 and 2002. Sediment samples were taken with an Eckman box corer with a sampling area of 225 cm², and subsamples were taken using plastic corers with a sampling surface of 7 cm². Sediment cores were subdivided vertically into separate 1 cm slices to a depth of 5 cm. Each slice was fixed with 10% formalin, and sieved through 500 and 63 µm sieves to separate macro- and meiofauna. Meiofauna was preserved in 70% ethanol and stained with Bengal Rose until further inspection. Meiofaunal major taxa were quantified and copepods (cyclopoids, poecilostomatoids and harpacticoids) were separated from the rest of meiofauna and stored in 70% ethanol for further investigation. Observation and drawings of the species described herein were made from whole and dissected specimens mounted in lactophenol, under 100× oil immersion objective using a Leica compound microscope equipped with drawing

tube and phase contrast. The type material was deposited in the collection of the Instituto de Ciencias del Mar y Limnología, Mazatlán Marine Station. The terminology proposed by Huys & Boxshall (1991) for the general description and armature formulae was adopted. Abbreviations used in the text and tables: P1–P6, first to sixth swimming leg; EXP, exopod; ENP, endopod.

Family Cletodidae T. Scott, 1904 sensu
Por (1986)

Genus *Enhydrosoma* Boeck, 1872

Enhydrosoma brevipodium, new species

Type material.—One female holotype preserved in 70% ethanol (EMUCOP-090301-73), one dissected male allotype (EMUCOP-090301-62), and one dissected female paratype (EMUCOP-090301-61); collected from station 10; 9 Mar 2001; leg. S. Gómez.

Type locality.—Urías system, Sinaloa, northwestern Mexico (23°09'–23°13'N, 106°20'–106°25'W).

Etymology.—The specific name alludes to the reduced exopodal lobe of female P5.

Female.—Body (Fig. 1A, 2A) tapering from posterior margin of cephalothorax, curved in lateral view; length of holotype, 420 μm from tip of rostrum to posterior margin of caudal rami. Cephalic shield about $\frac{1}{4}$ total length, with strongly folded lateral and dorsal surface, posterior margin plain, with sensilla arising from distinct cones. Rostrum triangular, fused to cephalic shield, with rounded tip, with two sensilla. Dorsal surface of free thoracic somites (P2–P4) smooth, with sensilla arising from distinct cones along plain posterior margin. First urosomite (P5-bearing somite) as preceding somites except for fewer sensilla. Surface of genital double somite smooth, with dorsolateral division between first and second genital somite (second and third urosomites), posterior margin of both genital somites plain, first somite with sensilla arising from distinct cones along posterior

margin, second somite as first one except for two additional tube pores (arrowed in Fig. 1A), both somites with additional sensilla arising from paired bulbous structures laterally; genital somites completely fused ventrally, first somite bearing pair of P6 and genital pore, the former each bearing a short spinulose spine, and with an associated tube-pore (arrowed in Fig. 2A), copulatory pore covered by integumental fold, ventral surface of second segment smooth, except for spinules and fragile setules along posterior margin between pair of sensillum-bearing cones. Dorsal surface of fourth and fifth urosomite as in preceding somite, except for lack of central pair of sensilla on posterior margin of fourth somite, and lack of sensilla along posterior margin of fifth urosomite, both somites with pair of tube pores (arrowed in Fig. 1A); ventral surface of fourth and fifth urosomite smooth, fourth urosomite ornamented with spinules and setules as in second genital somite, fifth urosomite with only spinules along posterior margin. Anal segment smooth, rounded anal operculum without ornamentation and flanked by pair of sensilla. Caudal rami cylindrical and about 8.3 times as long as wide, with seven setae in all, setae I and II located in proximal fifth, the former arising ventrally and about $\frac{1}{2}$ total length of seta II, the latter dorsal to seta I, seta III slightly longer than seta II and arising in the middle along outer margin of ramus, seta IV and V fused, seta VI located in distal inner corner and as long as seta II, seta VII arising in proximal third at the level between seta II and III.

Antennule (Fig. 2B). 5-segmented; surface of segments smooth except for spinular row on first, third and fourth segment. Armature formula 1-(1), 2-(7), 3-(7+ae), 4-(1), 5-(11+ae).

Antenna (Fig. 3A, B) with proximal and distal set of spinules on inner margin of allobasis; with very small distal abexopodal seta close to distal set of spinules, the latter difficult to see and can be easily mistaken for a setule (arrowed in Fig. 3A). Exopod

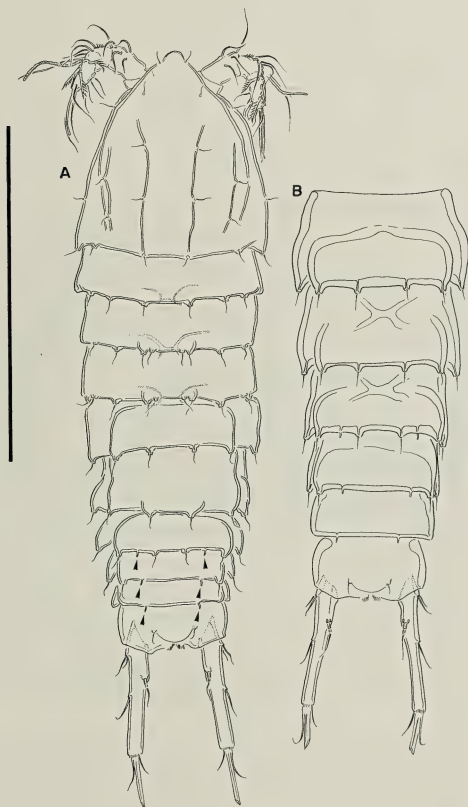


Fig. 1. *Enhydrosoma brevipodum*, new species. A, female, habitus, dorsal; B, male, urosome, dorsal. Scale bar: A, 200 μm ; B, 160 μm . A, paratype EMUCOP-090301-61; B, allotype EMUCOP-090301-62.

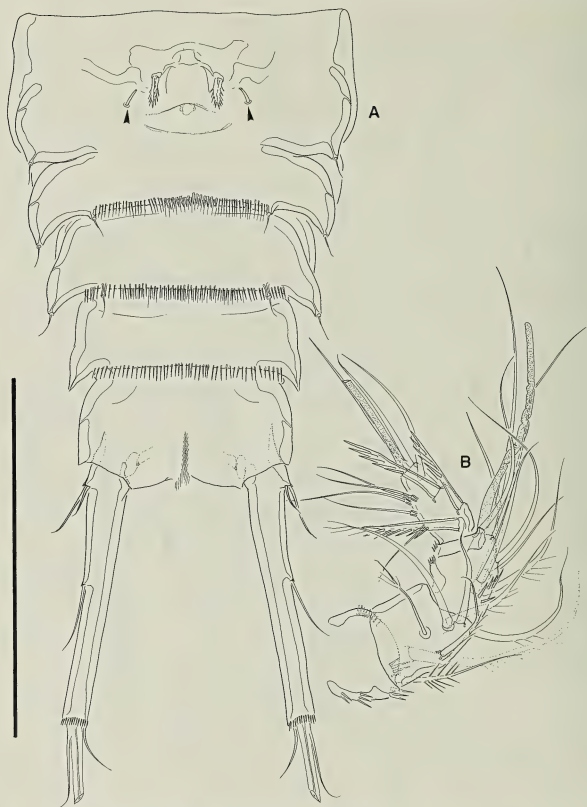


Fig. 2. *Enhydrosoma brevipodum*, female paratype EMUCOP-090301-61. A, urosome, ventral (P5 bearing-somite omitted; tube pores in genital field arrowed); B, antennule. Scale bar: A, 100 μm ; B, 75 μm .

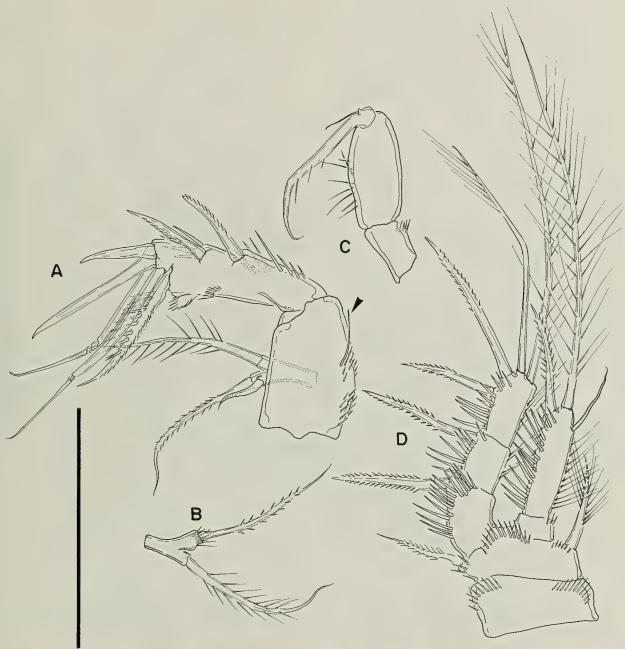


Fig. 3. *Enhydrosoma brevipodum*, female paratype EMUCOP-090301-61. A, antenna with aberrant exopod; B, normal exopod of antenna; C, maxilliped; D, Pl. Scale bar, 50 μ m.

1-segmented and armed with two bipinnate elements (Fig. 3B). Endopodal segment ornamented with two strong spines subdistally along inner margin; distal margin five setae/spines (outer pectinate spine seemingly without fused small seta), and ornamented with two hyaline frills on outer margin.

Mandible (Fig. 4A, B) with slender gnathobase; biting edge with uni- and multicuspitate teeth, and one bare seta at distal

inner corner. Palp well-developed, 1-segmented and armed with one endopodal and two basal setae (Fig. 4B).

Maxillule (Fig. 4C). Arthrite with five distal and two lateral elements, and two surface setae; coxal endite fused to basis and represented by one seta, basis represented by two distal setae, endopod and exopod represented by one seta each.

Maxilla (Fig. 4D) with short spinular row

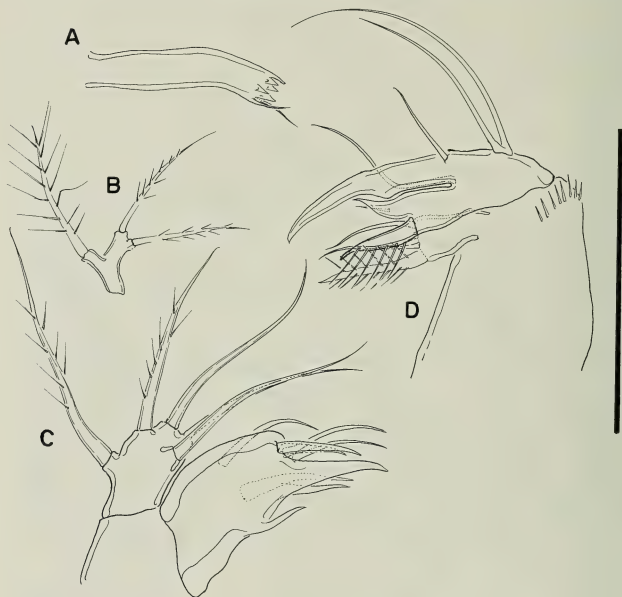


Fig. 4. *Enhydrosoma brevipodum*, female paratype EMUCOP-090301-61. A, mandible; B, mandibular palp; C, maxillule; D, maxilla. Scale bar: A, B, 50 μ m; C, D, 25 μ m.

on distal inner corner of syncoxa; proximal syncoxal endite with two slender and bare setae and one bipinnate element; distal syncoxal endite with two elements (inner strongly pinnate, outer anvil shaped, fused to endite and with only one pinnule). Allobasal endite with non-articulated spine and two setae. Endopod represented by two setae fused at base.

Maxilliped (Fig. 3C) prehensile, with short and unarmed syncoxa; basis with spinules along inner margin; claw slender and curved distally, with accessory seta.

P1 (Fig. 3D). Coxa and basis ornamented as depicted, the latter with inner and outer setae. Exopod three-, endopod 2-segmented, the latter reaching distal third of last exopodal segment.

P2-P4 (Figs. 5A, B, 6A) with coxa and basis ornamented as shown, the latter with outer plumose seta. Exopod three-, endopod 2-segmented. Endopod of P2 slightly longer than, of P3 as long as, of P4 clearly shorter than first and second exopodal segments combined. Armature formulae of P1-P4 as follows:



Fig. 5. *Enhydrosoma brevipodum*, female paratype EMUCOP-090301-61. A, P2; B, P3. Scale bar: 50 μm .

	P1	P2	P3	P4
EXP	I-0;I-0;II,2,0	I-0;I-0;II,2,0	I-0;I-0;II,2,1	I-0;I-0;II,2,1
EXP	0-0;I,1,1	0-0;0,2,0	0-0;I,2,0	0-0;I,2,0

P5 (Fig. 6B). Baseoendopod and exopod fused but with partial suture still visible on posterior face. Exopod almost square, with a few setules on outer margin, three setae (one minutely pinnate) on distal margin and a large tri-pinnate seta on inner margin.

Baseoendopod with transverse rows of spinules on endopodal lobe and at base of exopod; outer seta on long pedicel. Endopodal lobe reduced with three elements (a strong inner pinnate spine and a long pinnate seta on distal margin, and a slender pinnate seta on inner margin).

Male.—Total body length, 450 μ m. General dorsal body shape (not shown) as in female. Urosome (Fig. 1B) as in female dorsally; second and third urosomites distinct ventrally (Fig. 7A); first urosomite without ventral spinular ornamentation along posterior margin; second urosomite with P6 represented by one fused and one free plate close to posterior margin ventrally (Fig. 7A), and ornamented with spinules along posterior margin; third to fifth urosomites with spinules and fragile setules along posterior margin; fifth urosomite without sensilla. Caudal rami (Figs. 1B, 7A), mouth parts, and P1–P4 (not shown) as in female.

Antennule (Fig. 7B) 6-segmented, subchirocer; surface of segments smooth except for short spinules of first segment and longitudinal row of long spinules on fourth globose segment. Armature formula difficult to define.

P5 (Fig. 7A). Baseoendopod and exopod fused, the former with outer extension bearing outer seta and ornamented with spinules at base of exopod and distally on endopodal lobe, the latter small and armed with one inner seta and one outer spine. Exopod elongate, about 1.5 times as long as wide, and armed with two apical setae (outermost slender and about $\frac{1}{4}$ total length of innermost bipinnate seta).

Remarks.—In his outstanding preliminary revision of *Enhydrosoma*, Gee (1994) accurately stated that the armature complements of the second endopodal segment of P1 are not always reliable. This is true, as shown by Gee (1994), for *E. curticauda* Boeck, 1872, and also for *E. propinquum* (Brady, 1880) (compare Apostolov & Marinov (1988) and Sars (1909)). Also, Gee (1994) suggested that the often reduced inner seta on the P1 second endopodal segment could either be overlooked or mistakenly regarded as a spinule or setule in previous descriptions. On the other hand, it has to be noted that the males of some species (e.g., *E. intermedia* Chislenko, 1978, *E. ca-soae* Gómez, 2003 and *E. solitarium* Gómez, 2003) remain unknown and their position within *Enhydrosoma* regarding the male P3 endopod is still pending. Even when the male of a known species is found, the description of the P3 endopod is often omitted, e.g., Arlt (1983) for *E. longifurcatum* Sars, 1909 and *E. sarsi* (T. Scott, 1904); Bodin (1970) for *E. propinquum*; Apostolov & Marinov (1988) for *E. gariene* Gurney, 1930; Monchenko (1967), Apostolov & Marinov (1988) and Bodin (1970) for *E. caeni* Raibaut, 1965; Marinov & Apostolov (1985) for *E. longicauda* Marinov & Apostolov, 1983). Therefore, a thorough revision of the species currently assigned to *Enhydrosoma* is urgently needed to unravel the phylogenetic relationships within the genus.

The species herein described belongs to Gee's (1994) type 1 (being the male P3 endopod 2-segmented, with the same armature formula and form of armature elements as in the female), which seems to be rather common in *Enhydrosoma*. In fact, the unmodified condition of the male P3 endopod has been reported for 10 species—*E. migoti* Monard, 1926; *E. tunisensis* Monard, 1935 (considered as incertae sedis within *Enhydrosoma* by Wells 1965); *E. propinquum*, *E. sarsi*, *E. longifurcatum*, *E. latipes* (A. Scott, 1909); and *E. gariene*, *E. longicauda*, *E. pectinatum* Wells & Rao, 1987; *E. sor-*

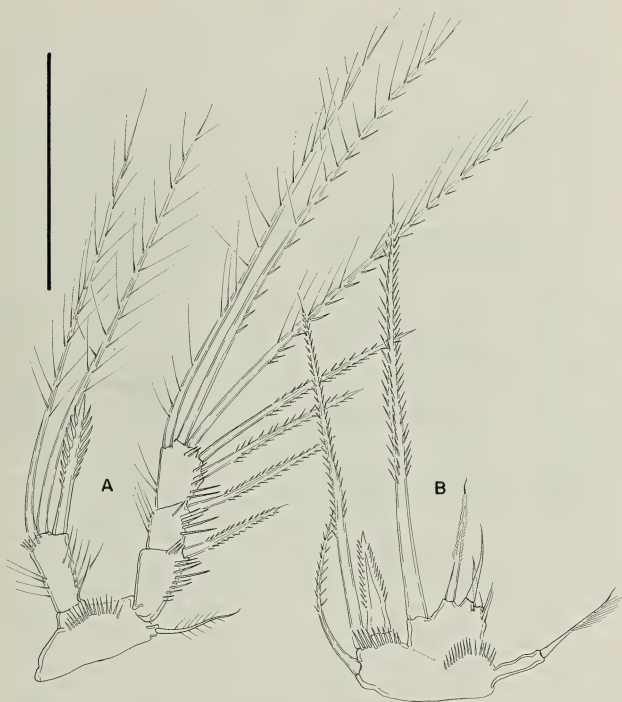


Fig. 6. *Enhydrosoma brevipodum*, female paratype EMUCOP-090301-61. A, P4; B, P5. Scale bar: 50 μ m.

didum Monard, 1926); and *E. caeni* and *E. rosae* Fiers, 1996. Of these, only Sars' (1909) *E. propinquum*, *E. latipes*, *E. rosae* and *E. migoti* have been reported bearing three setae on the second endopodal segment of P1 (although the armature formula of the endopod of P1 needs confirming in some other species), and *E. brevipodum*

could well be most closely related to the *E. longifurcatum* species-group (*E. longifurcatum*, *E. gariene*, *E. sordidum*, *E. caeni* and *E. pectinatum*) based on the combination of the following character states: (a) the caudal ramus shape and arrangement of setae I, II, III and VII, (b) rostrum, (c) number of setae on the mandibular palp, (d) fu-

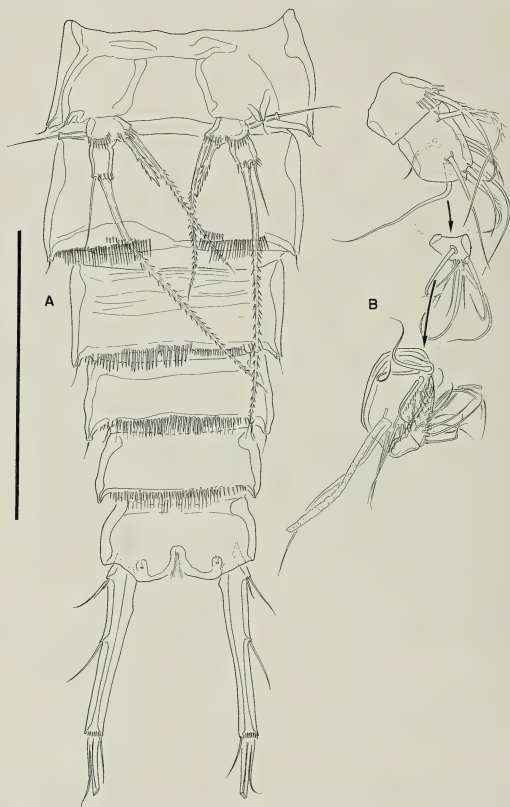


Fig. 7. *Enhydrosoma brevipodum*, male allotype EMUCOP-090301-62. A, urosome, ventral, showing P5 and P6; B, antennule. Scale bar: A, 100 μm ; B, 75 μm .

sion of coxal endite and basis and number of setae on the whole palp, (e) number of elements on distal syncoxal endite of the maxilla, (f) lack of sexual dimorphism on P3 endopod, (g) the fusion of exopod and baseopod on P5 of both sexes, and (h) number of setae on female P6. The species described herein differs from the other species of the *E. longifurcatum* species group in the following characters: (a) presence of a seta on abexopodal margin of the first endopodal segment of the antenna, (b) number of setae on the second endopodal segment of P1 (except for Sars' (1909) *E. propinquum*), (c) proportions of P5 exopod in both sexes and arrangement of setae in female (in all other species in this group the large inner seta is on distal margin and outer setae on outer margin, but in *E. brevipedum* the large seta is located internally and the others on distal margin. In this regard it has to be noted that *E. longifurcatum* and *E. sordidum* were reported to have only three setae on P5 exopod, but it is highly probable that there are four setae, being that the middle outer element is very small and weak (J. M. Gee, in litt.). The inner and outer elements of female exopod of P5 are strong and pectinate spines in *E. longifurcatum*, *E. gariene*, *E. sordidum*, *E. caeni* and *E. pectinatum*, but it is a pinnate seta in *E. brevipedum*. On the other hand, the genital field of *E. brevipedum* is similar to that described for *E. curticauda* by Gee (1994) in that the single copulatory pore is covered by an integumental fold, but differs in the armature formula of P6 (with two and one seta in *E. curticauda* and *E. brevipedum*, respectively), spinular ornamentation (with and without spinules in *E. curticauda* and *E. brevipedum*, respectively), and number and location of tube pores (with three tubular extensions arising from two pores in *E. curticauda*, and with two tubular extensions arising from two pores in *E. brevipedum*). The genital field of *E. brevipedum* seems to be similar to that described by Gee (1994) for *E. propinquum* in the number and location of the tube pores, and similar

to that described for *Strongylacron buchholzi* (Boeck, 1872) and *E. gariene* in the armature formula and lack of spinular ornamentation of P6 (see Gee, 1994:95, figs. 9C-E). Also, according to Gee (1994) the position of spinules and/or setules on the inner margin of the antennal allobasis could be used to discern which abexopodal seta has been lost in a given species. The distal abexopodal seta observed for *E. brevipedum* is very small and can be easily mistaken for a setule. However, careful examination revealed the presence of small spinules at the base of this element which, following Gee (1994), could indicate either the site where a seta is possibly attached or the site where the abexopodal seta must have been situated in those cases where the proximal (basal) or the distal seta was lost. All the above suggests the presence of a very reduced distal seta and loss of the proximal (basal) seta in *E. brevipedum*, which is also the case for most species within *Enhydrosoma* (Gee, 1994). It is interesting to note that a female paratype of *E. brevipedum* (EMUCOP-090301-61) was found to possess an aberrant antennal exopod bearing three setae (two well-developed and one dwarfed element) (see Fig. 3A). The same has been observed for a female of *E. curticauda* from East Finnmark (Gee, 1994:97). To the best of my knowledge, *E. brevipedum* is unique within the genus by the reduced exopod of the female P5.

