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STORTHYNGURA TORBENI, A NEW SPECIES OF HADAL ISOPOD FROM THE PUERTO RICO TRENCH AND AN HYPOTHESIS ON ITS ORIGIN (CRUSTACEA: EURYCOPIDAE)

Robert Y. George

Abstract.—A new species of deep-sea isopod crustacean, *Storthyngura torbeni,* is described from the floor of the Puerto Rico Trench at depths between 6800 and 8045 meters. Analysis of the diagnostic characters for this ultra-abyssal isopod indicates that the most closely related species occurs in the Antarctic abyss near the South Sandwich Islands. This Antarctic isopod, *S. eltaniae* George and Menzies, 1968b, has a similar pleotelson configuration. On the basis of similarities between these two species, an hypothesis is postulated to derive the origin of the Puerto Rico Trench species from its progenitor *S. eltaniae* from the Antarctic Abyss. Both species inhabit regions of Antarctic bottom water that originates in the Weddell Sea.

Our knowledge of the distribution pattern of animals inhabiting the deep sea is fragmentary because of the lack of adequate sampling in different abyssal regions. Nevertheless, certain groups of organisms are better known, particularly at the generic level. One such example is the deep sea isopod genus *Storthyngura* which is at present known to contain forty species occurring in all oceans except the Mediterranean and the Arctic Ocean (George and Menzies 1968a, b). This study revealed the global distribution pattern of this deep sea genus and also suggested, on the basis of morphological characters, that this isopod genus possibly originated in the Antarctic Ocean.

The question of centers of origin for deep sea animals has been discussed in recent years by several investigators (Madsen 1961, Kussakin 1973, Hessler and Thistle 1975, Thistle and Hessler 1976, Hessler et al. 1979, George 1980). Due to the absence of fossil evidence it is extremely difficult to trace the origin of crustaceans through any given geological scale. However, it is possible to determine the center of origin of the genus from present day species distribution. This paper takes the latter approach and reports upon a genus which shows evidence for possible origin in the Antarctic Ocean.

This study was initiated largely by the excellent collections made in the extreme depths of the Puerto Rico Trench. We encountered the new species of *Storthyngura* for the first time at the Gilliss Deep (George and Higgins 1979). Subsequently, the same species was also captured during the University of Miami expedition to the Milwaukee Deep at the western extremity of the Puerto Rico Trench. In addition, a recent Russian expedition aboard Akad. *Kurchatov* also collected 38 specimens of this ultra-abyssal species from the Brownson Deep of the Puerto Rico Trench. In this paper, I present a diagnosis and description of the new species with illustrations of important taxonomic features. I also postulate that the movement of the Antarctic Bottom Water