Enhydrosoma brevipedum was found in sandy sediments taken in the mouth of the Urfás brackish system. The sampling station (stn. 10) where the newly found species was taken is under the direct effects of marine water and is characterized by sandy bottom and low contents of chlorophyll "a" (3189.2 mg l^{-1}) and organic mater (2.8%).

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**New record of *Ophiosyzygus disacanthus* Clark, 1911
(Echinodermata: Ophiuroidea: Ophiomyxidae) in the Caribbean Sea**

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Abstract.—*Ophiosyzygus disacanthus* Clark, 1911 is reported for the first time in the Caribbean Sea; this is the third record of this species in the literature. A comparison with two other records from the southwestern coast of Japan (Clark 1911) and the Gulf of Mexico (Turner & Heyman 1995) is presented.

Ophiosyzygus disacanthus was described by Clark (1911) from the southwestern coast of Japan. This species was further documented by Turner & Heyman (1995), who revised the diagnosis of the monotypic genus *Ophiosyzygus* and the description of its type species, *O. disacanthus*, based on the type material (two specimens) and on new material (two specimens) collected recently from the Gulf of Mexico, off the southwestern coast of Florida. Among other characters, the genus was diagnosed by Clark (1911) as lacking radial shields and dorsal arm plates; but Turner & Heyman (1995) found these structures, and they emended the generic diagnosis, completed the original description of *O. disacanthus*, and commented on the family Ophiomyxidae, specifically about its small radial shields and thin dorsal arm plates, which have been often overlooked in this family. In this note, we record *O. disacanthus* from the Caribbean Sea, specifically off the Colombian coast.

Materials and Methods

As part of a project developed by the Marine and Coastal Research Institute (INVEMAR), designed to inventory the ben-

thic macrofauna from the continental shelf and upper slope region of the Caribbean coast of Colombia, two specimens of *Ophiosyzygus disacanthus* were collected at 9°46'61"N, 76°13'72"W in 155 m depth on 26 Apr 2001. Sampling was conducted on board the B/I *Ancón*; a 5 m opening trawl net was used. The material is deposited in the collection of the Museo de Historia Natural Marina de Colombia (MHNMC), catalogue number INV EQU01927. The specimens were measured, and photographs were taken, after fixing in 70% ethanol. The plates of the ventral interradius of the disc were measured after treatment with sodium hypochlorite, and also the disc granules were measured.

Family Ophiomyxidae Ljungman, 1867

Ophiosyzygus Clark, 1911

Ophiosyzygus disacanthus Clark, 1911

Fig. 1

Remarks.—The specimens of *O. disacanthus* collected off the Colombian coast agree with the diagnosis of the genus as emended by Turner & Heyman (1995), as well as with the characteristics included in the species description about the thornier arm spines, the presence of dorsal arm

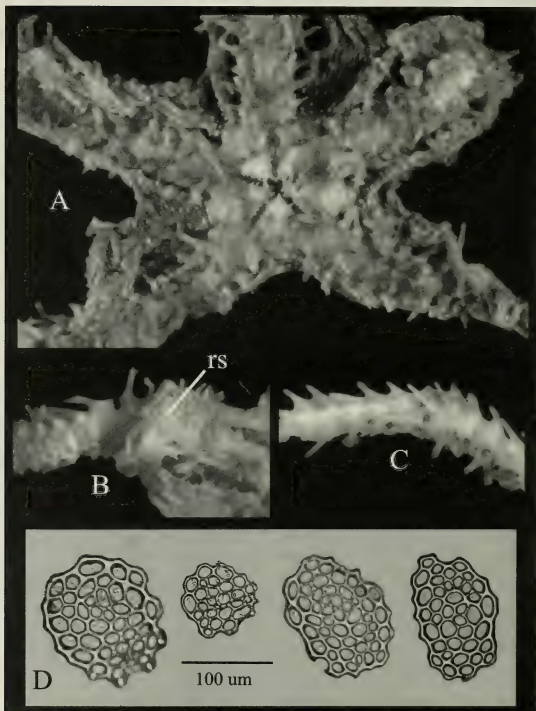


Fig. 1. *Ophiosyzygus disacanthus*. A. Ventral surface of disc (disc diameter: 15 mm). Note shape of oral papillae and white, opaque and irregular granules. B. Dorsal surface of disc and proximal part of arm. Note small radial shields (rs). C. Lateral view of arm. Note upper arm spines successively united by broad, thin, horizontal membrane. D. Four plates of ventral interradial plates of disc.

plates, and of flat and multiperforate plates embedded in the skin of the ventral interradial plates of the disc; these are visible after treatment with sodium hypochlorite (Fig. 1D). The ventral interradial plates are slightly

longer ($115.7 \pm 35.1 \mu\text{m}$, $n = 23$) than those of the Gulf of Mexico specimens ($111 \pm 22 \mu\text{m}$, $n = 24$) measured by Turner & Heyman (1995). The number of oral papillae is variable; 3–6 in the Colombian spec-

imens (Fig. 1A), 2–4 in those from Japan, and 2–5 in Florida specimens. The irregular granules of the disc are white, opaque, and are present in the ventral (Fig. 1A) and dorsal integument. One of the specimens has ventral granules larger ($155 \pm 34.6 \mu\text{m}$, $n = 16$) than the dorsal ones ($104 \pm 15.4 \mu\text{m}$, $n = 15$); in the other specimen, the dorsal and ventral granules are similar in size ($111.4 \pm 21.6 \mu\text{m}$, $n = 21$), but the dorsal granules are elongate. In general the granules of the two specimens from Colombia are smaller than those of the holotype ($232 \pm 67.8 \mu\text{m}$, $n = 34$) and paratype ($221 \pm 53.8 \mu\text{m}$, $n = 21$) and similar in size to the specimens from Florida ($84 \pm 21.9 \mu\text{m}$, $n = 9$; $124 \pm 32.8 \mu\text{m}$, $n = 10$) (Turner & Heyman 1995). The arms of both specimens are broken. The discs are damaged, disc diameters are 10 and 15 mm, 3 mm more than the maximum size of previously collected specimens (Clark 1911, Turner & Heyman 1995). The depth (155 m) where the Colombian specimens were taken is within the range recorded for other specimens: 188–278 m for the type material in the Pacific Ocean and 127–159 m for the specimens collected in the eastern Gulf of Mexico (Turner & Heyman 1995).

In accordance with previous findings, this species is found mostly in rocky and hard substrata, covered with a veneer of sand or in deep sand in the case of Gulf of Mexico samples. The station from which specimens were collected in the Colombian Caribbean was one of the most diverse among all those sampled in the INVEMAR project and produced a large number of fishes and invertebrates characteristic of hard substrata or reef bottoms. Among these, 39 species of echinoderms were found, collected from gorgonians (e.g., *Astrocnida isidis*, *Asteropora annulata*, *Astroschema* cf. *laeve*, *A. oligactes*) and other substrata (e.g., *Nemaster rubiginosus*, *Endoxocrinus parrae*, *Ophioderma appressum*, *Ophiothrix suensonii*). The most diverse taxa, in descending order, were echinoderms, cnidarians, fishes, decapods, crus-

taceans, and mollusks; also many individuals and possibly many species of sponges were collected, but they are not yet identified (Reyes et al. 2004). Turner & Heyman (1995) also reported a diverse habitat, with cnidarians, echinoderms, sponges, and crustaceans at one station and crustaceans, cnidarians, echinoderms, and sponges at the other station.

The world distribution of *O. disacanthus* is interesting because its presence in the Gulf of Mexico and the Colombian Caribbean might be a relict of a wider distribution in the Tethys Sea, as in the case of the genus *Quadratus*, a myxine fish that was considered restricted to the Western Pacific, but that was collected also during this project in the Western Atlantic (Mok et al. 2001).

Acknowledgments

We extend our gratitude to Dr. Richard Turner for his helpful suggestions and thorough revision of a draft of this note. This study was made possible by the financial support of the projects INVEMAR FON-AM, cod. 001065, INVEMAR COLCIENCIAS 2105-09-10401 and INVEMAR-COLCIENCIAS, cod. 210509-11248. This is contribution #849 from INVEMAR.

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***Sunagocia sainsburyi*, a new flathead fish (Scorpaeniformes: Platycephalidae) from northwestern Australia**

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Abstract.—Based on two specimens taken by bottom trawl from northwestern Australia, *Sunagocia sainsburyi* differs from its congeners in having: 4–5 preorbital spines; 5 total gill rakers on first arch; a bony expansion of suborbital ridge base on cheek bearing 1–2 rows of small spines; and no papillae on upper surface of eye. It also tends to have more spines on the ethmoid and on the supraorbital and suborbital ridges. A table compares features of the new species to the other three species currently included in the genus *Sunagocia*.

Imamura (1996) erected the genus *Eurycephalus* for three species formerly placed in the genus *Thysanophrys* Ogilby, 1898; *E. arenicola* (Schultz, 1966), *E. carbunculus* (Valenciennes in Cuvier & Valenciennes, 1833), and *E. otaitensis* (Cuvier (ex Parkinson) in Cuvier & Valenciennes, 1829). The primary features distinguishing the new genus were: suborbital ridge bearing four or more distinct spines; iris lappet finger-like or branched; lateral-line scale pores with two openings posteriorly; and sensory tubules weakly developed or absent from the cheek region. Recently, Imamura

(2003) learned that the name *Eurycephalus* was preoccupied by the cerambycid beetle genus *Eurycephalus* Gray in Cuvier & Griffith, 1832 and proposed *Sunagocia* as a replacement name.

During the trawling surveys of northwestern Australia conducted by the F/V *Courageous* in 1978 and by the F/V *Soela* in 1980, two small specimens of an undescribed species of *Sunagocia* were taken. Comparisons of features distinguishing these specimens from the other three species of *Sunagocia* appear in Table 1. The two collections of the new species represent

Table 1.—Comparison of features in species of *Sunagocia* (value for paratype in parentheses).

Character	<i>arenicola</i> n = 20	<i>carbunculus</i> n = 8	<i>otaitensis</i> n = 21	<i>sainsburyi</i> n = 2
SL (mm)	37–135	70–116	83–159	86 (97)
Total gill-rakers	6	6–7	6–7	5
Preocular spines	1	1	1	5 (4)
Preorbital spines	0, rarely 1–2	1, rarely 2	0, rarely 1	4
Maxilla reaches to	just past front of eye	anterior ¼ of eye	just past front of eye	mid-eye
Ocular flaps	absent	present	absent	absent
Labial papillae	absent	absent	present	absent
Suborbital ridge upper base	smooth, scaled	smooth, scaled	smooth, scaled	bony expansion with 1–2 rows of small spines

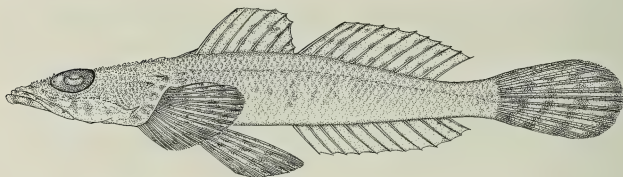


Fig. 1. Paratype of *Sunagocia sainsburyi*, CSIRO H 5856-01, Northern Australia, 97 mm SL.



Fig. 2. Cranial spines of holotype of *Sunagocia sainsburyi*, WAM 26230-007.

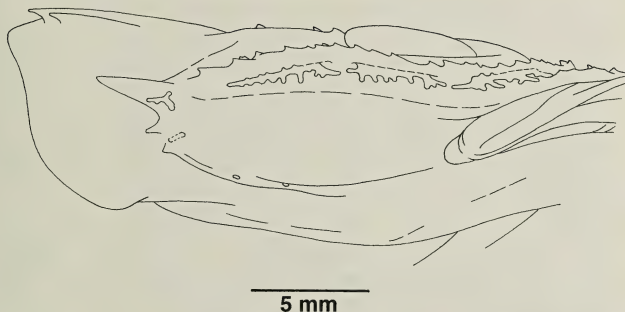


Fig. 3. Head of holotype of *Sunagogia sainsburyi*, right side, showing lack of sensory tubules on cheek below suborbital ridge.

the first records of the genus taken with trawling gear, the other species having typically been taken with rotenone and SCU-BA.

Methods

Counts and measurements were taken according to Hubbs & Lagler (1949). Measurements were made with calipers and rounded to the nearest mm. Vertebrae were counted from radiographs. Terminology of head spines follows Knapp et al. (2000). In-

stitutional acronyms follow Leviton et al. (1985) except for South African Institute for Aquatic Biodiversity (SAIAB), formerly RUSI. Standard length and head length are abbreviated as SL and HL, and lateral-line as LL.

Sunagogia sainsburyi, new species

Sainsbury's flathead

Fig. 1

Holotype.—WAM 26230-007, 86 mm SL, Western Australia, 125 km NE of Port Hedlund, 19°07'S, 119°25'E, F.V. *Courageous*, 28 May 1978, 73–74 m, K. Sainsbury et al.

Paratype.—CSIRO H 5856-01, 97 mm, Northern Australia, near Darwin, 11°53'S 131°15'E, F.V. *Soela*, Cr. 5, Sta. 49, 6 July 1980, trawl, 20–22 m.

Other material examined.—*Sunagogia arenicola*, USNM 362804 (12, 37–117 mm), Western Indian Ocean, Amirantes Is., D'Arros I., R/V *Anton Bruun* Cr. 9, 5°24'S, 53°13'E, 8 Dec. 1964, rotenone, 4–8 m, RS-40, R. D. Suttkus et al.; SAIAB 8219 (8, 46–131), Mozambique, Pinda Reef, Bay of Bocage, 14°10'S, Sept. 1956, M. M. Smith. *S. carbunculus*, USNM 99703 (8,

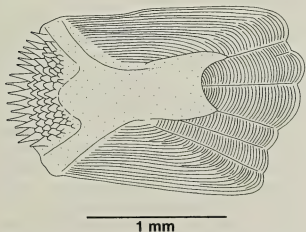


Fig. 4. LL scale, circa 22nd scale from right side of holotype of *Sunagogia sainsburyi*.

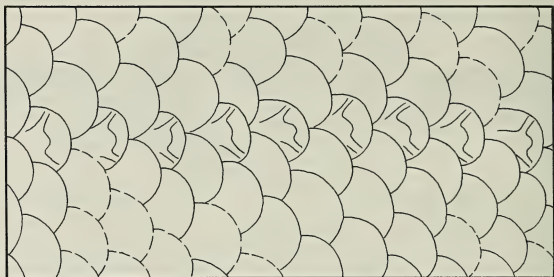


Fig. 5. Area around LL scales 19–27, right side of holotype of *Sunagocia sainsburyi*.

70–116), Malaysia, Sabah, North Borneo, Sandakan Bay, 2 Mar. 1908, U.S. Fisheries Steamer *Albatross*, seine. *S. otaitensis*, USNM 366402 (6, 106–151), Northern Philippines, Babuyan Is., Fuga I., circa 18°51'N 121°22'E, coral and tide pools, 11 Mar. 1990, rotenone, A. Ross; USNM 366403 (5, 83–159), Central Philippines, Negros, Apo I., 9°4.5'N 123°16.4'E, 18 May 1979, LK 79-20, rotenone, 0–2.4 m, L. W. Knapp et al.; ROM 42303 (10, 37–80) Indian Ocean, Chagos Arch., Peros Banhos, Isle du Coin, 5°26'21"S 71°46'52"E, 6 Feb. 1979, WE 79-06, rotenone, 0–7 m, R. Winterbottom et al.



Fig. 6. Sketch of iris lappet from right eye of holotype of *Sunagocia sainsburyi*.

Diagnosis.—A species of *Sunagocia* with 4–5 preorbital spines; 5 total gill rakers on the first arch; a bony expansion of the suborbital ridge upper base on cheek bearing 1–2 rows of small spines; maxilla reaching to below middle of eye; no papillae on upper surface of eye; a series of spines on the ethmoid and several pairs of nasal spines (Fig. 2); and smaller, more numerous spines on the supraorbital and suborbital ridges. Sensory tubules are absent from the cheek area below the suborbital ridge (Fig. 3).

Description.—Data for holotype given, followed by that of paratype in parentheses when differing. Dorsal-fin damaged in holotype, last 1–2 spines missing, VII(IX), 11; anal-fin rays 12; pectoral-fin rays 2 unbranched + 14 branched + 3 unbranched (2+13+4) = 19; pelvic fin with 1 spine and 5 rays, innermost is unbranched; caudal-fin branched rays 8; vertebrae 27; total gill rakers on first arch 5; pored scales in LL 52, anterior 3 scales bearing a small spine; 6 rows of scales between 2nd dorsal fin origin and LL. Number of oblique scale rows above LL about equal to number of LL scales. LL

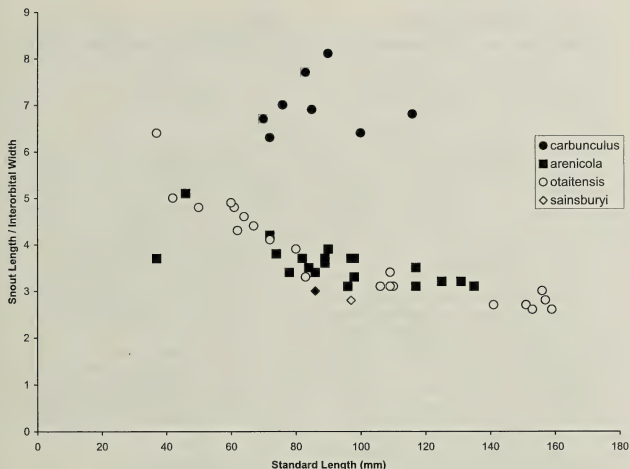


Fig. 7. Ratios of least interorbital width into snout length for the four species of *Sunagocia* (*S. sainsburyi* holotype, solid diamond).

scale pores with two openings to the exterior (Fig. 4). Relationship of LL scales to adjacent scale rows is shown in Fig. 5. Iris lappet bears short branches with bifurcate tips (Fig. 6). Lip margins without papillae.

Body depressed, upper body covered with ctenoid scales, breast scales largely cycloid. Interopercular flap lacking. HL 2.8 (2.9) in SL; orbit going 1.1 times in snout. Ratios of least interorbital width into snout length for the four species of *Sunagocia* appear in Fig. 7. Villiform teeth in bands on jaws and palatines, in two separate patches on vomer.

Top and sides of head armed with numerous spines (Fig. 2). Preopercular spines 3, uppermost longest, not bearing an accessory spine on base; a pair of stout nasal spines, with 2–3 smaller spines running anteriorly to each; base of opercular spines

covered by scales, not bearing serrae. Suborbital ridge with about 17–20 serrae.

Color observations were taken on the paratype after it thawed, prior to preservation. Dorsum brownish, with about six darker bands crossing back, venter whitish. Two brown infraorbital bands and two brown suborbital bands present. Cheek below suborbital ridge with a series of brown blotches. A brown band angling back from anterior ethmoid to front of eye. Dorsal-fin spines and rays bearing small dark spots; pectoral fin with several vertical brownish bands above, clear below; pelvic fin with four reddish-brown bands; and caudal fin with about four vertical dark brown bands.

Etymology.—The species is named in honor of Keith J. Sainsbury, collector of the holotype and other flatheads later during the F.V. *Soela* cruises.

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We thank the following individuals for the loan of specimens or other assistance: P. R. Last and A. Graham (CSIRO); J. B. Hutchins (WAM); R. Winterbottom and M. Rouse (ROM); P. C. Heemstra and V. Mthombeni (SAIAB) and S. Jewett (USNM). Thanks are also due J. Finan and S. Raredon, USNM, for considerable technical assistance. The fine drawing of the paratype was made by Keiko Hiratsuka Moore.

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Associate Editor: Carole Baldwin

**A new species of *Nannocharax* (Characiformes: Distichodontidae)
from Cameroon, with the description of contact organs and breeding
tubercles in the genus**

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Abstract.—*Nannocharax reidi*, new species, is described from several localities in the upper Cross River basin in Cameroon. The species possesses the synapomorphies of the clade comprising *Nannocharax* and *Hemigrammocharax*. It is assigned to *Nannocharax* on the basis of its possession of a completely-pored lateral line, a feature distinguishing that questionably monophyletic genus within the clade composed of these two genera. *Nannocharax reidi* is distinguished from its congeners on the basis of a combination of meristic and morphometric features and details of pigmentation on the body. Comparative studies revealed the presence of hook-shaped contact organs on the pectoral fins of some species of *Nannocharax* and epidermal breeding tubercles on the head, body, and fins of at least one species of the genus. These observations represent the first reports of contact organs and breeding tubercles in African members of the order Characiformes. Some species of *Nannocharax* were found also to possess variably-developed fields of hook-shaped contact organs on the exposed surfaces of scales of the midlateral portion of the body posterior of the pectoral girdle. This latter feature has not been previously reported among fishes.

Species of the African distichodontid genus *Nannocharax* are relatively small-sized fishes inhabiting the Nile River and many sub-Saharan rivers, with the greatest species-level diversity of the genus occurring in West Africa and the Congo River basin. Species of *Nannocharax* share a number of distinctive modifications relative to phylogenetically-proximate taxa including transversely-flattened ventral surfaces of the head and body, a down-turned mouth, and, in many species, expanded pelvic and pectoral fins; these features apparently correlate with their habits of resting on, and feeding off of, the substrate or vegetation (e.g., *Nannocharax fasciatus*, see Géry 1977:89). The most recent comprehensive

treatment of *Nannocharax* was that of Boulenger (1909:279) who discussed seven nominal species that recent authors have assigned to the genus. Subsequent decades saw the progressive descriptions of additional species of *Nannocharax*, resulting in 24 species being recognized in the compendium of the genus by Daget & Gosse (1984:200). Two treatments of the West African species of *Nannocharax* have been published (Daget 1961, Gosse & Coenen 1990), and recent decades have seen the description of several new species of the genus from that region (Vari & Géry 1981, Coenen & Teugels 1989, Van den Bergh et al. 1995). Numerous uncertainties, nonetheless, remain concerning the species-level

diversity within *Nannocharax*. Perhaps the major question is whether the geographically widespread *N. fasciatus*, whose distributional range in West Africa reportedly extends from Guinea to Gabon (Daget & Gosse 1984:201), is a single widely-distributed species or a complex of similar species. Reid (1989:24, 56), followed by Teugels et al. (1992:43), noted that population samples of an *N. fasciatus*-like form from the upper Cross River system in Cameroon differed from the more-typical *N. fasciatus* populations from that region, but those authors deferred from pursuing the question of the identity of these samples.

Studies of the species of *Nannocharax* in the lower Guinea region encompassing Cameroon, Rio Muni, Gabon, and the coastal portions of the Republic of Congo, Brazzaville demonstrate that some populations of an *N. fasciatus*-like form from the upper Cross River represent an undescribed species that we describe herein. We also describe unusual modifications of the scales, fins, and epidermis in some species of *Nannocharax* that were discovered during our comparative studies. These noteworthy modifications are either elaborations of some body scales of a form unique to the species of *Nannocharax* within the Characiformes (and perhaps fishes), or are elaborations of the fin rays and epidermis that were previously thought to be restricted to New World members within that order.

Materials and Methods

Measurements are given as a percentage of standard length (SL) except for subunits of the head that are presented as percentages of head length. Lateral-line scale counts include all pored scales along that series, including scales located posterior to the hypural joint. In fin-ray counts, lowercase Roman numerals indicate unbranched rays, and Arabic numerals indicate branched rays. The two posteriormost anal-fin rays, which are joined at their bases, were counted as one element. Morphomet-

ric and meristic data were taken following the procedures outlined in Fink & Weitzman (1974). Counts of gill-rakers, teeth, cteni, and branchiostegal rays were taken from two specimens that were cleared and counterstained following the method of Taylor & Van Dyke (1985). Vertebral counts were acquired via radiographs and include the four vertebrae of the Weberian apparatus and the terminal centrum. Institution abbreviations are: AMNH, American Museum of Natural History, New York; CU, Cornell University, Ithaca, New York; MRAC, Musée Royal de l'Afrique Centrale, Tervuren, Belgium; and USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Nannocharax reidi, new species

Fig. 1

Nannocharax sp. 1, Reid, 1989:24, 56 [Cameroon, upper Cross River system].

Nannocharax sp., Teugels et al., 1992:43 [upper Cross River system].

Holotype.—USNM 304046, 62.7 mm SL; Cameroon, Cross River system, collecting points on southern Munaya River draining northern Korup, on Basep River at junction with Munaya River (5°49'30"N, 9°03'30"E); collected by Gordon McG. Reid, 22 February 1988.

Paratypes.—20 specimens, 34.3–59.0 mm SL. USNM 375193, 16 specimens (2 cleared and counterstained for cartilage and bone), 34.3–59.0 mm SL; AMNH 233622, 2 specimens, 37.3–41.6 mm SL; MRAC A3-47-P-1-2, 2 specimens, 37.1–43.1 mm SL; collected with holotype.

Non-type specimens examined.—19 specimens, 33.3–44.7 mm SL. USNM 375195, 3 specimens, 34.5–38.8 mm SL; Cameroon, Many, Cross River system, collecting points on main Cross River, downstream of Mamfé, Mam River, junction with Cross (3°50'30"N, 9°14'50"E). USNM 375196, 1 specimen, 41.7 mm SL; Cameroon, Cross River system, collecting points on main Cross River below Mamfé

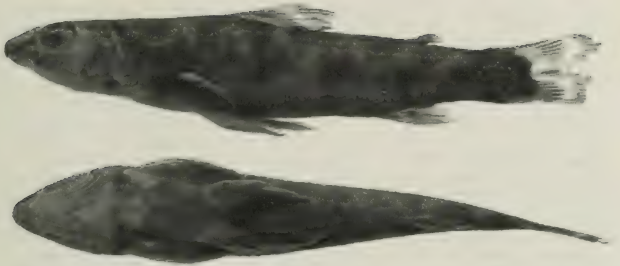


Fig. 1. *Nannocharax reidi*, holotype, USNM 304046, 62.7 mm SL; Cameroon, Cross River system, collecting points on southern Munaya River draining northern Korup, on Basep River at junction with Munaya River (05°49'30"N, 09°03'30"E); lateral and ventral views.

(5°51'25"N, 9°11'50"E). USNM 375197, 2 specimens, 36.4–44.5 mm SL; Cameroon, Cross River system, collecting points on southern Munaya River draining northern Korup, southern Munaya River, junction with Cross River (5°53'N, 9°00'E). USNM 375194, 6 specimens, 36.3–36.7 mm SL; Cameroon, Cross River system, collecting points on southern Munaya River draining northern Korup, on Basep River at junction with Munaya River (5°49'30"N, 9°03'30"E); collected with holotype. MRAC 88-053-P-0163-0168, 6 specimens, 33.3–44.7 mm SL; Cameroon, mainstream of Cross River, 5–15 km downstream of Mamfé (approximately 5°46'N, 9°17'E). MRAC 88-053-P-0170, 1 specimen, 42.4 mm SL; Cameroon, mainstream of Cross River, approximately 5 km downstream of Mamfé (approximately 5°46'N, 9°17'E).

Diagnosis.—*Nannocharax reidi* is distinguished from all congeners by the combination of: the lack of a large, dark, rounded spot extending from the posterior portion of the caudal peduncle to the basal portions of the middle caudal-fin rays; the lack of a distinct, dark, midlateral stripe extending from the snout at least to the rear of the caudal peduncle; the absence of a series of very narrow, vertical, dark bars positioned along

the lateral surface of the body; the location of the origin of the dorsal fin posterior to the vertical through the insertion of the pelvic fin; the possession of 47 to 49 scales along the lateral line, 5, rarely 6, scales dorsal of the lateral line to the origin of the dorsal fin, and 4 scales ventral of the lateral line to the origin of the anal fin; and the overall body form.

Descript on.—Morphometric values for holotype and paratypes are presented in Table 1. Body elongate, relatively wide transversely in region from rear of head to vertical through posterior terminus of base of dorsal fin and increasingly transversely-compressed posterior to latter region. Transverse widening of anterior portion of body proportionally more pronounced in larger examined individuals. Ventral region of head and body anterior to insertion of pelvic fin distinctly flattened; degree of flattening more pronounced in larger examined specimens. Dorsal profile of head gently convex from tip of snout to vertical through posterior margin of orbit, straight or very slightly convex from that point to posterior limit of supraoccipital spine. Predorsal profile of body slightly convex in all examined specimens. Dorsal profile of body slightly posteroventrally-inclined along base of dor-

Table 1.—Morphometrics and meristics of holotype and paratypes of *Nannocharax reidi*, new species, n = 21. Standard length is expressed in mm; measurements 1 to 14 are percentages of standard length; 15 to 18 are percentages of head length; mean includes holotype.

	Holotype	Paratypes	Mean
Morphometrics			
Standard Length	62.7	34.3–59.0	
1. Snout to anal-fin origin	75.6	72.1–76.3	74.3
2. Snout to pelvic-fin insertion	40.7	37.2–41.4	39.3
3. Snout to pectoral-fin insertion	23.4	23.2–26.3	24.8
4. Snout to dorsal-fin origin	43.7	42.1–45.9	44.3
5. Dorsal-fin origin to hypural joint	54.7	53.7–59.6	56.3
6. Dorsal-fin origin to anal-fin origin	35.4	32.3–36.7	34.3
7. Dorsal-fin origin to pelvic-fin insertion	20.2	17.9–20.0	18.8
8. Dorsal-fin origin to pectoral-fin insertion	26.2	23.9–27.1	25.7
9. Caudal-peduncle depth	10.2	9.8–10.4	10.1
10. Pectoral-fin length	25.2	23.9–27.2	25.6
11. Pelvic-fin length	25.4	22.4–25.6	23.8
12. Dorsal-fin length	21.9	21.5–25.4	23.7
13. Anal-fin length	17.1	15.9–17.8	16.8
14. Head length	25.8	24.5–27.5	25.8
15. Postorbital head length	37.8	37.8–44.7	42.1
16. Snout length	34.6	31.5–35.3	33.3
17. Bony orbital diameter	27.2	27.1–31.9	29.9
18. Interorbital width	21.0	16.3–20.9	19.2
Meristics			
Lateral-line scales	47	47–49	47.8
Scale rows between dorsal-fin origin and lateral line	5	5–6	5.1
Scale rows between anal-fin origin and lateral line	4	4	4.0
Predorsal median scales	10	10–12	11.2
Branched dorsal-fin rays	9	8–10	9.4
Branched anal-fin rays	6	6–8	7.0
Branched pelvic-fin rays	7	6–8	7.1
Pectoral-fin rays	14	13–15	14.1

sal fin and slightly convex from posterior terminus of base of fin to caudal peduncle. Ventral profile of head straight and slightly posteroventrally-inclined. Ventral profile of body nearly straight along prepelvic region and slightly convex from insertion of pelvic fin to caudal peduncle.

Mouth slightly subterminal. Lower jaw comparatively wide relative to condition in many congeneric species, with width of posterior portion of jaw equal to height of orbit in larger specimens. Jaw teeth elongate, bicuspid, and slightly expanded distally (see Daget 1961, fig. 4 for shape of teeth in genus), with single series of functional teeth in each jaw. Dentary with 5 or 6 teeth. Dentary teeth gradually decreasing

in size posteriorly with terminal tooth in series approximately one-half as long as tooth proximate to dentary symphysis. Replacement teeth on dentary arranged in single series within enlarged dentary replacement tooth trench. Dentary lacking segment of laterosensory canal system and movably attached to lateral surface of anterodorsal surface of angulo-articular. Contralateral dentaries immovably attached syndesmotically along medial surfaces. Premaxilla with 5 or 6 teeth of same morphology as dentary teeth. Premaxillary teeth gradually decreasing in size posteriorly with terminal tooth in series approximately one-half as long as tooth proximate to premaxillary symphysis. Premaxillary replacement teeth arranged in

single row embedded in fleshy covering of inner surface of premaxillae. Contralateral premaxillae immovably attached syndesmotically along medial surfaces; but with premaxillary complex vertically mobile on mesethmoid. Maxilla edentulous, with posterior portion of bone flat, plate-like, and extending nearly entirely under first infra-orbital bone when mouth closed. Pupil ovoid, with pronounced emargination of anterior portion of iris (see Vari & Géry 1981, fig. 2, for illustration of this condition in *Nannocharax maculicauda*). Snout and dorsal portions of upper lip and head covered with small papillae-like processes in holotype and to lesser extent in larger paratypes. Such papillae may represent intermediate developmental stages of well-developed breeding tubercles present in those regions and elsewhere on head, body, and fins in at least one congeneric species (see comments on breeding tubercles under "Contact organs and breeding tubercles in species of *Nannocharax*" below).

First gill arch with 13 or 14 gill rakers in 2 cleared and stained specimens. Branchiostegal rays 4.

Scales ctenoid (sensu Johnson 1984, Roberts 1993), with cteni formed by series of independent ossifications positioned along posterior margin of scale. Scales of lateral surface of body with 23 to 28 cteni along scale margin. Lateral-line scale series completely pored, with last scale in series horizontally elongate. Body scales extending onto base of middle rays of caudal fin in triangular pattern. Many smaller individuals with scaleless region on median portion of prepelvic region immediately posterior of ventral margin of pectoral girdle.

Largest examined specimens with lateral surface of scales in region posterior and posterodorsal to insertion of pectoral fin bearing some scattered, elongate, contact organs (sensu Collette 1977). Contact organs of scales most concentrated in region proximate to posterior margin of pectoral girdle and best developed in holotype, the largest examined specimen. Contact organs

elongate, laterally-directed, and with anteriorly-directed distal tips. Field of contact organs neither as dense as, nor as extensive as, pattern of hook-shaped processes present on that region of body in at least one congeneric species (see "Contact organs and breeding tubercles in *Nannocharax*" below).

Dorsal-rays ii,8 to 10. Distal margin of dorsal fin nearly straight. Anal-fin rays ii,6 to 8 or rarely iii,7. Distal margin of anal fin concave. Individual lepidotrichia of unbranched anal-fin rays anteroposteriorly expanded with overall form of distal portion of fin rays somewhat club-shaped; such rays proportionally more expanded in larger individuals. Anterior and lateral surfaces of first unbranched dorsal-fin ray and distal portions of second unbranched ray enveloped by overlying, thick, fleshy layer in many, but not all, specimens; fleshy covering more developed in holotype and larger paratypes. Caudal fin distinctly forked.

Pectoral and pelvic fins proportionally longer than in many congeneric species. Pectoral-fin rays ii,13 to 15. Dorsal surface of basal portions of second unbranched, and first through fifth branched rays of pectoral fin with basally-directed, hook-shaped, bony contact organs on basal one-half to two-thirds of rays in holotype, the largest examined specimen. Larger male paratypes with such contact organs developed to lesser degree, but still obvious. Hook-shaped processes on pectoral-fin rays apparently limited to mature males. Unbranched pectoral-fin rays and distal portions of first branched pectoral-fin ray with individual lepidotrichia widened, more so on distal portions of fin rays; expanded portion of fin rays consequently somewhat club-shaped. First unbranched pectoral-fin ray distinctly shorter than second ray, with second unbranched pectoral-fin ray somewhat shorter than first branched ray; latter ray longest of fin. Ventral and lateral surface of first unbranched pectoral-fin ray, and distal portions of second unbranched, and first branched, pectoral-fin rays with thick,

fleshy covering. Fleshy layer on fin rays thicker and extending farther basally along rays in larger individuals, and particularly well-developed in holotype. Tip of pectoral fin extending distinctly beyond vertical through insertion of pelvic fin in specimens of all sizes.

Pelvic-fin rays ii,6 to 8. Pelvic fin with unbranched rays and distal portion of first branched ray with individual lepidotrichia thickened, more so on distal portions of fin rays that consequently have a somewhat club-shaped form. Ventral and lateral surface of first unbranched, and distal portions of second unbranched and first branched pelvic-fin rays with thick, fleshy covering; fleshy layer also extending over dorsal surface of distal portions of ray. Fleshy layer on pelvic-fin rays thicker and extending further basally along rays in larger examined individuals. First unbranched pelvic-fin ray distinctly shorter than second unbranched ray; second unbranched ray somewhat shorter than first branched ray with medial branch of latter ray longest in fin. Tip of longest pelvic-fin ray reaching vent in smaller individuals, but falling slightly short of opening in larger specimens.

Vertebrae 36 to 38 [37 in holotype].

Coloration in alcohol.—Ground coloration light dusky-brown, with scattered dark chromatophores in holotype and paratypes; tan with fewer dark chromatophores in some more lightly-pigmented, non-type specimens. Lateral and dorsal surfaces of head with irregular field of small, dark chromatophores; chromatophore field more concentrated on upper lip, snout, and dorsal surface of head. Some larger individuals with concentration of dark chromatophores located posterior to orbit and on dorsal two-thirds of operculum. Ventral surface of head ranging from unpigmented to having scattered, small, dark chromatophores.

Body with pattern of relatively wide, irregular bars on dorsal and sometimes ventral surfaces; bars often narrowing towards midlateral region with dorsal and ventral bars variably in contact in that region. Re-

gions of contact between bars sometimes appearing as irregular, darker, midlateral patches of dark pigmentation. Smaller, more lightly-pigmented, non-type specimens with deep-lying, diffuse region of dusky pigmentation positioned along midlateral region, particularly on posterior two-thirds of body. Ventral surface of body ranging from pale with few, scattered, small, dark chromatophores in some smaller non-type specimens to dusky in holotype and paratypes. Some darker specimens with variably-shaped, unpigmented, typically scaleless area on anteroventral portion of body immediately posterior of margin of pectoral girdle.

Dorsal fin with transverse band of dark pigmentation located slightly dorsal of bases of fin rays and second, more distally-positioned, wider band of dark pigmentation extending across entire fin. Wider band of pigmentation distinctly separated from distal margin of fin anteriorly, but angling toward and reaching margin of fin along distal portions of first or second branched dorsal-fin rays. Anal fin with variably-developed patch of dark pigmentation on basal portions of anterior rays and with dark band extending from more distal portions of anterior rays across fin to its posterior margin. Caudal fin with patch of dark pigmentation situated basally and with variably-shaped and -positioned patches of dark pigmentation located on both lobes of fin. Pectoral-fin rays overlain dorsally by small, dark chromatophores; dark pigmentation most intense on lateral most fin rays, more so distally. Pelvic fin with pattern of dark chromatophores on distal portion of unbranched rays and more central sections of branched rays. Individual patches of dark pigmentation forming broad, interrupted, dark band across pelvic fin. Adipose fin dark distally in smaller, more lightly-pigmented individuals, dark throughout in larger specimens.

Coloration in life.—Photos of specimens taken soon after capture show that the species has the same pattern of dark pigmen-

tation as described above, but with the hyaline regions of head, body, and fins of preserved specimens having a rosy tint in life.

Remarks.—Vari (1979:332) noted that the monophyly of *Nannocharax* had yet to be demonstrated. That author further commented that although *Nannocharax* and *Hemigrammocharax* share a series of hypothesized synapomorphies (Vari 1979:331), the single feature that has been utilized to distinguish *Nannocharax* from *Hemigrammocharax* (the possession of a completely- versus incompletely-pored lateral line, respectively) may not serve to delimit monophyletic assemblages in light of the independent reduction in the degree of development of the lateral line in various groups of characiforms. The possession of various derived characters in a subset of the species of *Nannocharax* and *Hemigrammocharax* to the exclusion of other members of each genus (Vari & Géry 1981:1082), furthermore, apparently delimits a monophyletic lineage. That hypothesis suggests that both *Nannocharax* and *Hemigrammocharax* as now defined are non-monophyletic.

More recently, Coenen & Teugels (1989:317) documented that population samples of some nominal species within the *Nannocharax*-*Hemigrammocharax* clade demonstrated a continuum between distinctly-shortened and fully-developed lateral lines. Such continuity in the degree of development of the poring of the lateral-line scale series bridges the gap that purportedly distinguished *Nannocharax* from *Hemigrammocharax*, thereby casting further doubt on the utility of a complete versus incomplete lateral line as a generic delimiter for these taxa. Above and beyond the uncertainty about the naturalness of *Nannocharax* and *Hemigrammocharax*, we are also encumbered by the limitation that the phylogenetic relationships within the clade formed by these two genera are yet to be critically examined within the context of a comprehensive analysis. In the absence of such a phylogenetic study, we follow current taxo-

nomic practice and assign the new species to *Nannocharax* on the basis of its completely-pored lateral line, in conjunction with the possession of the synapomorphies for the clade formed by *Nannocharax* and *Hemigrammocharax* (see Vari 1979:331, synapomorphies 96 to 107).

Distribution.—All examined population samples of *Nannocharax reidi* were collected in the upper portions of the Cross River basin in Cameroon.

Etymology.—The specific name, *reidi*, is in honor of the collector of the specimens that served as the basis of the description of the species, Dr. Gordon McGregor Reid, of the North of England Zoological Society, who first reported that these samples might represent an undescribed form and who has contributed broadly to our knowledge and conservation of African freshwater fishes.

Ecology.—*Nannocharax reidi* was typically captured in the swiftly-flowing main-stream portions of rivers, usually in association with submerged logs and branches. In all such localities the water is clear and brown-tinged. The new species was collected together with *N. fasciatus* at the type locality and at three other localities in the upper Cross River. Those two species of *Nannocharax* were sympatric with *N. latifasciatus* at two of those sites.

Contact Organs and Breeding Tubercles in Species of *Nannocharax*

Examination of other species of *Nannocharax* revealed the presence of hook-shaped contact organs on the pectoral-fin rays and on the scales in the region of the body proximate to the insertion of the pectoral fin, along with the occurrence of breeding tubercles on the head, body, and fins of at least some species. The hook-shaped contact organs on the fin rays and breeding tubercles of these species of *Nannocharax* had been previously reported within the Characiformes only in some Neotropical members of the order. The hook-shaped contact organs on some scales

of the body in the genus are unknown in any other member of the Characiformes.