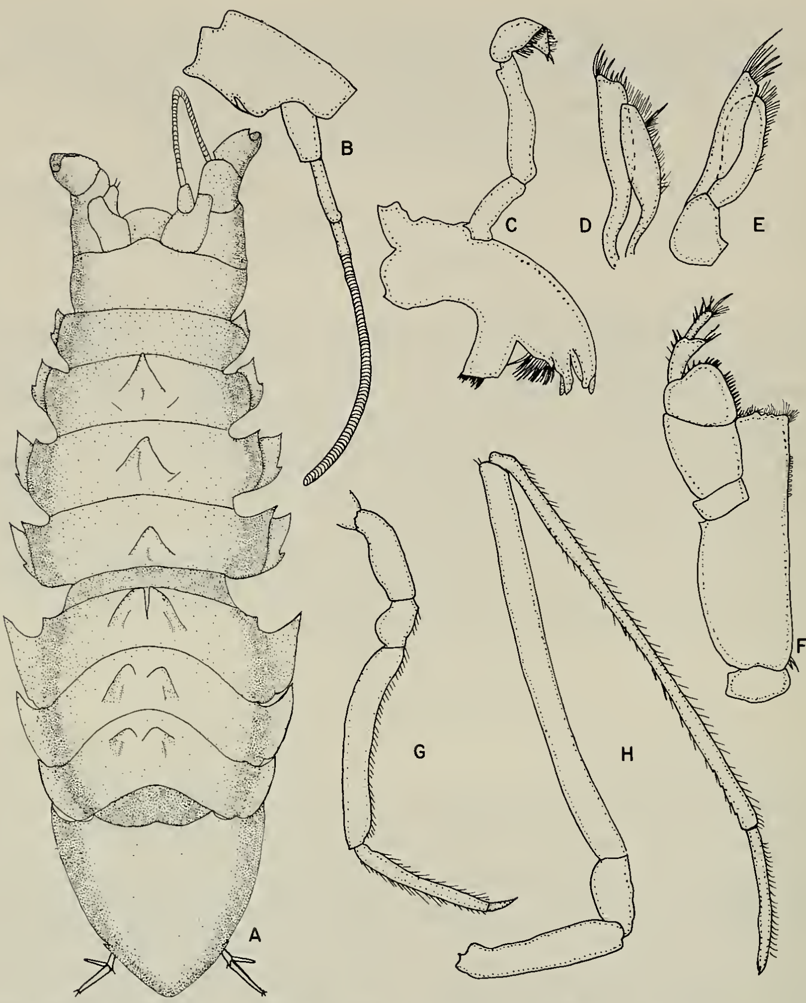

Fig. 1. *Storthyngura torbeni,* holotype male, length 19 mm: A, Dorsal view; B, First antenna; C, Mandible; D, Maxillule; E, Maxilla; F, Maxilliped; G, First peraeopod; H, Second peraeopod.

has significantly contributed to the evolution of this genus from its origin in the Antarctic Ocean.

Storthyngura torbeni, new species
Figs. 1, 2

Material.—Holotype male: length 19 mm, width 8 mm. Allotype female: length 22 mm, width 9 mm.

Type locality.—Milwaukee Deep of the Puerto Rico Trench. *Pillsbury* sta 1406, 19°31.8′N, 68°07.5′W, 7850–7810 m, 17 Jul 1971. Holotype male USNM 231361, allotype female USNM 231362. In addition to the *Pillsbury* collection, *S. torbeni* was also collected from the Gilliss Deep of the Puerto Rico Trench: *Gilliss* sta 24, 19°24.5′N, 66°19.7′W, 8045 m, 18 Jul 1976, 2 male specimens 20 mm long. During the Soviet expedition to the Puerto Rico Trench, *S. torbeni* was collected from Akad. *Kurchatov* sta 1182, 42 specimens (27 males, 12 females, 3 juveniles and 4 fragments), 19°53′N, 68°11′W, 6400 m, 3 Feb 1973, and Akad. *Kurchatov* sta 1194, 19°49′N, 68°08′W, 6800–7030 m, 9 Feb 1973, 11 specimens (3 males, 7 females and 1 juve-

Fig. 2. *Storthyngura torbeni,* holotype male, length 19 mm: A, Third peraeopod; B, Fifth peraeopod (dactyl broken); C, Sixth peraeopod; D, Seventh peraeopod; E-1, Male first pleopod; E-2, Distal edge of first pleopod; F, Second pleopod; G, Uropod.

nile). The *Kurchatov* specimens are deposited in the Universitets Zoologiske Museum in Copehagen, Denmark.

Diagnosis.—*Storthyngura* with cephalon totally devoid of any spines on dorsal surface. First peraeonal somite lacking dorsal spines; somites 2 to 4 each with single dorsal spine; somites 5 to 7 each with pair of median dorsal spines. Pleonal somite present, without dorsal spine. Pleotelson lacking lateral spines, apex somewhat rounded. Pleotelson with smooth dorsal surface, lacking spines or tubercles. Basis of uropod longer than endopod; exopod about one-half length and width of endopod.

Etymology.—This new species is named in honor of the isopodologist, Dr. Torben Wolff, who graciously loaned me the *Kurchatov* collections of this species for study.

Description.—General body shape oval, about 2 times longer than wide. Cephalon smooth, lateral margin slightly concave, frontal margin not truncated.

First pereonal somite lacking spines. Anterolateral margin rounded, coxal plate small and bilobed. Second pereonal somite with prominent median spine, anterolateral margin rounded. Coxal plates well developed, bilobed with anterior lobe produced. Third and fourth somites each with large median spine; anterolateral margin acutely produced, coxal plates prominent and bilobed. Somites 5 to 7 with paired median spines; anterolateral margin with minute tubercles. Anterolateral margin acutely produced, coxal plates lacking.

Pleon with short, flat anterior pleonal somite which smooth and lacking spines; pleotelson shieldlike. Anterolateral angle of pleotelson produced into sharp spine exhibiting minute tubercle at anterolateral angle. Lateral margin entire with indication of fused posterior lateral spine; telsonic apex slightly rounded. Pleotelson smooth, devoid of spines or tubercles.

First antenna with broad basal article with prominent spine on inner margin. Peduncle composed of 1 broad basal article; 3 narrow and elongate terminal articles; flagellum annulated, composed of more than 50 minute articles. Second antenna with basal article broad and lacking marginal spines. Mandible with well developed palp of 3 articles; second article twice as long as first; third article deflected upward into cuplike configuration, inner margin furnished with dense row of setae. Cutting face well developed with prominent truncate molar and middle row of approximately 21 movable spines. Incisor process tridentate; lacinia mobilis robust and bidentate.