Presence of hooks on pectoral-fin rays.—In their recent analysis of the phylogenetic relationships of various groups of Neotropical characids, Malabarba & Weitzman (2003:73) enumerated a series of generic and suprageneric taxa within the Characiformes that bear hook-shaped processes on various combinations of the paired and unpaired fins, including the pectoral fin. These hook-shaped processes were termed contact organs by some authors (e.g., Wiley & Collette 1970, Collette 1977), who discussed the distribution and possible functions of these structures. In their commentary on contact organs on the fins of characiforms, Malabarba & Weitzman (2003) noted that such bony processes on individual segments of lepidotrichia were known to be present in diverse Neotropical components of the order, but were unknown in Old World characiforms, including the family Distichodontidae. Although Malabarba & Weitzman (2003) were correct that contact organs on the fins had not been previously reported for Old World characiforms, we found that larger, apparently male, individuals of *Nannocharax reidi* have a series of hook-shaped, distally slightly anteriorly-bent bony processes arranged in a single series along the dorsal surface of the basal one-half to two-thirds of the medial rays of the pectoral fin. As is the case with many Neotropical characids, each lepidotrichium of the pectoral-fin rays with a hook-shaped contact organ bears a single such process.

The extent of the field of hook-shaped contact organs on the pectoral-fin rays differs both among specimens of *N. reidi* and between species of *Nannocharax*. In *N. reidi*, the hook-shaped processes on the dorsal surface of the pectoral-fin rays are more highly-developed in larger individuals, but even at their maximum observed degree of development these structures are limited to the basal one-half to two-thirds of the second unbranched and first through fifth branched pectoral-fin rays. Mature males of

N. rubrolabiatus (MRAC 95-022-P-001-007), in contrast, have hook-shaped contact organs on a greater number of fin rays (second unbranched through eighth branched) and have these processes nearly to the distal tips of the fin rays. The presence of these hook-shaped contact organs on the pectoral fin in specimens of *N. rubrolabiatus* is correlated with other apparently breeding-associated modifications of the scales and fins (the presence of hook-shaped contact organs on the lateral surface of the scales in the region medial to the pectoral fin and the possession of epidermal breeding tubercles distributed over the head, body, and fins; see discussion of next two characters). This correlation of apparently sexually-dimorphic features in conjunction with the relatively few examined specimens of the species of *Nannocharax* that demonstrate these modifications indicate that the hook-shaped contact organs on the pectoral-fin rays of *N. reidi* and *N. rubrolabiatus* may be restricted to mature males only during the height of the breeding season.

Hook-shaped processes on scales.—The holotype and larger male paratypes of *Nannocharax reidi* possess a form of contact organ (sensu Wiley & Collette 1970, Collette 1977) involving an elaboration of the scales in the region of the body medial to the adpressed pectoral fin that is apparently unique not only within the Characiformes, but perhaps throughout bony fishes. The typical form of the scales among members of the Distichodontidae (sensu Vari 1979) is a laterally-unelaborated, relatively flat ossification with the posterior margin of the main body of each scale bearing a series of smaller, independent ossifications (see Vari 1979, figs. 38b and c), that form a distinctly-serrate posterior margin to the scale. These independent ossifications, which constitute true cteni (sensu Johnson 1984, Roberts 1993:70), vary both in number and form across the members of the Distichodontidae, but such elaborations, nonetheless, are nearly invariably limited to the posterior margin of the scale. The single ex-



Fig. 2. *Nannocharax rubrolabiatus*, MRAC 95-022-P-001-007, 56.1 mm SL; showing breeding tubercles on the head, anterior two-thirds of the body, and dorsal, pectoral, and pelvic fins. Arrow indicates the midlateral region of the body lacking breeding tubercles, but with hook-shaped contact organs on the lateral surface of the scales.

ception to that generality that we have discovered, involves the form of the scales on the portion of the body medial to the pectoral fin in some species of *Nannocharax*. In larger specimens of *N. reidi* the scales of the portion of the body medial to the basal portion of the pectoral fin (see description above), particularly those scales in the region of the body immediately dorsal to the posteriorly-directed process of the cleithrum, have the cteni along their posterior margins complemented by hook-shaped processes arising from the lateral surface of the scales. These scale processes have the form of moderately elongate spines with slightly anteriorly-directed distal hooks. Although such processes are obvious in the larger examined specimens of *N. reidi*, they nonetheless are somewhat scattered across, and fail to completely cover, the lateral surface of the involved scales.

A dramatically greater degree of development of such contact organs in the region

of the body posterior to the insertion of the pectoral fin characterizes mature males of *Nannocharax rubrolabiatus* (Fig. 2). Contrary to the situation in all other examined distichodontids, males of *N. rubrolabiatus* lack distinct cteni along the posterior margins of the scales on the anterior portion of the midlateral surface of the body. More strikingly, the specimens in this population sample have the lateral surface of the scale variously covered by fields of laterally-directed, elongate, hook-shaped contact organs with anteriorly-curved distal tips. Continuity between the fields of hook-shaped processes of adjoining scales varies across the portion of the body with such lateral elaborations of the scales. Those scales positioned closer to the posterior margin of the pectoral girdle have patches of contact organs that together with those of adjoining scales form a nearly uninterrupted, brush-like expanse continuing approximately five scales posteriorly from the

posterior margin of the pectoral girdle and extending dorsally to the horizontal running through the dorsal margin of the opercular opening. Farther posteriorly, the hook-shaped processes on the lateral surface of the scales are restricted to the posterior one-half of the exposed portion of the scale and, thus, form discrete patches of such contact organs, with these patches distinctly separated from each other. These posteriorly-positioned scales with separate patches of contact organs on their lateral surfaces also differ from the more anterior scales characterized by the possession of such processes in retaining independent, variably posteriorly-directed cteni along at least a portion of the posterior margin of the scale. Such cteni are, however, often somewhat more laterally-directed than are the homologous ossifications in other members of the Distichodontidae.

We are unaware of any laterally-positioned, hook-shaped contact organs of a comparable morphology on the body scales, elsewhere either within the order Characiformes or among other groups of fishes. The only other report of an African freshwater fish with laterally-directed hook-shaped processes on the scales involves the gonorhynchiform *Phractolaemus ansorgei*, an ostariophysan that is phylogenetically distant from the Characiformes. *Phractolaemus* differs significantly from *Nannocharax* in the distribution, morphology, and number of such hook-shaped processes per scale (see Thys van den Audenaerde 1961a, fig. 2; 1961b, fig. 2) and the elaborations of the scales in the two genera, thus, are appropriately considered to be non-homologous. As a consequence of their apparent unique morphology, the presence of the dense patches of hook-shaped processes on the anterior portion of the midlateral scales of *Nannocharax* is a likely synapomorphy for at least a subunit of that genus, albeit one perhaps restricted to fully mature, sexually-active males during the height of the breeding season.

Breeding tubercles.—The presence of

epidermal breeding tubercles has been reported in a number of New World members of the Characiformes including the families Characidae, Parodontidae, and Lebiasinidae (Wiley & Collette 1970:164–167, Collette 1977:236–241), but not within any of the African families within that order, an apparent absence that included the Distichodontidae. One series of *Nannocharax rubrolabiatus* (MRAC 95-022-P-001-007) examined during this study has, however, very well-developed epidermal breeding tubercles distributed over the head, body and fins (Fig. 2). The degree of development of the tubercles correlates somewhat, albeit not absolutely, with the size of the specimens. The smallest specimen in the lot (45.5 mm SL) has both fewer tubercles than most of the larger conspecific individuals captured with it and, furthermore, those tubercles are proportionally less-developed than those in larger specimens. In larger, apparently male, individuals of *N. rubrolabiatus*, the breeding tubercles are broadly distributed in large numbers across the snout and the dorsal and lateral surfaces of the head (Fig. 2). On the ventral surface of the head, the tubercles are arranged in discrete rows along the ventral surfaces of the branchiostegal rays. Scales on the surface of the body have one to four tubercles, other than those scales medial to the pectoral fin whose surfaces are covered with the hook-shaped contact organs (described in the previous section and indicated by white arrow of Fig. 2). When present, the tubercles on the scales are positioned toward the posterior margin of the scale, and when three or four tubercles occur on an individual scale, these structures are arranged in an arch paralleling the posterior margin of the scale. The size and number of tubercles tend to be reduced on the scales of the ventrolateral portion of the body. An extensive series of tubercles occurs, however, on scales of the prepelvic region of the body, with a less concentrated field of tubercles present in the region from the insertion of the pelvic fin to the origin of the anal fin.

Breeding tubercles are present on all fins of *Nannocharax rubrolabiatus* with the exception of the adipose fin. The tubercles on the caudal fin are less developed than those on the remaining fins, being apparent solely as small, raised areas along the basal and middle portions of the caudal-fin rays. Tubercles are present on all of the dorsal-fin rays with the exception of the first unbranched and last branched rays. At their maximum degree of development, such breeding tubercles extend along nearly the entire length of each dorsal-fin ray. Some larger examined specimens of *N. rubrolabiatus* have indications of poorly-developed breeding tubercles on the basal portions of the second unbranched anal-fin rays, with better-developed tubercles present on all but the terminal branched anal-fin ray. The pectoral fin has tubercles on the dorsal surface of the unbranched rays, but tubercles are absent on the portions of the second unbranched through eighth branched rays with anteriorly-directed, hook-shaped contact organs. The ventral surface of the pectoral fin has at most a few tubercles distributed along the unbranched rays, but such structures are completely absent in some individuals. Variably-developed series of tubercles extend along the length of the ventral surfaces of each of the branched pectoral-fin rays. The pelvic fin has a series of tubercles arranged along the dorsal surface of the branched rays, and along the ventral surfaces of the last unbranched fin ray and all of the branched fin rays with the exception of the medialmost branched ray.

Our comparative studies failed to reveal any comparably well-developed breeding tubercles in the other examined species of *Nannocharax*. Larger examined specimens of *N. reidi* do, however, have a pattern of small, papillae-like processes on the upper lip, snout, and dorsal surfaces of the head that have an arrangement comparable to the pattern of the breeding tubercles that occur in those regions in most examined specimens of *N. rubrolabiatus*. It will be necessary to examine additional population

samples of *N. reidi* captured during the height of the breeding season in order to determine whether the papillae-like processes present in that species would develop into the distinctly larger breeding tubercles that typify the examined sample of *N. rubrolabiatus*. Broader comparative studies would possibly also yield insight in the range of the distribution of breeding tubercles across the species of *Nannocharax*.

Comparative material examined.—*Nannocharax altus*: MRAC 78-22-P-801-804, 4 specimens, Republic of the Congo, Mayala, Niola Creek.

Nannocharax fasciatus: USNM 303754, 5 specimens; USNM 303756, 2 specimens; USNM 303811, 1 specimen; USNM 303847, 3 specimens; USNM 303867, 2 specimens; USNM 303908, 4 specimens; USNM 303995, 2 specimens; USNM 304081, 3 specimens; USNM 375192, 5 specimens; Cameroon, upper Cross River system.

Nannocharax intermedius: CU 80570, 2 specimens, Gabon, Motoboi Village, Kine-né Creek; CU 90276, 3 specimens, Gabon, Okolville; MRAC 91-79-P-202-206, 4 specimens, Gabon, Riviere Loukénini; MRAC A2-006-P-0826-0828, 3 specimens, Gabon, Ivindo basin, Balé Creek.

Nannocharax maculicauda: USNM 224524, 3 paratypes; Gabon, upper Ivindo River (1°20'N, 13°12'E); CU 80621, 1 specimen, Gabon, Woleu-Ntem, Ngomo River (1°42'N, 11°38'E).

Nannocharax parvus: CU 80148, 19 specimens, Gabon (0°34'S, 10°12'E). CU 80163, 1 specimen; CU 80185, 2 specimens; CU 80184, 3 specimens; Gabon, Bi-roundou Creek (2°13'S, 11°28'E). CU 80191, 1 specimen, Gabon, Mimboumbou Creek, near Franceville (1°38'S, 13°31'E). CU 80279, 5 specimens, Gabon, Okolville. CU 80607, 6 specimens, Gabon, stream at Okolville (1°29'S, 13°31'E).

Nannocharax rubrolabiatus: MRAC 95-22-P-001-007, 7 specimens, Cameroon, Sanaga River basin, Mi River (6°12'N, 14°23'E).

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***Rhamdia guasarensis* (Siluriformes: Heptapteridae), a new species of cave catfish from the Sierra de Perijá, northwestern Venezuela**

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Abstract.—*Rhamdia guasarensis* n. sp. is described from subterranean waters in the Río Guasare drainage of northwestern Venezuela. The new species is distinguished from congeners by its concave head profile; medially sutured frontal bones; small, circular vestige of the anterior cranial fontanelle; and troglomorphic characters such as absence of eyes and pigmentation, wide cephalic laterosensory pores, and wide fossae of preoperculo-mandibular sensory canal in preopercle and dentary. Cave catfish diversity in the Sierra de Perijá region of Venezuela is reviewed and compared to cave catfish diversity elsewhere in South America.

Resumen.—Se describe *Rhamdia guasarensis* sp. n. proveniente de aguas subterráneas de la cuenca del Río Guasare en el noroccidente de Venezuela. La nueva especie se diferencia de las restantes especies que conforman el género por su perfil dorsal de la cabeza cóncavo; huesos frontales suturados medialmente; fontanela craneal anterior reducida a un pequeño foramen circular; y caracteres troglomórficos tales como ausencia de ojos y pigmentación, poros cefálicos latero sensoriales anchos, fosas ensanchadas del canal sensorial preoperculo-mandibular en el preopérculo y dentario. La diversidad de bagres cavernícolas de la Sierra de Perijá es revisada y comparada con la diversidad de bagres cavernícolas de otras regiones de Suramérica.

The family Heptapteridae has invaded and adapted to hypogean waters multiple times. Among Neotropical catfish families, heptapterids have the greatest diversity of truly troglobitic taxa: *Phreatobius cisternarum*, *Pimelodella kronei*, *Rhamdia laluchensis*, *Rhamdia laticauda typhla*, *Rhamdia macuspanensis*, *Rhamdia quelen urichi*, *Rhamdia redelli*, and *Rhamdia zongolicensis*. Trajano & Bockmann (2000) described the ecology and behavior of *Taunayia* sp., a troglobitic catfish, inhabiting caves of northeastern Brazil, but the species has not been formally named. *Pimelodella spelea*

Trajano, Reis & Bichuette, 2004 is a recently described troglophile without marked specializations for hypogean life. Taxonomic practice has shifted away from assigning supra-specific rank to cave-dwelling fishes solely on account of their troglobitic adaptations. Among Heptapteridae, the nominal monotypic genera *Caecorhamdia*, *Caecorhamdella*, and *Typhlobagrus* have long been treated as synonyms of *Rhamdia* and *Pimelodella* respectively. Furthermore, Silfvergrip (1996) synonymized all cave populations of *Rhamdia* described as separate species with *R. quelen* or *R.*

laticauda, both wide-ranging epigean species.

In this paper we describe a new troglobitic heptapterid species in the genus *Rhamdia*. Our placement of the new species is more a matter of convenience than firm phylogenetic resolution. *Rhamdia* is taxonomically complex. In the latest revision of the genus, Silfvergrip (1996) consolidated its approximately 100 nominal species into eight and he described three new species. In 1998, Weber & Wilkens described the blind species *R. macuspanensis*, and in 2003, Weber et al. described *Rhamdia laluchensis*, another troglobitic species from Mexico. In the most thorough phylogenetic study of Heptapteridae to date, Bockmann (1998) concluded that *Rhamdia* is non-monophyletic but he did not attempt to resolve the genus into phylogenetically diagnosable units. As it stands, *Rhamdia* is a non-monophyletic assemblage of common fishes with an immense geographic distribution in South and Middle America from the lower Paraná Basin in Argentina to central México.

The new species, from a cave in the Sierra de Perijá region of northwestern Venezuela, is distinct both in its typical troglobitic specializations and other apomorphic features, but overall it is most similar to other *Rhamdia*. Discovering the relationships of the new species and, more generally, resolving the relationships of *Rhamdia* species are major problems quite beyond our present scope. Our immediate concern is to name and describe this previously unseen species that has a highly restricted distribution in a marginal and potentially fragile habitat. We comment also on the subterranean catfish fauna of the Perijá region.

Material and Methods

Morphometric measurements follow the criteria set out by Lundberg & McDade (1986) and Bockmann (1994). Terminology of cephalic laterosensory canals and branches follows Arratia & Huaquin's de-

scription of *Diplomystes* and *Nematogenys* (1995). However, our numbering of sensory pores in *Rhamdia* reflects anteroposterior or mesiolateral pore order, and does not imply individual homologies of pores among catfishes. All measurements were made on the left side of the specimens using a Mitutoyo digital, needlepoint caliper at a precision of 0.1 mm. For osteological observation one paratype (101.1 mm SL) was cleared and stained using the method of Taylor & Van Dyke (1985). A second paratype (93.4 mm SL) was radiographed. Only these two specimens were used for counts of vertebrae, branchiostegal rays, ribs, and pterygiophores. The vertebral count includes the first five vertebrae incorporated into the Weberian apparatus whereas the compound caudal centrum is counted as one. Institutional abbreviations follow Leviton et al. (1985). Other abbreviations are: SL—standard length, HL—head length, CS—cleared and stained skeletal preparation, alc—whole specimen preserved in alcohol.

Rhamdia guasarensis, new species

Figs. 1–4

Holotype.—MBUCV-V-29604: 106.8 mm SL; Surgencia del Tigre at 2.5 km W of Cerro Yolanda, Río Guasare basin, Sierra de Perijá, Estado Zulia, Venezuela (10°52'53"N, 72°30'03"W). Elevation 200 m asl; collected by J. Lagarde, 3 April 1999.

Paratypes.—All collected with the holotype: MBUCV-V-29622, two specimens, 87.2–101.1 mm SL, the second cleared and stained; ANSP 179878, one specimen, 93.4 mm SL.

Diagnosis.—*Rhamdia guasarensis* is distinguished from congeneric species by two characters: dorsal profile of head concave (Fig. 1, vs. convex or straight); and frontal bones broadly sutured to each other anterior to small, circular remnant foramen of anterior cranial fontanelle that is anteriorly adjacent to epiphyseal bar (Fig. 2, vs. frontals separated by anterior fontanelle widely

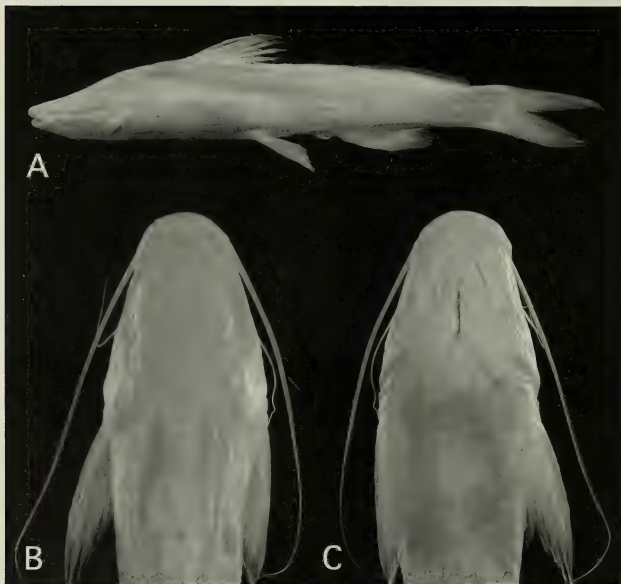


Fig. 1. *Rhamdia guasarensis*. Holotype MBUCV-V-29604, 106.8 mm SL. A, lateral view; B, dorsal view of head; C, ventral view of head.

open from mesethmoid to epiphyseal bar). *Rhamdia guasarensis* differs from all epigean *Rhamdia* by the following troglomorphic characters: absence of eyes, complete depigmentation, widened cutaneous pores of the cephalic laterosensory system, preoperculomandibular sensory canal forming wide fossae in the dentary and preopercle (Fig. 3, vs. narrow pores and canals).

In addition to these characteristics, *R. guasarensis* can be distinguished from other species of the genus by the following combination of characters: pectoral fins with a spine and ten branched rays (vs. modally

eight or nine soft rays in other species, data from Silfvergrip 1996); both lobes of the caudal fin pointed (vs. at least one lobe rounded); caudal skeleton with three hypural plates, PH; 1 + 2; 3 + 4 + 5 (vs. modally four PH; 1 + 2; 3 + 4; 5 in the other species with the exception of *R. laukidi* and *R. jequitinhonha*, see Silfvergrip 1996).

Description.—Morphometric data are presented in Table 1. Body elongate, strongly depressed anteriorly and gradually more compressed from origin of pectoral fins to caudal peduncle. Shape approximately tri-

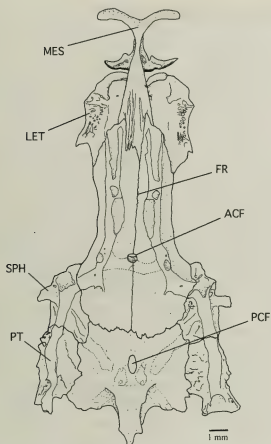


Fig. 2. *Rhamdia guasarensis*. Skull roof illustrating reduction of the anterior cranial fontanelle and midline contact of frontal bones. MBUCV-V-29622, 101.1 mm SL. Abbreviations: ACF, anterior cranial fontanelle; FR, frontal bone contact on midline; LET, lateral ethmoid; MES, mesethmoid; PCF, posterior cranial fontanelle; PT, pterotic; SPH, sphenotic.

angular in transverse section at dorsal-fin origin. Dorsal profile sinusoidal anterior to dorsal fin, then approximately straight to middle of adipose fin, then slightly concave along caudal peduncle. Ventral profile nearly straight to anal-fin origin, then slightly concave posteriorly.

Head depressed, its dorsal profile concave, its lateral and ventral profiles nearly straight. Mouth terminal, upper jaw slightly in advance of lower jaw. Rictal folds little developed. Upper and lower lips with weak sulci, slightly evident in holotype, forming single labial fold. Premaxillaries with single band of diminutive teeth, arranged in ten irregular tooth rows, the posterolateral corners rounded, not produced. Dentition of

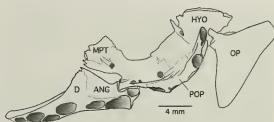


Fig. 3. *Rhamdia guasarensis*. Enlarged preoperculo-mandibular laterosensory canal and associated foramina. MBUCV-V-29622, 101.1 mm SL. Abbreviations: ANG, anguloarticular; D, dentary; HYO, hyomandibula; MPT, metapterygoid; OP, opercle; POP, preopercle; Q, quadrate.

lower jaw similar to premaxillary teeth, in six irregular tooth rows. Palatine and vomer edentulous. Maxillary barbels long, extending beyond base of pelvic fins. Mental barbels relatively short, inner mentals scarcely reaching posterior border of branchial membrane; outer mentals surpass pectoral fin bases. Inner mental barbel bases inserted slightly in advance of outer mental barbel bases. Anterior nares tubular, near border of snout. Posterior nares with elongated orifices, bounded anterolaterally by membrane of fine skin. Internarial length less than width between posterior nares. Eyes completely absent. Branchial membranes overlapping medially; united to isthmus only anteriorly.

Cephalic lateralis sensory system with paired supraorbital (SO), infraorbital (IO), preopercular (POP), mandibular (MA), otic (OT), and post-otic (POT) canals, without tubular commissure connecting supraorbital canals. Sensory pores simple, not branched and multiple. SO canal with six pores: SO1–SO3 associated with nasal bone, SO1 medially adjacent to anterior naris, wide and delimited by membrane of fine skin, SO2 between anterior and posterior nares, slightly closer to first, SO3 posteromedially near posterior naris. SO4 near dorsal midline at end of short medial tube and separate from its counterpart of opposite side. SO5 lateral to its canal midway between SO4 and union of SO and IO canals. SO6 medial to its canal a little posterior to union of SO and IO canals.

Table 1.—Measurement data for the type series of *Rhamdia guasarensis*. Measurement 1 expressed in mm. Proportional measurements expressed as thousandths of standard length (2–19; 26–28) or head length (20–25).

	Holotype MBUCV-V-29604	Paratype MBUCV-V-29622	Paratype MBUCV-V-29622 (CS)	Paratype ANSP 179878
1. Standard length	106.8	87.2	101.1	93.4
2. Total length	1057	1093		1083
3. Body depth	162	178		167
4. Body width	171	180	168	173
5. Predorsal length	351	367	352	359
6. Preanal length	645	653	659	656
7. Prepelvic length	462	458		490
8. Preadipose length	555	545		530
9. Caudal peduncle length	211	210	214	224
10. Caudal peduncle depth	97	104		105
11. Dorsal fin spine length	85	86		108
12. Length of first branched dorsal fin ray	172	176	183	187
13. Dorsal fin base	115	121	104	113
14. Adipose fin length	387	411	432	394
15. Dorsal fin to adipose fin	99	72		68
16. Anal fin base	141	127	127	143
17. Pectoral fin spine length	121	111		123
18. Length of first branched pectoral fin ray	204	197	195	216
19. Pelvic fin length	169	153	159	169
20. Head length	259	262	256	276
21. Head width	661	645	631	633
22. Head depth	550	522	538	528
23. Internarial length	137	144		147
24. Anterior internarial width	173	169		187
25. Posterior internarial width	156	152		165
26. Maxillary barbel length	541	610	557	578
27. Outer mental barbel length	205	262	258	262
28. Inner mental barbel length	98	121	108	121

IO canal with four pores; IO1–3 wide like SO1. IO1 posterior to anterior nostril; IO2 emerges dorsal to groove for maxillary barbel, posterior to base of barbel; IO3 near point where IO canal curves dorsally; IO4 at tip of short posterior tube near union with SO canal. Holotype and one paratype (87.2 mm SL) have different single supernumerary IO pores; extra pore of holotype from left canal between the IO2 and IO3; extra pore of paratype from right IO canal between IO3 and IO4.

POP canal with four pores; MA canal with seven pores; all except MA1 and POP4 originate from much enlarged cavities in dentary and preopercular bones. MA1 in mental position near to midventral line at tip of its branch from lower jaw symphysis.

POT canal with two pores, POT1 over pterotic dorsal to gill opening; POT2 dorsal to supracleithrum and above main lateralis canal at level of first pore. First pore of lateralis canal at end of ventral branch dorsal to postcleithral process. Several following pores also at tips of short postero-ventral branches. Lateral line canal complete to base of middle upper-lobe caudal rays.

Dorsal fin with a spinelet, spine and six branched rays; its margin rounded. Dorsal spine weakly developed, only its basal part rigid and unsegmented; dentations diminutive and scarcely visible, limited to basal part of anterior margin. The distal two-thirds of dorsal spine flexible and obliquely segmented. Adipose fin long and low, its origin near tip of depressed dorsal fin, and extending posteriorly to approximately 80%

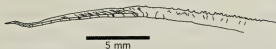


Fig. 4. *Rhamdia guasarensis*. Pectoral spine in dorsal view. Holotype MBUCV-V-29604, 106.8 mm SL.

of caudal peduncle length; posterior end of adipose fin adnate to caudal peduncle without a free fleshy tab. Caudal fin deeply forked; both caudal lobes pointed; upper lobe slightly longer than lower; membrane uniting innermost caudal rays complete. Principal caudal rays i,7-8,i, except i,7-7,i in one paratype. Anal fin with 12 rays, anteriormost two or three rays simple, others branched; its margin rounded.

Pectoral fins with a spine and ten branched rays. Pectoral spine (Fig. 4) with weak dentations proximally on anterior margin; distal half of spine flexible and obliquely segmented. First branched pectoral-fin ray longest, posterior branched rays diminishing in length. Postcleithral process short, sharp. Pelvic fins with one simple ray and five branched rays, its origin posterior to end of dorsal fin.

Skull roof (Fig. 2) with anterior cranial fontanelle extremely reduced to a small circular foramen located in front of epiphyseal bar; mesethmoid posteriorly lacking concave notch of fontanelle, and frontals meeting medially along most of their length. Posterior cranial fontanelle reduced to oval foramen near center of supraoccipital. Supraoccipital process short, its length about equal to length of supraoccipital body.

Anus and urogenital papillae separated, anus located equidistant between medial edge of pelvic-fin base and urogenital papilla, approximately at midlength along pelvic fins; urogenital papilla conspicuous and elongated, located closer to base of anal fin than to base of pelvic fin.

Total vertebrae 40-42; neural spines of vertebrae 6-10 bifid; hemal arch closed in vertebra 12 or 13, first hemal spine on vertebra 14, 15 or 16; eight pairs of ribs borne on vertebrae 6-13. Seven dorsal-fin ptery-



Fig. 5. The Lago de Maracaibo—Sierra de Perijá region, Venezuela, showing type locality (star) of *Rhamdia guasarensis*. Map based on shaded relief image PIA03388, Shuttle Radar Topography Mission, National Aeronautics and Space Administration (NASA).

giophores preceded by small supraneural; first dorsal-fin pterygiophore inserted between rami of neural spine of fourth vertebra. Eleven anal-fin pterygiophores, first inserting posterior to hemal spine of vertebra 21. Caudal skeleton with three hypural plates: rectangular parhypural; triangular hypurals 1 + 2; triangular hypurals 3 + 4 + 5.

Color in alcohol.—Body and fins completely depigmented; most of skin, rayed- and adipose-fin membranes hyaline and translucent; musculature appearing yellowish, particularly jaw adductors and dorsal trunk myomeres; parts of head and fin bases whitish.

Distribution and habitat.—*R. guasarensis* is known only from the Surgencia del Tigre (Zu. 23), in the middle basin of the Río Guasare, north of the Sierra de Perijá in northwestern Venezuela (Fig. 5). The cave is near the margin of Río Guasare and is the source of a spring during seasonal rains (Sociedad Venezolana de Espeleología

1991). The cave's lower conduit has a 280 m course, 2–3 m wide and 1–2 m high, narrowly communicating with the access gallery. The underground river is permanently fed by a spring about 60 m into the lower gallery. At the time the cave was surveyed, the average depth of this water course was 1.5 m with deeper pools along its course where the catfishes were observed (Sociedad Venezolana de Espeleología 1991).

Etymology.—The name is based on Río Guasare, parent stream of the subterranean waters in which this endemic catfish species lives.

Discussion

Rhamdia guasarensis is placed in Heptapteridae by its possession of four synapomorphies identified for the family (Lundberg & McDade 1986, Ferraris 1988, Bockmann & Guazelli 2003): posterior limb of fourth transverse process expanded and notched; posterodorsal corner of hyomandibula greatly expanded for attachment of levator operculi muscle; dorsal margin of quadrate free, not sutured to hyomandibula and metapterygoid; ventrolateral corner of mesethmoid anteriorly recurved. However, the new species lacks a fifth synapomorphy of heptapterids: a straight-edged vertical bony lamina on the Weberian complex centrum. Instead, the vertical lamina has a concave margin in *R. guasarensis*.

Except for the obvious lack of a free orbital rim, *R. guasarensis* possesses the character combination presented as diagnostic of *Rhamdia* by Silfvergrip (1996:74). This includes: three pairs of barbels, double lip fold, vomer without teeth, transverse processes of fourth vertebra expanded branched distally, supraoccipital process not contacting anterior nuchal plate, adipose fin with free posterior margin, posterior fontanelle closed and postcleithral process well developed. However, none of these are unambiguous synapomorphies of the group of species comprising *Rhamdia*. Instead, some characters are heptapterid or

higher level synapomorphies, and others, some of uncertain polarity, have wider and variable distributions among heptapterids. Thus, placement of this new species in *Rhamdia* must be considered provisional because the genus has not been supported as monophyletic. Bockmann's (1998) phylogenetic analysis of Heptapteridae placed one representative species, *R. laticauda*, sister to *Pimelodella* but a second species, *R. quelen*, is deeper in his cladograms. In this context *R. guasarensis* has one derived, although non-unique, feature listed by Bockmann as diagnostic for *R. quelen*. This is the highly reduced posterior cranial fontanelle, long used as one of the diagnostic characters of *Rhamdia*. Indeed, we find the posterior fontanelle closed or reduced to a small foramen in the supraoccipital in most other *Rhamdia* examined: *R. laukidi*, *R. nicaraguensis*, *R. quelen* (including specimens originally identified as *R. guatemalensis*, *R. hilarii*, *R. vilsoni*, *R. wagneri*) and some *R. laticauda*. Silfvergrip (1996) reported the fontanelle to be variably open or reduced in *R. laticauda*, and our sample also shows such variability among specimens. We find that *R. muelleri* has an open posterior fontanelle. The fontanelle is also closed in the heptapterids *Brachyglanis*, *Brachyrhamdia*, *Leptorhamdia*, and *Myoglanis* (Bockmann 1998, pers. obs.). Furthermore, *R. guasarensis* has an uncinat process on hypobranchial 1, unlike *R. quelen* that lacks the process (listed as a second non-unique derived feature of *R. quelen* by Bockmann 1998). Accordingly, we do not take the foregoing as evidence for a particularly close phylogenetic relationship between *R. guasarensis* and *R. quelen*. The midline union of frontal bones (Fig. 2) and concomitant extreme reduction of the anterior fontanelle are a distinctive apomorphic character of *R. guasarensis*. Although not all species have been examined for this feature, we have not observed it in any *Rhamdia* nor has it been previously reported, and in his description of the genus, Silfvergrip (1996:74) reported the anterior fontanelle to

be invariably open. This is at least a diagnostic autapomorphy of the species, although these features are potentially informative about relationships. Bockmann (1998) illustrated a variety of conditions of anterior fontanelle narrowing and closure in other heptapterids including *Myoglanis*, *Taunayia*, *Imparfinis pristus*, and an undescribed species, but all of these are structurally different from that in *R. guasarensis*.

Another peculiar character of the new species is the concave dorsal profile of the head. In general, *Rhamdia* species, including most cave populations, have convexly rounded heads. The cave species *R. macuspanensis* recently described from Mexico (Weber & Wilkens 1998) has a straight dorsal head profile, somewhat more similar to that of *R. guasarensis* than to other congeners. *Rhamdia macuspanensis* is readily distinguished from *R. guasarensis* by its strong development of pectoral spine denations and rounded tips of the caudal lobes.

Rhamdia guasarensis possesses typical reductive characteristics in common with other cave-dwelling species and populations of the genus. Furthermore, the greater relative length of the head and elevated number of pectoral-fin rays are also shared by other troglotic species of the genus (Weber 1996). It has been suggested that larger head size is related to an increase in the development of the cephalic laterosensory system (Langecker & Longley 1993, Weber 1996), and the greater number of pectoral-fin rays is possibly correlated with the increased mass of the anterior part of the body, compensating this increase with a greater fin area for hydrodynamic lift (Weber 1996). If there is a functional relationship between head size and pectoral-fin area in cave dwelling *Rhamdia*, it does not extend to the heptapterid genus *Pimelodella*, wherein the large-headed *P. kronei* has eight or nine pectoral-fin rays (Trajano 1997, Trajano & Britski 1992) and the small-headed *P. spelaea* has ten pectoral-fin rays (Trajano et al. 2004).

No *Rhamdia* species are known from the

surface waters of Río Guasare, thus *R. guasarensis* is not a cave-dwelling ecotype of a proximate epigeal species. Two *Rhamdia* species have been reported from northwestern Venezuela. From the Lago de Maracaibo Basin, Schultz (1944) published on specimens now identified as *R. quelen* (Silfvergrip 1996). Fernández-Yépez & Martín (1953) reported *R. wagneri* based on specimens collected in the Río Negro in the southern part of the Perijá range. One of us (CDN) has reidentified these specimens at the Museo de Historia Natural La Salle as *R. quelen*. As noted above, there is no evidence for a uniquely close relationship between *R. guasarensis* and *R. quelen*.

The fauna of troglotic catfishes of the Sierra de Perijá region includes: *Ancistrus galani* Pérez & Vilorio, 1994, *Trichomycterus spelaeus* DoNascimento, Villarreal & Provenzano, 2001, and *Rhamdia guasarensis*. There is another hypogean population of *Trichomycterus*, possibly an undescribed species, living in a cave drained by the Río Yasa (Río Negro system) in the southern part of the Sierra de Perijá (DoNascimento, in prep.).

The diversity of three cave catfishes of the Río Guasare system is among the highest of any Neotropical karst region, although the species are not found syntopically in the same cave. By contrast Bichuette & Trajano (2003) list five troglotic species in caves of the São Domingos karst area, Goiás, Brazil. *Ancistrus cryptophthalmus* and the trichomycterid *Ituglanis passensis* coexist in the São Vicente cave, Tocantins Basin, Goiás, Brazil (Trajano & Souza 1994, Fernández & Bichuette 2002). Also, the inundated caves of the Formosinho karst region of Bodoquena, Mato Grosso do Sul, southeastern Brazil, are co-inhabited by *Ancistrus formoso* and an undescribed troglomorphic population of *Trichomycterus* (Sabino & Trajano 1997).

Cave-dwelling and specialized troglotic neotropical catfishes belong to the families Astroblepidae, Heptapteridae, Loricariidae, and Trichomycteridae. Within the last three

of these families the genera *Rhamdia*, *Ancistrus*, and *Trichomycterus* are most commonly represented in cave faunas. Their prevalence suggests possession of morphological, physiological, behavioral, and ecological features (preadaptations) that facilitate existence in cave waters (Eigenmann 1919, Norman 1926, Hubbs 1936).

Wilkens (1986) proposed a correlation between degree of morphological reduction and time of subterranean evolution based on a neutral mutation model for the regressive evolution of eyes and pigmentation in cave fishes and crustaceans. The subterranean catfishes of the Sierra de Perijá, especially *Trichomycterus spelaeus* and *R. guasarensis*, are highly advanced in their troglotic features, suggesting that they are not new arrivals in their subterranean environment. Ocular and pigmentation reduction of *R. guasarensis* and *T. spelaeus* are complete. These species exhibit additional autapomorphies such as extremely elongate barbels in *Trichomycterus* and much enlarged head laterosensory organs in *Rhamdia*. These characters, too, may indicate a long period of hypogean evolution. Indirect evidence suggests the availability of an ample period of time for the evolution of the Perijá cave fishes. Paleogeographic reconstructions of northwestern Venezuela suggest that uplift of the Sierra began in the early Cenozoic (González de Juana et al. 1980). It is reasonable to assume that these fishes originated in situ after subterranean waters carved out their habitat within Cretaceous limestones of the Sierra de Perijá. On the fish side of the equation, the only fossil record of *Rhamdia* are fin spines of relatively young Pleistocene age (Cione 1982). However, based on much older Miocene fossils of phylogenetically related pimelodid and pseudopimelodid catfishes, the heptapterids are expected to have originated and diversified long before the late Pleistocene (Lundberg 1998). Thus it is possible that subterranean aquatic habitats and cave fishes have been present in this region for tens of millions of years.

Comparative material.—*Rhamdia laticauda*: ANSP 104034, one specimen, X-ray and alc, 86 mm SL, Panama, Cocle; UMMZ 197078, two dry skeletons, 131–146 mm SL, Honduras. *R. laukidi*: ANSP 139184, one of three specimens, X-ray and alc, 127 mm SL, Colombia, Meta. *R. muelleri*: ANSP 162521, two of four specimens, X-ray and alc, 109–110 mm SL, Venezuela, Amazonas. *R. nicaraguaensis*: ANSP 8444, one specimen, alc, 135 mm SL, Nicaragua, Lago Nicaragua. *Rhamdia quelen*: ANSP 141578, two of five specimens, X-ray and alc, 100–105 mm SL, Venezuela, Bolívar; ANSP 45365 (original identification *R. guatemalensis*), one specimen, X-ray and alc, 120 mm SL, Panama, Canal Zone; ANSP 172138 (original identification *R. hilarii*), two of 37 specimens, X-ray and alc, 107–110 mm SL, Brazil, Minas Gerais; ANSP 16020 (original identification *R. vilsoni*), one specimen, alc, 200 mm SL, Trinidad; ANSP 71621 (original identification *R. wagneri*), one specimen, X-ray and alc, 125 mm SL, Colombia, Magdalena; DU-F1021, one dry skeleton, 202 mm SL; MBUCV-CT-561, eight specimens, CS, 23–57 mm SL, Venezuela, Zulia; MHNLS-1645, two specimens, alc, 59–223 mm SL, MHNLS-1734, three specimens, alc, 107–228 mm SL, Venezuela, Zulia.

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**Taxonomic review of the fossil Procellariidae (Aves:
Procellariiformes) described from Bermuda by R. W. Shufeldt**

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Abstract.—The literature and specimens relevant to the three new species of petrels (Procellariidae) proposed by R. W. Shufeldt from Quaternary fossils from Bermuda were re-examined. A case is made for citing all three binomials as dating from Shufeldt's earlier preliminary publication (1916) rather than his later monograph (1922). *Aestrelata vociferans* Shufeldt, 2 October 1916, was correctly synonymized with *Aestrelata cahow* Nichols & Mowbray, 31 March 1916, and a lectotype is designated here. *Puffinus mcgalli* Shufeldt, 1916, was correctly synonymized with *Puffinus puffinus* Brünnich, 1764, with the holotype evidently representing a casual occurrence. A lectotype is designated for *Puffinus parvus* Shufeldt, 1916. This taxon is not synonymous with *Puffinus lherminieri* Lesson, 1839, being much smaller, and is provisionally retained until its status relative to other taxa in the *Puffinus assimilis/lherminieri* complex can be assessed.

Because seabirds of the family Procellariidae are usually the most prevalent members of the fossil avifaunas recovered in Bermuda, it is desirable to resolve several taxonomic and nomenclatural problems that were introduced in two papers by R.W. Shufeldt (1916, 1922) in which he named three new species of petrels and shearwaters from fossil remains of uncertain age obtained in several caves in Bermuda. Although his names were all subsequently synonymized, these actions were taken without reference to Shufeldt's original material, most of which is now to be found in the Carnegie Museum of Natural History, Pittsburgh (not the British Museum, as surmised by Brodkorb, 1963). The objectives of this review are: (1) to establish the original citation for each of Shufeldt's names; (2) to attempt to identify at least parts of the type series upon which each species was based and designate lectotypes where appropriate; and (3) to determine autoptically the identity and validity of each of Shufeldt's taxa.

Considering the deficiencies of the comparative osteological material available to Shufeldt, his studies of Bermudan fossils are quite exemplary. Regardless of the ultimate fate of Shufeldt's names, his analysis of the specimens and his conclusions were for the most part meritorious—something that cannot be said for many of his other studies of fossil birds. Shufeldt's first contribution to Bermudan paleontology (Shufeldt 1916) was intended only as a preliminary introduction to a larger work. He had progressed at least as far as mounting the plates for this proposed monograph, as at this point he refers specifically to the plate and figure numbers of the unpublished larger manuscript. The figure numbers mentioned at this time correspond exactly with those published later (Shufeldt 1922), although the plates were renumbered according to the sequence necessitated by the journal in which they appeared. Publication of the definitive paper was originally to have been through the American Museum of Natural History, but this never took place;

the paper was delayed (7 years) and eventually was issued in the Carnegie Museum series. That a delay was forthcoming must have been apparent to Shufeldt in 1916, as he included an addendum to his preliminary paper in which he named his new taxa, although the descriptions accompanying the names were very spare. Some of the names have been construed as *nomina nuda* at this point (e.g., Brodkorb 1963:246), but for reasons given below I consider all of Shufeldt's names to date from the 1916 publication.