Maxillule with inner lobe broad and setose, outer lobe narrow with terminal spines. Inner lobe of first maxilla with dense setae. Maxilliped with 9 coupling hooks on endite; palp with short and broad basal article, second and third articles somewhat enlarged; fourth article distally produced, terminal article narrow with tuft of apical setae.

First peraeopod with short dactylus; propodus narrow and shorter than carpus; merus short and broad; ischium about twice as long as merus.

Second and third peraeopods twice as long as first; dactylus long. Both propodus and carpus elongate. Merus short; ischium more than twice as long as merus. Peraeopods 5–7 very similar with propodus and carpus expanded into paddle-like configuration with dense marginal plumose setae. Dactylus relatively long and narrow.

First male pleopod broadening distally into somewhat truncated apex with distinct left and right divisions; each division showing 3 discrete lobes, with exterior lobes having triangular spine. Second male pleopod with well developed copulatory organ.

Uropod with basis longer than endopod; exopod one-half length and width of endopod.

Affinities.—In general shape, *S. novaezelandiae* (Beddard 1885), from 2012 meters in the southwest Pacific is somewhat similar but has a conspicuous process on the exterior margin of the second segment of antenna 1 and lacks dorsal spines on peraeonal somites 3–5. Amongst all known species of *Storthyngura,* only *S. eltaniae* and *S. intermedia* have a simple pleotelson configuration that resembles the general shape of the pleotelson in species of the confamilial genus *Eurycope. Storthyngura intermedia* was originally described by Beddard (1885) on the basis of deepsea specimens captured during the expedition from 5011 meters in the North Pacific. *Storthyngura eltaniae* was described originally by George and Menzies (1968a) from specimens captured off the South Sandwich Islands in the Antarctic ocean at 5449 meters. The new species, *S. torbeni,* also has a simple pleonal configuration without any well developed lateral spines as found in all other *Storthyngura* species. However, this new species differs from *S. intermedia* in that *S. torbeni* lacks the spines both on the cephalon and the first peraeonal somite that are found in *S. intermedia.* These two species have a smooth pleotelson without any dorsal spines or tubercles. However, the most closely related species to *S. torbeni* is *S. eltaniae.* These two species are also related by the absence of dorsal spines on the first peraeonal somite. The major morphological difference is that *S. torbeni* does not have any spines on the cephalon while *S. eltaniae* has a pronounced spine on the cephalon. In addition, *S. eltaniae* has an anterior spine and a pair of posterior tubercles on the pleotelson; these characters are not found in the Puerto Rico Trench species, *S. torbeni.*

Hypothesis on the Origin of *Storthyngura torbeni*

The genus *Storthyngura* belongs to the family Eurycopidae which includes both shallow and deepsea species. However, most of the eurycopid shallow-water species tend to occur in the cold waters of the high latitudes. Species belonging to the genus *Storthyngura* are exclusively found in the deep sea and in trenches at ultra-abyssal depth. George and Menzies (1968b) presented evidenced that the Antarctic Ocean is the center of origin for *Storthyngura.* This conclusion was based on the prolific presence of species belonging to the five morphological clusters that are represented in the Antarctic Ocean. This genus has also successfully colonized the major trenches of the Northwest Pacific Ocean (Birstein 1963) and also the Peru-Chile Trench of the Southeast Pacific Ocean (Menzies and George 1972). This paper reports that the genus *Storthyngura* has colonized depths exceeding 8000 meters in the Puerto Rico Trench, North Atlantic Ocean. I believe that this evolutionary process of colonization into the Puerto Rico Trench was somehow associated with the flow of the Antarctic Bottom Water into the trench. The Antarctic Bottom Water possibly originated during the miocene glaciation in the Antarctic Ocean. This hypothesis is further supported by the fact that the most closely related species to *S. torbeni, S. eltaniae* is found in the Antarctic Ocean; both species also possess a primitive plesiomorphic pleotelson configuration. From an evolutionary point of view, the question of colonization of the deepsea environment, particularly the ultra-abyssal trenches, is certainly an intriguing problem that calls for further studies.

Acknowledgments

I wish to thank the National Science Foundation, the Office of Naval Research and the University of Miami for sponsoring the R/V *Gilliss* expedition to the Gilliss Deep of the Puerto Rico Trench in 1976. I also thank Dr. Gilbert Voss for graciously providing *Storthyngura* specimens from the 1971 *Pillsbury* collections, obtained under the sponsorship of the National Geographic Society and the University of Miami Deep Sea Biology Program, in the Milwaukee Deep of the Puerto Rico Trench. I am also grateful to Dr. Torben Wolff of the Copenhagen Museum for generously giving me the *Storthyngura* specimens collected during the 1973 Russian Expedition of Akad. *Kurchatov* to the Puerto Rico Trench.