There were several collections of Bermudan fossils upon which Shufeldt based his descriptions of *Aestrelata vociferans*, *Puffinus mcgalli*, and *P. parvus*. The original one, upon which he had been invited to work by F. A. Lucas "Director of the American Museum of Natural History" (Shufeldt 1916:623), had been obtained by L. L. Mowbray. Material from this collection was identified by Shufeldt (1922) as being from the American Museum (AMNH). Another collection was obtained by Edward McGall and was referred to in Shufeldt (1922) as the McGall Collection. Apparently the AMNH material was never returned and most of Shufeldt's material that has been traced so far is in the collections of the Carnegie Museum. Furthermore, at least one specimen identified in Shufeldt (1922) as coming from the AMNH collection was exchanged from the Carnegie Museum to the Smithsonian Institution in 1932 (USNM 320059, accession no. 117209). (All USNM and CM catalog numbers refer to series in the ornithological rather than paleontological collections.)

Identifying Shufeldt's type material is made more difficult by the fact that none of the specimens involved had been cataloged or numbered. It should be noted that McGall and Anthony Tall evidently sent additional specimens to Harvard University, the British Museum, and perhaps elsewhere (Shufeldt 1922:384), but Shufeldt never examined these specimens and they certainly have no claim as types.

Pterodroma cahow (Nichols & Mowbray, 1916)

Aestrelata cahow Nichols & Mowbray, 1916 (31 March):194.

Aestrelata vociferans Shufeldt, 1916 (2 October):633, Shufeldt, 1922:365.

Oestrelata vociferans: Lambrecht, 1933: 271.

Pterodroma cahow: Bent, 1922 (19 October):112 (new combination with *A. vociferans* in synonymy); Brodkorb, 1963: 246.

Lectotype (here designated).—*Aestrelata vociferans* Shufeldt 1916, skull (neurocranium with attached maxillary rostrum and right quadratojugal) included with USNM 320059. Measurements: total length 74.7 mm; cranium length 40.2, cranium width at postorbital processes 29.5, cranium depth 21.1; least width interorbital bridge 10.4, width at naso-frontal hinge 10.3; length of rostrum from naso-frontal hinge 36.2; length of nostril 11.4; length of premaxilla anterior to nostril 20.0.

This specimen can be identified unequivocally as the fossil of *Aestrelata vociferans* illustrated in Shufeldt (1922) as Figure 5 on Plate 16, by the shape of the small flange of bone projecting ventrally nearly across the ventral interorbital fenestra. This flange is extremely variable in *Pterodroma cahow* and may range from a small pointed projection to a continuous bridge across the fenestra. The distinctive shape in USNM 320059 is exactly as shown in Shufeldt's figure (Fig. 1a, b), and all other variations, such as positions of small foramina, correspond exactly as well. In Shufeldt (1916: 635) it is stated that "The differences in the osseous mandibles of a Petrel (*Aestrelata vociferans*) and a Shearwater (*Puffinus lherminieri*) are easily appreciated upon comparing those parts in figs. 5 & 6 of pl. i." This reference is to figures in the then unpublished manuscript. The plates were renumbered in Shufeldt 1922, so that plate 1 became plate 16g in which Fig. 5 is the specimen designated here as lectotype. In

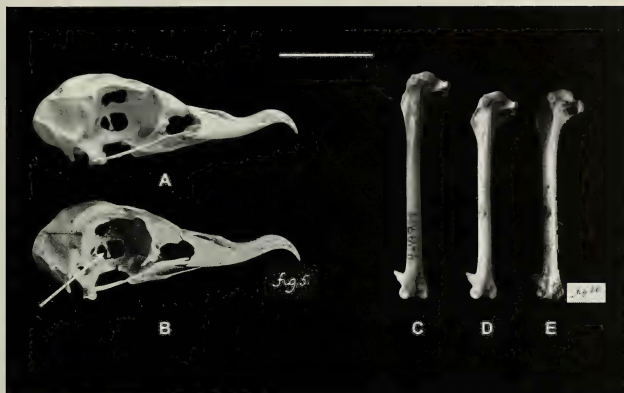


Fig. 1. A, lectotype of *Aestrelata cahow* Shufeldt (1916), USNM 320059; the quadratojugal and quadrate were separated from the rest of the skull subsequent to Shufeldt's photograph and may not have been rejoined in exactly the same position; the quadrate is not necessarily from the same individual as the skull and is not to be considered as part of the lectotype. B, Shufeldt's illustration (1922: fig. 5, plate 16) of the same specimen; arrow indicates the diagnostic flange of bone in the interorbital foramen that identifies the photograph with USNM 320059. C, left humerus of *Puffinus lherminieri* USNM 428934 from Bermuda. D, left humerus, lectotype of *Puffinus parvus* Shufeldt (1916), CM 16539. E, Shufeldt's illustration (1922: fig. 56, plate 25) of the same specimen; the markings on the shaft and bit of matrix in the olecranal fossa identify the photograph with CM 16539.

the legend, this was identified as being part of the series that was supposed to be in AMNH (see above).

USNM 320059 was received from the Carnegie Museum in exchange in 1932. The label with this specimen reads "Skeleton of adult 'Cahow' | *Aestrelata vociferans* sp. nov. Shuf. | Made as perfect as the bones in the | collection would allow R. W. S[hufeldt]. | 11 Dec. '15."

Paralectotypes.—Because of adhering matrix, discolorations, or individual osteological variation, the following specimens can be identified with photographs in Shufeldt (1922) and are therefore unequivocally part of his type series. Shufeldt's figure number follows the current museum number: skulls CM 16533 (fig. 1), 16534 (fig.

2), 16535 (fig. 3); sterna 16537 (fig. 26), 16538 (fig. 27). Skull CM 16536 may be the one illustrated in fig. 4, but if so, both quadratojugals are now lacking and I did not detect any peculiarity of the specimen that would allow it to be certainly identified with the figure.

Remarks.—Of the new names for Bermudan petrels introduced by Shufeldt, the citation for *Aestrelata vociferans* presents the most difficulties, as no characters of the species itself are actually mentioned and no specimens were illustrated in Shufeldt (1916). Nevertheless, he did discuss osteological characters of the fossils that definitely refer them to *Aestrelata* (= *Pterodroma*) as opposed to *Puffinus*. Only one species of *Pterodroma* has ever been found

in fossil deposits on Bermuda, and Shufeldt identified his new species with the "cahow" of legend, which was later definitely established as being a species of *Pterodroma* (Murphy & Mowbray 1951). Furthermore, Shufeldt specifically refers to bones of the new species illustrated in plates prepared for his monograph published later (Shufeldt 1922) and unequivocally identifies them by figure number and plate number. Therefore, it is now possible to identify particular specimens of Shufeldt's new species based on information given in the 1916 publication. Thus, it may be argued, as I believe, that *Aestrelata vociferans* is valid as of Shufeldt 1916 rather than Shufeldt 1922. It is a moot point, however, as *A. vociferans* Shufeldt 1916 is still a junior synonym by 6 months of *A. cahow* Nichols & Mowbray, 1916. If *A. vociferans* is dated from Shufeldt 1922, Bent (1922: 114), who had access to Shufeldt's manuscript, effectively synonymized Shufeldt's name 17 days later by saying that it was "apparently the same bird" as *A. cahow* of Nichols & Mowbray.

The unravelling of the identity of the bird known to Bermuda's early settlers as the "cahow" is well summarized by Murphy & Mowbray (1951). This bird was once incredibly abundant and provided the early colonists with a ready supply of food. But it was so overexploited by man and introduced mammals that it had seemingly disappeared before its identity could be made known to naturalists. A living example of a *Pterodroma* was taken in Bermuda in 1906 by L. L. Mowbray, but was referred to a species that breeds in New Zealand (Bradlee 1906). Not until a decade later was this specimen described as the type of a new species, *Aestrelata cahow* (Nichols & Mowbray 1916), almost simultaneously with Shufeldt's (1916) preliminary note. Shufeldt deserves a fair amount of credit for developing our knowledge of the Cahow, as his paleontological studies were as seminal as any in providing documentation that the Cahow was one of the gadfly pet-

rels now recognized in the genus *Pterodroma*.

Puffinus puffinus puffinus (Brünnich, 1764)

Puffinus puffinus bermudae Nichols & Mowbray, 1916 (31 March):195.

Puffinus mcgalli Shufeldt 1916 (2 October): 630; Shufeldt, 1922:354.

Puffinus puffinus puffinus: Dwight 1927: 243 (with *P. p. bermudae* in synonymy).

Puffinus puffinus: Wetmore, 1931:407 (footnote; suggested synonymy of *P. mcgalli*); Lambrecht, 1933:269; Wetmore, 1962: 16; Brodkorb, 1963:246.

Holotype.—*Puffinus mcgalli* Shufeldt 1916, sternum CM 16531, with a split in the carina from which a piece of bone is missing, also lacking the tip of the carina and tips of some of the posterior processes.

Referred specimen.—In an addendum, Shufeldt (1922:381, footnote) identified what he believed to be a pedal phalanx 2.8 cm in length that he thought "belonged to an adult specimen of *Puffinus mcgalli*, and possibly to the same individual" as the holotypical sternum. This specimen (CM 16532) is still in the same box with the holotype and measures 28.7 mm. It is actually the left tibiotarsus of a juvenile passerine bird with the proximal end quite porous and incompletely ossified. It has no status whatsoever as a type.

Remarks.—Shufeldt (1916) based *Puffinus mcgalli* on a sternum that was stated to be larger than that of *P. lherminieri* and smaller than that of *P. major* (= *P. gravis*), in addition to which a measurement of the holotype was provided. This is quite sufficient to establish the name *P. mcgalli* at this point. Wetmore (1931:407), presumably on the basis of size and geographical probability, suggested that *P. mcgalli* was probably synonymous with *P. puffinus* and was followed by Lambrecht (1933). Later, Wetmore (1962:16) considered that Shufeldt's figures of the sternum of *P. mcgalli* "agree exactly with a sternum of a female *Puffinus puffinus puffinus*." Brodkorb (1963) fol-

lowed Wetmore's lead, but no one since Shufeldt had ever critically examined the specimen.

The shape of the manubrial area, the angle of the sterno-coracoidal processes, and other features establish that the holotype is correctly referred to the genus *Puffinus*, as opposed to *Pterodroma*. In size, it is within the range of *Puffinus puffinus puffinus*: length along midline 58.0 mm, width across posteriormost costal facets 25.4 mm. In a series of 10 skeletons of *Puffinus puffinus puffinus* the length was 52.2–58.0 (avg. 55.1) and width 23.9–27.2 (avg. 25.7). This is larger than *Puffinus lherminieri* but smaller than any of the other Atlantic species of *Puffinus*. Thus *Puffinus mcgalli* Shufeldt, 1916, was correctly synonymized with *Puffinus puffinus* Brünnich, 1764.

This occurrence of *Puffinus puffinus* as a fossil in Bermuda is unique, as no other fossils of the species have ever been encountered among the thousands of bones of seabirds collected so far. Although this species is a common offshore visitor to Bermuda, there are only three records of attempted breeding (Bradlee et al. 1931, Bourne 1957). The first was a specimen "captured while sitting on its solitary egg in a rocky hole on a small island in Castle Harbor, in April, 1864" (Reid 1884:274). The second record, more doubtful, was another bird sitting on an egg in an island in Castle Harbor in May 1877 tentatively recorded as *Puffinus opisthomelas* (Reid 1884:276). The final record was a specimen taken "March 10, 1905, sitting on a single white egg in a crevice in Gurnet Head Rock" (Nichols & Mowbray 1916). This was described as a new subspecies, *Puffinus puffinus bermudae* Nichols & Mowbray, 1916, that was later definitively synonymized with *Puffinus puffinus puffinus* by Dwight (1927).

In an instance perhaps similar to those on Bermuda, a single incubating Manx Shearwater was found in June 1973 on Penikese Island, Massachusetts, west of Martha's Vineyard (Bierregaard et al. 1975), but breeding evidently did not continue there

(Lee & Haney 1996). The first North American breeding colony of the species was established in 1977 on Middle Lawn Island, southern Newfoundland, and by 1981 the population had grown to an estimated 350 individuals (Storey & Lien 1985). There is no evidence that *Puffinus puffinus* was ever able to establish such a colony on Bermuda at any time in the last 400,000 years and all the records, including the fossil sternum described as *Puffinus mcgalli*, appear to have resulted from single individuals or pairs.

Puffinus parvus Shufeldt, 1916

Puffinus parvus Shufeldt, 1916:632; Shufeldt, 1922:356.

Puffinus lherminieri: Wetmore, 1931:407 (footnote; suggested synonymy of *P. parvus*); Lambrecht, 1933:270; Wetmore, 1962; Brodkorb, 1963:246.

Lectotype (here designated).—*Puffinus parvus* Shufeldt, 1916, left humerus, CM 16539 (fig. 56 of Shufeldt 1922). Measurements: Total length 58.8 mm; proximal width 10.7, depth of head 3.3, width and depth of shaft at midpoint 3.8×2.6 , distal width 7.9.

Paralectotypes (figure numbers from Shufeldt 1922 in parentheses).—CM 16540 right humerus (fig. 55), 16541 right humerus, 16542 left humerus, 16543 left humerus, 16544 right ulna (fig. 43), 16545 right ulna, 16546 left ulna (fig. 44), 16547 left radius (fig. 45), 16548 right carpometacarpus (fig. 67), 16549 right phalanx 1 of major alar digit (fig. 74), 16550 left coracoid (fig. 92), 16551 incomplete furcula (fig. 79), 16552 right tibiotarsus (fig. 119), 16553 left tibiotarsus (fig. 120), 16554 right tarsometatarsus (fig. 107), 16555 right femur, 16556–58 left innominates.

Remarks.—The name *Puffinus parvus* dates from Shufeldt (1916), as there this taxon was specifically characterized as being smaller than *P. lherminieri* and as belonging to a group of small shearwaters having a short, rather than an elongate sternum. The type material he listed (p. 632)

as 12 bones from what he called the AMNH series (of which only one certainly, and three probably, can now be accounted for) and the following from the McGall collection: "five perfect humeri, three ulnae, a radius, a carpo-metacarpus, a proximal joint of an index digit, a coracoid, an inferior mandible, an imperfect os furculum, a tarso-metatarsus, an os innominatum of the left side; subsequently there also came to light an imperfect cranium." These lists were repeated nearly verbatim in Shufeldt (1922:356) save that the last imperfect cranium is omitted and that specimen is no longer present, so perhaps he subsequently re-identified it. In an addendum, Shufeldt (1922:385) listed and identified a further series of 77 specimens of *Puffinus parvus* collected by McGall and Tall that also was deposited in the Carnegie Museum, where all but the 5 sterna and 2 of the fragmentary furculae may still be found. It is very clear from Shufeldt's statements (e.g., 1922:385), however, that the first two collections constituted the type series and that the additional specimens were referred only subsequent to his 1916 paper and thus have no status as types.

In the CM collections was a container of bones labelled in Shufeldt's hand "McGall Collection | *Puffinus parvus* Shuf. sp. nov | Nov. 27 1915 | Fragile." This series corresponds exactly to Shufeldt's list of this collection, less the cranium mentioned above, except that it has been augmented by a right and left tibiotarsus, a right femur, and an additional two innominate bones. Although no tibiotarsus was listed for the McGall collection in either of Shufeldt's publications, the legend for Shufeldt's (1922) fig. 119 of a right tibiotarsus identifies it as being from the McGall collection, whereas the left tibiotarsus in fig. 120 is identified as being from the AMNH series, in which there was only a single tibiotarsus. The femur and the additional two innominates are doubtless the femur and two of the four innominates listed for the AMNH series, which has otherwise disappeared.

I think that there can be no question that all 21 of these bones may be safely regarded as syntypes of *Puffinus parvus* Shufeldt. Several can be identified with photographs in Shufeldt (1922) and from these I have selected as lectotype a humerus with distinctive markings making it individually identifiable (Fig. 1d, e). All of the remaining bones in this series may be considered paralectotypes and have been listed above with their current catalog numbers and reference to the figure numbers in Shufeldt (1922) where appropriate.

Without having seen the material, Wetmore (1931) suggested in a footnote that *Puffinus parvus* was probably the same as the living Audubon's Shearwater *Puffinus lherminieri* Lesson, 1839, in which he was followed by Lambrecht (1933). Later, in examining a few remains of small *Puffinus* found in 1958 on Cockroach Island, Harrington Sound, Bermuda, Wetmore (1962) noted what seemed to be two size classes but considered that the smaller one consisted of juveniles. Although he stated (p. 16) that "Shufeldt (1916 p. 632) noted two apparent size groups and named the smaller one *Puffinus parvus*," I cannot interpret anything in Shufeldt's publication as indicating that he thought there were two size classes. Wetmore also noted that Shufeldt's (1922) photographs of the bones of *P. parvus* were not to the scale indicated, as Shufeldt himself had pointed out, however (p. 362 footnote). Wetmore concluded that *P. parvus* was not a valid taxon and synonymized it with *P. lherminieri*, and he was followed by Brodkorb (1963).

After having examined Shufeldt's type-series and much more extensive fossil material from Bermuda dating from the middle Pleistocene onward, I have concluded that *Puffinus parvus* is indeed a much smaller species than *P. lherminieri* (Fig. 1c, d). The systematics of the *Puffinus lherminieri*/*P. assimilis* assemblage is very complex and imperfectly understood. *Puffinus parvus* needs comparison with the Atlantic taxa known as *Puffinus affinis baroli*, which oc-

curs in the Azores, Madeira group, and Canary Islands, and *Puffinus lherminieri boydi* of the Cape Verde Islands (Jouanin & Mougin 1979). Unfortunately, there is almost no skeletal material of these taxa available for comparison. Apparently, *P. parvus* was exterminated after human arrival in Bermuda, after which *P. lherminieri* was able to colonize the island for a brief period before it became extinct itself as a breeding-bird in the late 20th century. Ironically, both species are present in the Cockroach Island material. Further investigation of the small shearwaters of Bermuda is under way, but for now *Puffinus parvus* Shufeldt, 1916, is retained as a taxon that is clearly distinct from *P. lherminieri*.

Acknowledgments

I thank Kenneth C. Parkes and Robin Panza, Carnegie Museum of Natural History, Pittsburgh (CM), for making Shufeldt's material available and for supplying catalog numbers. The figure is by Brian Schmidt, Division of Birds, National Museum of Natural History, Smithsonian Institution (USNM).

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Revision of the genus *Squamigera* (Insecta: Zygentoma: Nicoletiidae) with descriptions of two new species

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Abstract.—The genus *Squamigera* was described in 1999 from a single male. Understanding of the genus was therefore limited. After several unsuccessful expeditions, new material has finally been collected from the same cave. New material of related *Squamigera* species was also found while reviewing museum collections. From these specimens two new species, *S. cumcalcaris* and *S. jaureguii*, are described, and a better description of the diagnostic characters of the genus is provided.

In 1988, a single male thysanuran was collected by R. Espinasa-Closas in a Mexican cave (Cueva de las Pozas Azules). The specimen is unique in many ways. Measuring 22 mm, it is one of the largest specimens in the family Nicoletiidae, but more diagnostically, it has spines on the cerci and scales cover its body and head. All other members of the subfamily Cubacubaninae lack this combination. Despite many subsequent visits to the same locality, no other specimens were found. Eleven years after the original discovery, the specimen was described (Espinasa 1999a) and the new nicoletioid genus *Squamigera*, was established. By necessity, the description of *Squamigera* lacked a description of the female morphology or of postembryonic development. Comparison of the genus with other members of the subfamily was difficult because it was unclear which characters were unique to the specimen (species variation) and which characters had phylogenetic/taxonomic value.

Fortunately, the situation has changed. A revision of the nicoletioid collection of the American Museum of Natural History provided a single female from a surface locality collected in 1976 by Reddell and Grubs. Also, the Sbordoni collection of cavernicole organisms from Chiapas provided two

males and one female from two caves. And finally, an additional male has been collected from the type locality. This male is considerably larger than any other American nicoletioid described.

From these specimens, two new species are described and a revision of the taxonomic characters for the genus is provided.

Materials and Methods

The live specimen was found crawling on the cave wall and was preserved in 96% ethanol. Dissections were made with a stereo microscope and the body parts were mounted in fixed preparations with Hoyer's solution. The female and juvenile male from Chiapas, and the new Pozas Azules specimen were not dissected. All illustrations were made with aid of a camera lucida attached to a compound microscope. The types were deposited in the Zygentoma collection of the American Museum of Natural History.

Squamigera Espinasa, 1999

Diagnosis (amended).—A member of the subfamily Cubacubaninae with mucronate to emarginate scales with smooth to serrate borders. Cerci of males with modified

spines. Parameres without a cleft on the apex.

Description (amended).—Body proportions normal to robust. Head, thorax, abdomen, and proximal articles of legs with scales and setae. Distal articles of legs, mouthparts and abdominal stylets only with setae. Scales numerous and multiradiate, their form mucronate to emarginated, with smooth to highly serrated borders.

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

Tarsi with four articles. Praetarsi with three simple claws. Middle claw glabrous, slender and smaller than lateral claws. Urosterna II–VII subdivided into coxites and sternite. Urosterna VIII and IX of male entire. Middle portion of sternites with 1 + 1 sublateral macrochaetae at hind borders, as well as 1 + 1 near suture at about middle of segment. Coxites on segments II–IX with stylets. Eversible vesicles on segments II–VI, pseudovesicles on VII. Urosterna III of adult males sometimes with modified coxites. Urosterna IV apparently without articulated submedian appendages. Urosterna VIII with a wide and not too deep posterior emargination. Posterior projections acute to slightly round, pointing slightly outward. Tergum X very protruding, almost straight on posterior border. Posterior angles with several subequal macrochaetae.

Point of insertion of parameres relatively deep and with modified setae on internal face of coxal processes. Parameres with specialized setae on apex, but without a cleft or other modifications. Stylets IX apparently without spines. Opening of penis longitudinal. Cerci of male with modified spines. Median filament with or without spines. Females with a subgenital plate and gonapophyses of adult females apparently with numerous articles.

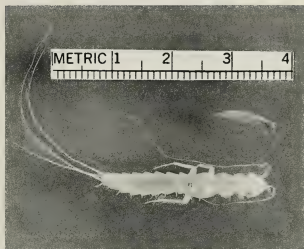


Fig. 1. *Squamigera latebricola*, male topotype (larger individual, dorsal view) and *Squamigera* sp., juvenile male (smaller individual, ventral view). Comparison of body proportions to illustrate the large size of *S. latebricola*.

Type species.—*Squamigera latebricola* (Fig. 1).

Distribution.—All specimens to date come from south-central Mexico. It is currently unknown but likely that members of the genus occur in South America and the Antillean islands. Their distribution is probably restricted to the neotropics.

Remarks.—Several amendments were made to the original description of the genus: 1. Body proportions are not always robust. 2. Scales are not only slightly serrated, but can be highly serrated. 3. Size of spur on male pedicellus can be variable. 4. Urosterna II subdivided into coxites and sternite. In the fixed preparation of the holotype it was unclear if the urosterna was divided. 5. Urosterna III of adult males can have modified protuberances similar to those found in some *Cubacubana* (Espinasa 1991) and *Prosthecina* (Espinasa 2000). 6. Number of macrochaetae in posterior angles of tergum X can be variable. 7. Point of insertion of parameres relatively deep and with modified setae on internal face of coxal processes. 8. Parameres without a cleft. In the fixed preparation of the holotype, the parameres were broken as an artifact of the preparation, giving the impression of a cleft (The

cleft/break was not represented in the original figures, it was only mentioned in the text). 9. Central filament sometimes with spines. 10. Females with a subgenital plate and gonapophyses of adult females apparently with numerous articles. There were no female samples available when the original description was made.

Squamigera belongs to a group of nicoletioid genera, the Cubacubaninae (Mendes 1988), characterized by subdivided urosterna II–VII and fused coxites VIII and IX of males. *Squamigera* is distinguished from almost all genera of this subfamily by having scales. It differs from *Texoreddellia* (Wygodzinsky 1973), the only other genus with scales, by the morphology of scales (in *Texoreddellia* scales have three pointed borders instead of smooth to serrated borders), and by having scales in the head and modified spines in cerci, which are both absent in *Texoreddellia*.

Squamigera cumcalcaris, new species

Figs. 2A–G, 3A–E

Type material.—"Grotta I Finca S. Anita" cave, Finca S. Anita, Simojovel de Atilende, Chiapas, México. 830 m above sea level. 10/IX/1973 V. Sbordoni col. Male holotype, female paratype.

Description.—Body length 15 mm. Maximum conserved length of antennae 12 mm and of caudal appendages 11 mm. General color: light yellow to white. Morphology of the body as in generic description. Scales similar to Fig. 5B.

Male antennae as in Fig. 2A–B. Pedicellus slightly more than one half as long as basal article. On ventral side with approximately six clusters of unicellular glands arranged in two long rows, surrounded by microchaetae forming a "U" shape. Outside this microchaetae, another two clusters of unicellular glands and a downward pointing robust spine, opposite to an extension of the basal article (Fig. 2B). Base of female antennae simple and pedicellus half as long as basal segment.

Head with approximately 5 + 5 macrochaetae on border of insertion of antennae (Fig. 2A). Mouthpart appendages relatively short. Labial palp as in Fig. 2D. Apical article slightly wider than long and barely longer than penultimate article. Penultimate article with bulge containing macrochaetae. Labium and first article of labial palp with macrochaetae. Maxilla as shown in Fig. 3D. Last article slightly longer than penultimate. Apex of maxillary palp with two conules of similar width and a 3rd minute extra conule similar to Fig. 4G. Two teeth on lacinia. Mandibles chaetotaxy as in Fig. 2C.

Thoracic nota with scales and macrochaetae on lateral borders apart from several setae of varied sizes (Fig. 3B), but no small sclerotized spines on posterior borders. Legs relatively short and stout. Tibia on 2nd leg with five macrochaetae, some of them stout, and approximately 3.5× longer than wide and 1/3 shorter than tarsus (Fig. 2E). Tibia on 3rd leg with five macrochaetae, and approximately 4.5× longer than wide and 1/5 shorter than tarsus (Fig. 2F). Claws relatively short.

Urosterna III and IV of male without modifications in the samples examined. It is currently unknown if more fully adult specimens will develop them. Urosterna VIII posterior projections acute to slightly rounded, subtriangular (Fig. 3A). Urotergite X posterior angles with several long macrochaetae and setae of different sizes. On the borders some prominent scales (Fig. 2G).

Urosterna IX of male similar to some *Anelpistina*; point of insertion of parameres deep and setae slightly more sclerotized on internal face of coxal processes and above insertion of parameres (Fig. 3A). Stylets IX bigger than the others, with 4–5 macrochaetae and an extra subapical pair. In both males and females without spines or other modifications. Other stylets have only three macrochaetae plus the subapical pair.

Penis and parameres as shown in Fig. 3A. Parameres attaining 1/2 of stylets IX. Parameres globular and with a distinct group of microchaetae on the tip. Overall

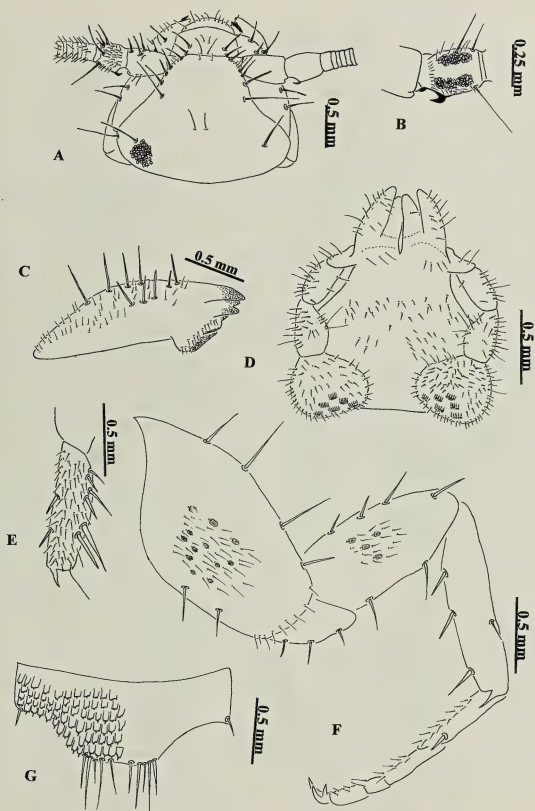


Fig. 2. *Sqv imigera cumcalcaris*. Male holotype. Scales and microchaetae partially shown; A, Head; B, Pedicellus; C, Mandible; D, Labial palp and labium; E, Tibia of 2nd leg; F, 3rd leg; G, Urotergum X.

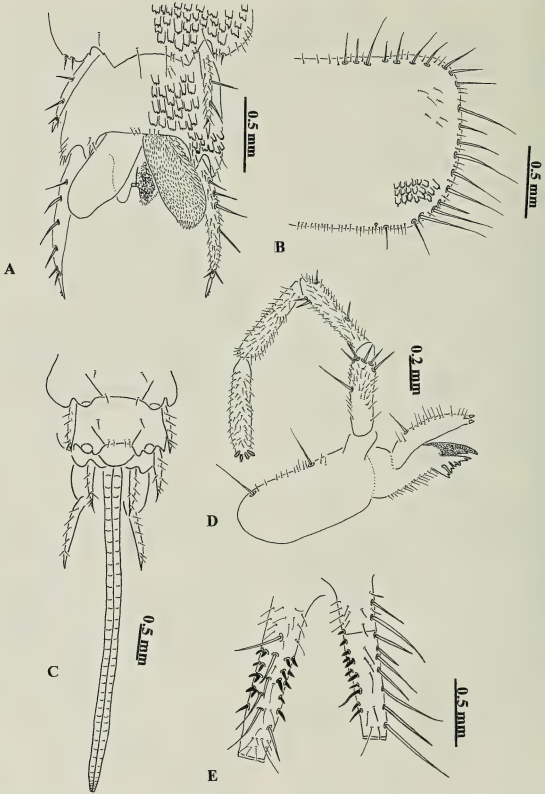


Fig. 3. *Squamigera cumcalcaris*. Male holotype except C, female paratype. Scales and microchaetae partially shown; A, Genital area; B, Thoracic tergum; C, Ovipositor; D, Maxilla; E, Median filament (left) and cercus (right).

appearance similar to some *Prosthecina* (Wygodzinsky 1946). Subgenital plate of female parabolic (Fig. 3C). Ovipositor surpassing apex of stylets IX by thrice the length of stylets (Fig. 3C). Gonapophyses with approximately 38 articles.

Male caudal appendages as in Fig. 3E. Inner side of cerci in males with spines of varied sizes. Some spines arranged even in a double row. The central filament also with spines of subequal size arranged on multiple rows facing both cerci. Female caudal appendages without modifications.

Postembryonic development unknown because of the scarcity of samples. It is assumed that specimens examined are adult based on the development of sexual secondary characters. Comparison to other species within the subfamily indicates that in younger instars we could expect that spines, modifications of antenna, and size of parameres to be reduced in younger males. In females a smaller ovipositor could be expected.

Known range.—Known only from the type locality.

Etymology.—The name is derived from the Latin "cum+calcaris" for with+spur, alluding to the prominent curved spur in the pedicellus of the antennae in males.

Remarks.—*Squamigera cumcalcaris* can be differentiated from all species of subfamily Cubacubaninae by the spines on the central filament. Such spines until now were described only in Nicoletiids in the subfamilies Coletiniinae and Subnicoletiinae (Mendes 1988). Adult males can be further differentiated by the large curved spur oriented toward the base of antennae in the pedicellus, which in *S. latebricola* is reduced to a small spine. Adult females can be differentiated from *S. jaureguii* by a parabolic instead of trapezoidal subgenital plate and by a considerably less subdivided gonapophyses.

Squamigera jaureguii, new species

Figs. 4A–H, 5A–F, 6A–D

Type material.—Puente Actopan, 5 km SE Actopan, Veracruz, Mexico. 25 Dec

1976. J. Reddell and A. Grubbs cols. Female holotype.

Description.—Body length 9.5 mm. Antennae and caudal appendages broken. Maximum conserved length of antennae 4 mm and of caudal appendages 5 mm. Body proportions as in Fig. 4A. General color: light yellow to white. Morphology of the body as in the generic and *S. cumcalcaris* descriptions, unless otherwise stated. Scales as in Figs. 4D and 5B.

Antennae as shown in Fig. 4B. Basal article without projections. Pedicellus slightly less than one half as long as the basal article. Head with approximately 8 + 8 macrochaetae on border of insertion of antennae (Fig. 4C). Labial palp as in Fig. 4E. Maxilla as shown in Fig. 4F–G. Last article $\frac{1}{2}$ longer than penultimate. Apex of maxillary palp with two conules of similar width and a 3rd minute extra conule (Fig. 4G). Mandibles chaetotaxy as in Fig. 4H. Thoracic nota as in fig. 5A. Legs relatively short and stout (Fig. 5C–D). Tibia on 2nd leg with five macrochaetae, some of them stout, and approximately 3.2× longer than wide and $\frac{1}{4}$ shorter than tarsus, and five macrochaetae. Hind leg broken in the specimen. Claws relatively short (Fig. 5E).

Urosterna I and II as in Fig. 5F. Urotergite X posterior angles with 2–3 long macrochaetae and setae of different sizes and on borders some prominent scales (Fig. 6A). Stylets IX bigger than the others, with 5–6 macrochaetae and an extra subapical pair (Fig. 6B). Subgenital plate of female trapezoid, outer border almost straight (Fig. 6B). Ovipositor surpassing apex of stylets IX by thrice the length of stylets (Fig. 6B). Apex as in Fig. 6C. Gonapophyses with approximately 53 articles. Cerci without modifications (Fig. 6D).

Males unknown. Postembryonic development unknown because only a single female individual could be examined. It is assumed that this individual is an adult based on its large ovipositor. Comparison to other species within the subfamily indicates that

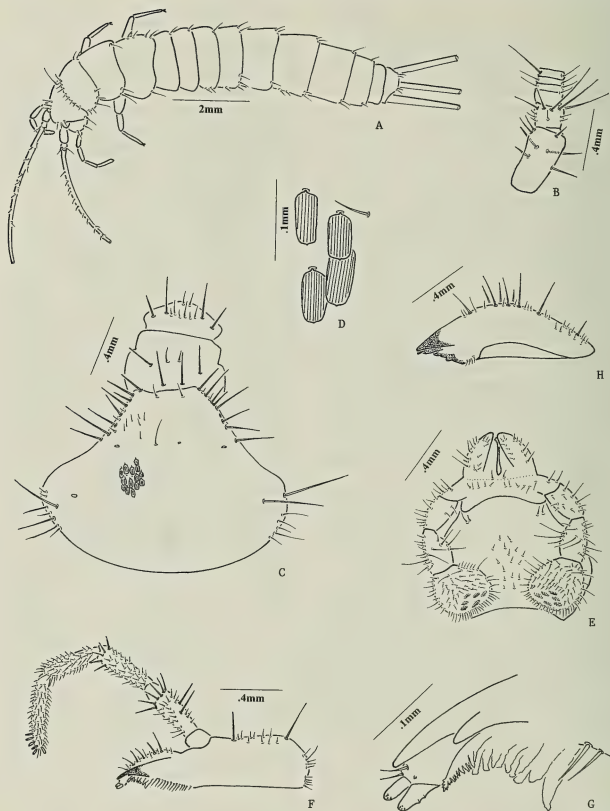


Fig. 4. *Squamigera jauregui*. Female holotype. Scales and microchaetae partially shown. A, Body; B, Basal portion of antennae; C, Head; D, Scales on head; E, Labial palp and labium; F, Maxilla; G, Apical portion of maxilla; H, Mandible.

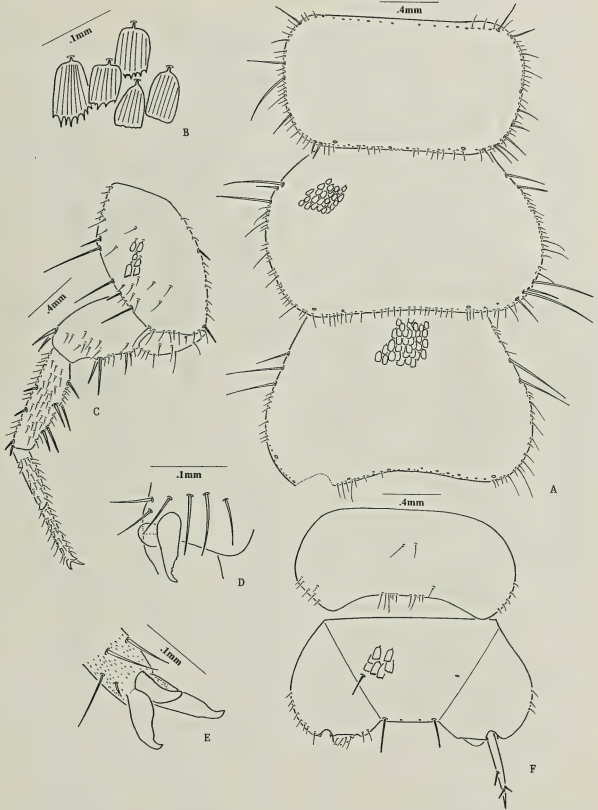


Fig. 5. *Squamigera jaureguii*. Female holotype. Scales and microchaetae partially shown. A, Thoracic tergum; B, scales of urotergum I; C, 2nd leg; D, Apex of 2nd tibia; E, Claws of 2nd leg; F, Urosternum I and II.

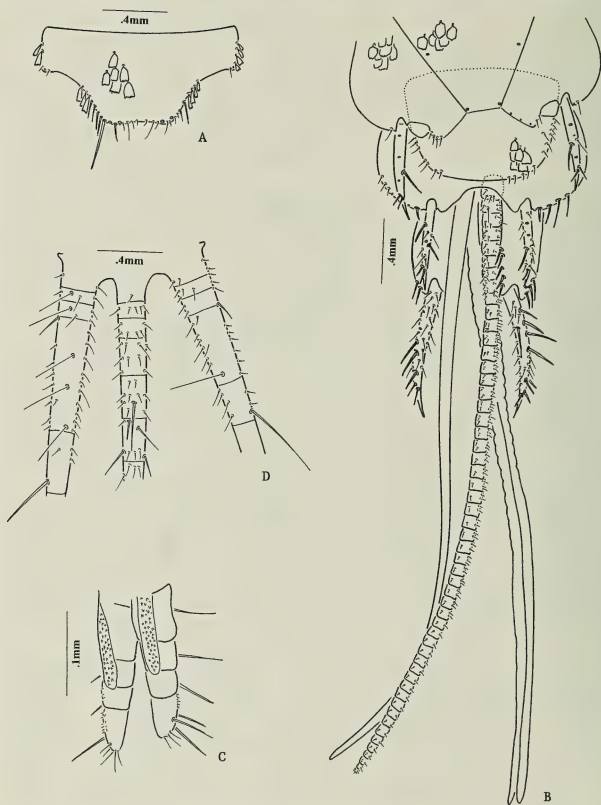


Fig. 6. *Squamigera jaeregui*. Female holotype. Scales and microchaetae partially shown. A, Urotergum X; B, Subgenital plate and ovipositor; C, Apex of ovipositor; D, Caudal appendages.

in younger instars we could expect a smaller ovipositor.

Known range.—Known only from the type locality.

Etymology.—This species is dedicated to Sergio Jáuregui to recognize his enthusiastic, long time participation in cave colelepid collecting and field work.

Remarks.—*Squamigera jaureguii* can be differentiated from other described *Squamigera* by having more macrochaetae on the head at the border of the insertion of antennae, and a shorter body and appendages. Adult females can be differentiated from *S. cumcalcaris* by the trapezoidal instead of parabolic subgenital plate and by a considerably more subdivided gonapophyses. No *S. latebricola* females are available for comparison.

Squamigera latebricola Espinasa
Fig. 7A–G

Topotype.—"Cueva de las Pozas Azules" cave (Espinasa-Pereña 1989), Taxco de Alarcón Municipality, Guerrero State, México, 18°36'40"N, 99°33'25"W. April 2001. L. Espinasa col. Male.

Description.—Body length 29 mm. Maximum conserved length of antennae 29 mm and of caudal appendages 35 mm. Body proportions as in Fig. 1. General color: light yellow to white. Morphology of body similar to *S. cumcalcaris* and *S. jaureguii*, unless otherwise stated. Scales with slightly less serrated borders.

Pedicellus with clusters of unicellular glands and a small spur (Espinasa 1999a; Fig. 1C) instead of long hooked spine of *S. cumcalcaris*. Mouthpart appendages relatively thin and long. Apical article of labial palp barely longer than wide and barely shorter than penultimate (Espinasa 1999a; Fig. 1D). Penultimate article's bulge not too prominent. Maxilla as in Fig. 7D. Last article shorter than penultimate. Apex of maxillary palp with two conules of similar width and a 3rd small extra conule (Fig. 7E).

Thoracic nota with small sclerotized spines on lateral and posterior borders (Espinasa 1999a; Fig. 3A). Legs relatively long (Espinasa 1999a; Fig. 2A). Tibia on 2nd leg with seven thin macrochaetae, and approximately 4.5× longer than wide and ½ shorter than tarsus. Tibia on 3rd leg with eight thin macrochaetae, and approximately slightly over 5× longer than wide and ¼ shorter than tarsus. Trochanter on 3rd leg with a protuberant spine projection (Fig. 7B) which is not present in the smaller sized (22 mm) holotype. Claws of normal size.

Coxites in urosterna III (Fig. 7C) with protuberances similar to those found in some *Cubacubana* (Espinasa 1991) and *Prosthecina* (Espinasa 2000). Urosterna III in smaller holotype also with a slight protuberance (not reported in original description), similar to nascent protuberance found in some immature individuals of the aforementioned *Cubacubana* and *Prosthecina*. Urosterna IV without modifications (Fig. 7A). Urosternum IX as in Fig. 7F. In this specimen the point of insertion of parameres is slightly deeper than in the holotype and closer in appearance to some *Anelpistina* (Espinasa 1999b). Stylets IX with five macrochaetae and an extra subapical pair but otherwise without any other modifications. Penis and parameres as shown in Fig. 7F. Parameres attaining less than ½ of stylets IX and curved outward. Cerci as in Fig. 7G. Females unknown.

Postembryonic development only partially understood since only two fairly large male individuals are available, the holotype (22 mm) and this new topotype (29 mm). In the smaller specimen, projections of urosterna III are only starting to develop, spines in cerci are less prominent and trochanter of hind leg has no projection.

Known range.—Known only from the type locality.

Remarks.—Being 3 cm in length (10 cm if antennae and caudal appendages are included), *S. latebricola* can easily be differentiated from all species of the subfamily

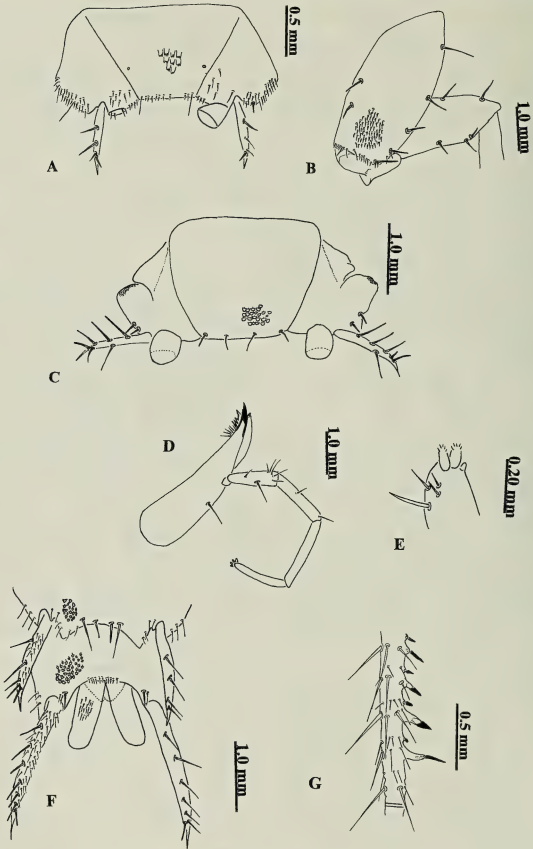


Fig. 7. *Squamigera latebricola*. Male topotype. Scales and microchaetae partially shown. A, Urosternum IV; B, 3rd leg. Notice projection in trochanter (scales not shown); C, Urosternum III; D, Maxilla; E, Apical portion of Maxilla; F, Genital area; G, Spines in cercus.

Cubacubaninae by its large size. This is the longest species among the nicoletiids, which typically measure 1 cm or less. Enlargement of body and appendages is common among cave adapted organisms and it is certainly the case for this species. This species can further be differentiated from *S. cumcalcaris* and *S. jaureguii* by the small sclerotized spines on lateral and posterior borders on thoracic nota (Espinasa 1999a; Figs. 1G and 3A), and by the morphology of its sexual secondary characters.

Squamigera sp.

Fig. 1

Material examined.—"El Chorreadero" cave, Chiapa de Corzo Municipality, Chiapas, México. 650 m above sea level. 10/11-VIII-73. V. Sbordoni col. Male.

Description.—Body length 10 mm. Antenna and caudal appendages broken. Middle filament missing. Scales as in other members of the genus. No apparent spines in pedicellus, sterna III, or cerci. Parameres curved outward, similar to the holotype of *S. latebricola* (Espinasa 1999a, Fig. 2C), but attaining less than $\frac{1}{5}$ of stylets IX. This single individual is probably not a mature adult. Chorreadero cave is visited relatively often by speleologists and hopefully more samples will be available one day for a formal description of this population.

Acknowledgments

We thank Dr. Randall T. Schuh, curator and chair of the Division of Invertebrate Zoology of the American Museum of Natural History, for kindly giving access to the

museum collection and facilitating examination of the specimens. We also thank Valerio Sbordoni for facilitating acquisition of specimens from Chiapas. Work was done with support from CEAMISH-Universidad Autónoma del Estado de Morelos, in facilities of the American Museum of Natural History and Shenandoah University.

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Associate Editor: Wayne Mathis

BIOLOGICAL SOCIETY OF WASHINGTON

131st Annual Meeting, 15 June 2004

President Roy McDiarmid called the meeting to order at 10:30 a.m. in the Waldo Schmitt Room, National Museum of Natural History (NMNH). Council members and editorial staff present: Marilyn Schotte (Elected Council), Ron Heyer (Acting President Elect), Chad Walter (Treasurer), Carole Baldwin (Secretary), Richard Banks, Stephen Cairns, Bruce Collette, and Storrs Olson (Past Presidents), and Steve Gardiner, Carol Hotton, and Ed Murdy (Associate Editors).

Minutes of the 130th Annual Meeting were summarized by Secretary Baldwin. Those minutes are scheduled to appear in Volume 117(1) of the *Proceedings*, which had not been published at the time of the annual meeting. Following approval of the minutes, McDiarmid summarized recent Society activities. McDiarmid announced that *Proceedings* Editor Richard Sternberg submitted his resignation as Editor on 9 October 2003 but agreed to remain in the position until a replacement could be found. Past President Richard Banks has agreed to serve as interim Editor beginning 1 July 2004. In view of declining manuscript submissions to the *Proceedings*, McDiarmid is appointing a committee to investigate electronic publishing. To investigate declining Society membership, he is re-establishing a Membership Committee. McDiarmid also noted that he met recently with NMNH Director, Cristián Samper, and new NMNH Associate Director for Research and Collections, Hans Sues, to inform them of the existence of the Society and its historical relationship with and support from the museum. Those administrators are in favor of the museum's continued support of the Society and are interested, in principal, in hosting the Society's website on the muse-

um server, but they indicated that a final decision about the website should not be made until the museum's new information-technology director is hired. Associate Editor Steve Gardiner, who has produced the Society's web pages on the server at Bryn Mawr College, announced that his institution is agreeable to leaving the Society's website on its server if necessary. McDiarmid concluded his summary of recent Society activities by noting that the Society will publish a special Bulletin this year entitled *Study of the Dorsal Gill-Arch Musculature of Teleostome Fishes, with Special Reference to the Actinopterygii*, by Victor G. Springer and G. David Johnson. This 800+ page Bulletin will comprise two volumes and be published in an 8½" × 11" format.

President McDiarmid then called on Chad Walter for the Treasurer's Report (Table 1). Income for the period 1 January 2003 to 31 December 2003 was \$93,105.92, and expenses for the same period were \$74,024.02. Total Society assets as of 15 April 2004 were \$99,705.40. The value of the endowment fund increased by \$12,307 in 2003. The Audit Committee, Don Wilson and Neal Woodman, indicated that they had reviewed the books and ledgers of the Treasurer and found all financial records to be accurate and in good order. The Treasurer's report was approved.

Proceedings Editor Richard Sternberg reported at the Society's Council meeting on 17 May 2004 that four issues of Volume 116 were published comprising 75 papers and 1007 pages. As of 1 June 2004, there were 34 submissions, but neither 117(1) nor 117(2) had yet been published. Issue 117(1) was submitted in January 2004, but because of the low number of submissions (8), that

Table 1.—Summary Financial Statement for 2003.

	General Fund	Endowment Fund	Total Assets
Assets: January 1, 2003	18,365.23	66,277.07	84,642.30
Total Receipts for 2003	78,473.46	14,631.94a	93,105.40
Total Disbursements for 2003	71,698.63	2,325.39b	74,024.02
Assets: December 31, 2003	<u>25,140.06</u>	<u>78,583.62</u>	<u>103,723.68</u>
Net Changes in Funds	6,774.83	12,306.55	19,081.38

a: Annual gain in value of Endowment.

b: Annual loss in value of Endowment.

issue would have been unusually small. Publication was delayed until more manuscripts were ready for publication. A decision was then made to split 117(1) into 117(1) and 117(2), both to be published approximately the same time and very soon. Sternberg acknowledged that the decrease in submissions reported last year finally caught up with us. Furthermore, he noted that the delayed publication of the first issues of volume 117 also was attributable to slower-than-normal production of page proofs and page-proof mailing errors. Issue 117(3) is on track for timely production. The Editor's report was approved by the Council.

Custodian of Publications Storrs Olson reported little activity with back issues but noted that he had filled a few orders. The print run of the *Proceedings* was reduced previously from 1000 to 850 copies, but since membership is 730, the print run could be reduced again, perhaps to 800.

Frank Ferrari noted that the Finance Committee (Stephen Cairns, Oliver Flint, Chad Walter, and Ferrari) had consulted an attorney about tax laws regarding member contributions to the Society. The Finance Committee recommends three categories of gifts: Contributor (\$100–\$499), Sponsor (\$500–\$999), and Benefactor (\$1000 and higher). Donors will receive a letter from the Society that indicates the donor received nothing for his/her contribution, and names of donors will be listed in four consecutive issues of the *Proceedings*. The Committee is currently working on an announcement of the gift-fund categories.

Secretary Baldwin indicated that a vote was needed on a change to Article 8 of the Bylaws proposed last year by the Finance Committee. Regarding the Society's Endowment Fund, the first sentence of Article 8 currently states: "There shall be an Endowment Fund which shall consist of contributions from members, miscellaneous gifts, and surplus funds from operations." The proposed change would remove "and surplus funds from operations," and the amended first sentence would read: "There shall be an Endowment Fund which shall consist of gifts from members and miscellaneous gifts." The proposed change was unanimously approved.

Baldwin also noted that results of the 2004 election of officers could not be announced as usual at the annual meeting because the ballots, which are part of *Proceedings* issue 117(1), have not been mailed. Results of the election will be added as an addendum to these minutes.

President McDiarmid then announced that in hopes of increasing attendance at the annual meetings, he had decided this year to add a program at the conclusion of the annual meeting. Uncharacteristically for Society meetings, the Waldo Schmitt room was nearly full as McDiarmid introduced the scheduled program. McDiarmid remarked that the purpose of the program was to honor Past President Bruce Collette, whose activities in our Society are a reflection of his attitude, activities, and devotion to promoting science. The program began with Division of Fishes ichthyologist David Smith presenting *The Natural History of*

Bruce B. Collette, a talk Dave had written as an introductory talk for a symposium honoring Collette held at the May 2004 meetings of the American Society of Ichthyology and Herpetologists in Norman, Oklahoma. Following Dave's thoughtful and entertaining presentation, Bruce was invited by McDiarmid to speak. Bruce's comments reflected his love of his job and the thrill of being able to work on so many interesting fish groups, such as tunas ("warm-blooded fish!"). At the core of his message was the fact that seeking answers to simple natural history questions, rather than hypothesis testing, had led him to so many years of study and a lot of publications. Bruce concluded with a plea for Society members to work to conserve diversity and habitats. The meeting was adjourned at 12:15 p.m.

Respectfully submitted,
Carole C. Baldwin
Secretary

Addendum to Minutes.—Results of the 2004 election of officers are as follows: President-Elect—W. Ronald Heyer; Secretary—Carole C. Baldwin; Treasurer—T. Chad Walter; Elected Council—Michael D. Carleton, W. Duane Hope, Marilyn Schotte, F. Christian Thompson, Jeffrey T. Williams, and Neal Woodman. Additionally, a proposed amendment to Article 5 was passed. This amendment allows the Council to elect a replacement President-Elect to finish the term if the President-Elect is unable to carry out the duties of office, and then both the President and President-Elect positions are voted on at the next scheduled election.

THE BIOLOGICAL SOCIETY OF WASHINGTON

CONSTITUTION AND BYLAWS

Adopted 3 December 1884
(As amended August 2004)

Article 1. Name

The name of this Society shall be the Biological Society of Washington

Article 2. Purpose

The purpose of this Society shall be for the furtherance of taxonomic study of organisms and for the increase and diffusion of biological knowledge among interested persons.

Article 3. Membership

Membership in this Society shall be open to persons and organizations interested in the promotion of systematic biology. The following classes of members shall be recognized: Associate Members, Active Members, Life Members and Emeritus members. Changes of status of membership may be effected at any time by the payment of appropriate dues. Membership shall become effective upon payment of dues.

Associate Members shall pay annual dues, shall receive notices of meetings and be eligible to vote at meetings of the Society and in ballots by mail.

Active Members shall pay annual dues, shall receive the publications of the Society, shall receive notices of meetings, and shall be eligible to vote at meetings of the Society and in ballots by mail.

Life Members shall be recognized as such by the payment of a fee established by the Council. This fee shall be paid either in one lump sum or in four equal, consecutive annual installments. During their lifetime, Life Members shall receive the publications of the Society, shall receive notices of

meetings and shall be eligible to vote at meetings of the Society and in ballots by mail.

Emeritus Members. Any member who has been an Active or Associate Member may, at the discretion of the Council, be accorded the privileges of Emeritus Membership. These persons shall then be granted the same status as a Life Member.

An organization which is a member may designate a representative who may cast a single vote in its behalf.

Article 4. Dues

Annual dues for Associate and Active Members shall be fixed by the Council and may be changed by the Council.

Article 5. Officers and Elections

The Officers shall be a President, a President-Elect, a Secretary and a Treasurer. The President-Elect shall succeed the President upon the expiration of the latter's term of office. The President-Elect, Secretary, and Treasurer shall be elected for a term of two years by a majority of the members voting by means of a mail ballot. The officers shall take office at the end of the annual business meeting. A slate of candidates shall be prepared by a Nominating Committee appointed by the President. Ballots shall be mailed to all members at the time of billing for annual dues in an election year.

If, for any reason, the President shall be unable to carry out the duties of the office, he/she shall be succeeded by the President-Elect until the Council judges him/her to be competent to resume the duties of the of-

fice. If, for any reason, the President-Elect shall be unable to carry out the duties of office, the Council will elect a replacement to fill the term; both the President and President-Elect positions will be voted on at the next scheduled election. Vacancies in the other offices shall be filled temporarily or until the next election by a majority vote of the Council.

Article 6. Council

The Council shall consist of the President, the President-Elect, the Secretary, the Treasurer, the Chairmen of Standing Committees, the ex-Presidents, and six additional members who shall be nominated by the Nominating Committee and elected at the same time the Officers are elected and have two year terms of office.

The Council shall be the governing body of the Society. It shall be responsible for matters of policy and procedure. It shall meet at the discretion of the President and shall always meet prior to the annual business meeting. It shall receive and act on reports from the Committees of the Society. It shall receive and act on the annual budget prepared by the Finance Committee. It shall fix the time and place of the annual business meeting.

Actions of the Council may be emended at any annual meeting of the Society by a three-fourths vote of the members present. Actions of the Council may be approved or rejected at any annual meeting of the Society by a majority vote of the members present.

The President, with the approval of the Council, shall appoint *ad hoc* committees which shall report to the Council.

Article 7. Meeting

The Society shall hold at least one scheduled meeting each year except in an emergency as decided by a three-fourths vote of the Council members present.

Reports of Standing Committees, the Treasurer, the Auditor, and the Council shall

be presented to the members at the annual meeting.

Should the Council declare an emergency, these reports may be made to the members in printed form. The Council shall install officers in the event there shall be no annual meeting.

Article 8. Publications

The publications of the Society shall be *The Proceedings of the Biological Society of Washington* and any other publication that the Council authorizes. The *Proceedings* shall be managed by an Editorial Committee, consisting of an Editor, who shall serve as Chairman, and not less than three Associate Editors.

Article 9. Bylaws

The Society may enact bylaws which interpret and implement this Constitution. Such bylaws, when approved by the Council, may be adopted, amended, or repealed by a two-thirds majority of those voting at an annual meeting of the Society or in a mail ballot, provided that in either case, notice of the proposed action shall have been sent to each voting member of the Society at least thirty (30) days before the date of the vote.

Article 10. Amendments

This Constitution may be amended by a two-thirds majority of members voting, either at an annual meeting of the Society, or in a mail ballot, provided that in either case notice of the proposed action, when approved by the Council, shall have been sent to each voting member of the Society at least thirty (30) days before the date of the vote.

Article 11. Limitation

The purposes of the Society are listed in Article 2 of the Constitution. Lobbying or activities specifically designed to influence legislation are not among the objectives of

the Society and no official group within the Society shall engage in such activity.

Article 12. General Prohibitions

Notwithstanding any provision of the Constitution or Bylaws which might be susceptible to a contrary construction:

- a. The Biological Society of Washington shall be organized exclusively for scientific and educational purposes;
- b. The Biological Society of Washington shall be operated exclusively for scientific and educational purposes;
- c. No part of the net earnings of the Biological Society of Washington shall or may under any circumstances inure to the benefit of any private shareholder or individual;
- d. No substantial part of the activities of the Biological Society of Washington shall consist of carrying on propaganda, or otherwise attempting to influence legislation;
- e. The Biological Society of Washington shall not participate in, or intervene in (including the publishing or distribution of statements) political campaigns on behalf of any candidate for public office;
- f. The Biological Society of Washington shall not be organized or operated for profit;
- g. The Biological Society of Washington shall not: 1) lend any part of its income or corpus; without the receipt of adequate security and a reasonable rate of interest to; 2) pay any compensation, in excess of a reasonable allowance for salaries or other compensation for personal services actually rendered, to; 3) make any part of its services available on preferential basis, to; 4) make any purchase of securities or any other property, for more than adequate consideration in money or money's worth from; or 6) engage in other transactions which result in substantial diversions of its income or corpus to; any officer, member of the Council, or substantial contributor to the

Biological Society of Washington. The prohibitions contained in this subsection (g) do not imply that the Biological Society of Washington may make such loans, payments, sales or purchases to anyone else, unless such authority be given or implied by any other provisions of the Constitution or Bylaws.

Article 13. Distribution or Dissolution

Upon dissolution of the Biological Society of Washington, the Council shall distribute the assets and accrued income to one or more organizations as determined by the Council, but which organization or organizations shall meet the limitations prescribed in subsections (a)–(g) inclusive, of Article 12, immediately preceding.

BYLAWS

1. **Quorum.** Five Council members shall constitute a quorum at a meeting of the Council.
2. **The Secretary.** The Secretary shall keep minutes of the meetings of the Council and of the Society and shall present a yearly summary to the Society and Council. He/she shall issue notices for the meetings of the Society and the Council, shall notify members of their election, and shall conduct the correspondence of the Society and Council.
3. **The Treasurer.** The Treasurer shall be in charge of the funds and keep the financial records of the Society. He/she shall be authorized by the Council to make necessary disbursements, within the limits set by the budget. The Treasurer shall preserve a receipted bill, or bill and cancelled check for each payment. He/she shall present a statement of financial accounts, audited by the Finance Committee at the time of the annual business meeting.
4. **The President.** The President shall preside at meetings of the Council and of the Society, and perform such other functions that may adhere to the office.

5. The President-Elect. In cases of illness, incapacities, death or absence of the President, the President-Elect shall assume all duties incumbent on the President until the Council judges the President to be competent to resume the duties of the office. In the event of the death of the President, the President-Elect shall automatically become President.

6. Budget. Prior to the annual meeting, a budget for the next year shall be prepared by the Finance Committee and submitted to the Council for action. No financial obligation against the Society may be contracted by any officer or member except as specified in the annual budget or as provided for by special action of the Council upon recommendation of the Finance Committee.

7. Committees. The Society shall maintain the following committees. They shall be provided with such needed financial support, to be designated in the budget, as the funds of the Society may warrant. The chairmen of the standing committees shall be appointed by the President following the annual meeting.

A. The Finance Committee shall consist of the Treasurer and two members to be appointed by the President. The Treasurer shall not serve as the Chairman. It shall prepare the annual budget for submission to the Council and shall advise the Council in all matters affecting the finances of the Society, including

the deposit and investment of funds, endowments, and long-term financial policies.

B. The Editorial Committee shall be composed of the Editor, who shall serve as Chairman, and not less than three Associate Editors. This Committee shall advise the Council on all matters affecting publication. The Editor shall be appointed by the Council. The Associate Editors shall be appointed by the Editor. Terms for the members of the Editorial Committee shall be at the discretion of the Editor.

C. The Membership Committee shall consist of a Chairman and not less than three members and shall be responsible for the Society's effort to increase or maintain the membership. The Chairman shall be appointed by the President, the other members shall be appointed by the President upon recommendation of the Chairman.

8. Endowment Fund. There shall be an Endowment Fund which shall consist of contributions from members and miscellaneous gifts. At the discretion of the Council, the principal of this fund may be used in publishing the Society's journal or for the general operations of the Society. At the discretion of the Council, the principal of this fund may also be used in the publication of symposia, monographic studies, or other special publications; however, such a decision must be reached only during a regularly scheduled meeting of the Council.

PROCEEDINGS
of the
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Washington

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Content.—The *Proceedings of the Biological Society of Washington* publishes original research bearing on systematics in botany, zoology, and paleontology, and notices of business transacted at Society meetings. Except at the direction of the Council, only manuscripts by Society members will be considered. Papers are published in English (except for Latin diagnoses/descriptions of plant taxa), with an Abstract in another language when appropriate.

Submission of manuscripts.—Manuscripts may be submitted in one of three ways. You may mail three paper copies of the manuscript complete with tables, figure captions, and figures (do not submit original figures unless/until the manuscript is accepted for publication) to the Editor, Dr. Richard C. Banks, MRC-116, National Museum of Natural History, P. O. Box 37012, Washington, DC 20013-7012 USA. Manuscripts (in Word or WordPerfect) and figures may be sent on separate computer diskettes or CDs to the same address. For courier delivery, the museum address is 10th and Constitution Ave., NW, Washington, DC 20560 (telephone no. 202-633-0783). Finally, manuscripts and figures may be submitted electronically, as attachments to email, to Banksr@si.edu. Mailing and email addresses of the corresponding author must be clearly indicated. Most communication about the manuscript will be by email.

Presentation.—Requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of such papers. Telegraphic style is recommended for descriptions and diagnoses. The style for the *Proceedings* is detailed in "Guidelines for Manuscripts for Publications of the Biological Society of Washington," a Supplement to vol. 114, no. 4, December 2001. Authors may wish to consult those guidelines before manuscript preparation, but study of articles in recent numbers should be helpful. The establishment of new taxa must conform to the requirements of appropriate international codes of nomenclature. Descriptions of new species-group taxa must cite a type specimen deposited in an institutional collection.

Review.—The Society strives to publish peer-reviewed research results of its members promptly. The Editor evaluates manuscripts for general content and appropriateness and sends them to an Associate Editor, who in turn sends them to at least two referees who are knowledgeable in the particular taxonomic area. Associate Editors may return manuscripts to authors with reviews and suggestions for improvement.

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Publication charges.—The Society is a non-profit organization with limited funds. Depending on available financial resources, the Society may subsidize up to 12 pages per author per year (one author per paper). This 12-page waiver is not automatic with membership, but must be justified in a request to the editor and treasurer when a manuscript is accepted. Even with a waiver, the author will be required to pay full costs of figures, tables, author's changes in proofs, and reprints. Payment of full costs is strongly encouraged and will facilitate speedy publication.

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Bulletins.—The Society publishes appropriate monographic length manuscripts as *Bulletins* on an irregular basis. Please send inquiries about possible *Bulletins* to the Editor.

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