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PARAEUPOLYMNIA, A NEW GENUS OF TEREBELLID (POLYCHAETA: TEREBELLIDAE) FROM BELIZE

Martha W. Young and Henry Kritzler

Abstract.—A new genus of terebellid, *Paraeupolymnia,* and species, *P. carus,* collected by the senior author in Belize are described.

Paraeupolymnia, new genus

Type species.—*Paraeupolymnia carus,* new species.

Diagnosis.—The genus *Paraeupolymnia,* placed in the subfamily *Amphitritinae,* is characterized by the virtual absence of ventral glandular scutes, by lateral lappets only on the second segment, by thoracic setigers bearing smooth-tipped winged capillaries on segments 3 through 19, by avicular uncini without long basal shafts in single rows on setigers 2 through 7, in double rows face to face on setigers 8 through 17, and single rows throughout the abdomen, and by a pair of dichotomously branched gills on both segments 2 and 3. The new genus is erected on the ground that, although it resembles *Eupolymnia* Verrill, 1900, in some respects, it differs in several important characters, most particularly in that all of the undamaged specimens examined by us have two pairs of gills, not three as in *Eupolymnia.*

Paraeupolymnia carus, new species
Fig. 1

Material examined.—Caribbean Sea off Belize, main channel separating the two mangrove islands constituting the Twin Cays, 16°50′N, 88°06′W, 2¼ m, 9 Mar 1984, coll. D. K. and M. W. Young. Holotype, USNM 098908, 2 paratypes, USNM 098909, many others in the collections of the senior author.

Description.—The holotype, a complete specimen with 19 thoracic and about 30 abdominal segments, is 11 mm long and about 1 mm wide. The tentacular lobe consists of a low semicircular dorsal flap and a collar that encircles the mouth. It bears two dorsolateral clusters of 4 to 6 grooved tentacles (Fig. 1A). A row of eyespots is situated at the base of each group of tentacles. The latter have numerous single and paired pigment spots. The second segment bears prominent lateral lappets. From its dorsal anterior edge arises the first pair of quite regularly dichotomously branched gills. The second pair is similarly situated on the third segment. The anterior pair is larger and has up to 4 or 5 levels of dichotomous branching. The posterior, smaller pair has fewer, not more than 3. A pair of nephrostomes is situated on both segments 3 and 4, dorsal to the notopodia. There are no distinct ventral glandular scutes (Fig. 1B). Narrow-winged, smooth-tipped capillary setae are borne on small, undistinguished notopodia on segments 3 through 19. The wings have diagonal striations visible under oil (Fig. 1C). Avicular uncini, none of which have long basal shafts, appear in single rows on setigers 2 through 7, in double rows face to face on setigers 8 through 17 (Fig. 1F). Uncini continue in single rows on well-developed tori throughout the abdomen (Fig. 1G). Each torus bears a low cirrus and, especially toward the posterior, prominent suspensory ligaments. The thoracic uncini have a single tooth surmounted by a row of 3 to 5 denticles, above the main fang (dental formula MF: 1: 3–5) (Fig. 1D–F). The abdominal uncini are variable, the dental formula being mainly as in the thorax but, occasionally in

Fig. 1. *Paraeupolymnia carus,* holotype. A, Anterior end, dorsal view; B, Anterior end, ventral view; C, Capillary seta; D, Thoracic uncinus, lateral view; E, Thoracic uncinus, frontal view; F, Uncini, eighth thoracic setiger; G, Uncini, second abdominal segment; H, Uncinigerous torus, twenty-seventh abdominal segment.

the same row and increasingly toward the posterior, they read MF: 2: 4–6 or MF: 3: 5–6 (Fig. 1G, H).

The anus is terminal on a low eminence devoid of distinguishing characteristics.

The foregoing description applies equally well to the paratypes and to virtually all of the other specimens examined by us.

Biology.—Paraeupolymnia carus lives in mucus tubes adorned with miscellaneous debris and attached to the blades of turtle grass (*Thalassia testudinum*) growing in a mixture of coarse and fine mainly calcareous sediment with varying amounts of mangrove detritus. It is associated with a species-rich benthic assemblage. Its population constitutes a conspicuous portion of the seagrass epibenthos in the Twin Cays mangrove habitat. Of 47 individuals from one station, which ranged from 2.5 to 11 mm in length and from which the holotype and the paratypes were segregated, there were 36 with two pairs of gills and 11 with fewer. All of the latter were small and appear to have been damaged by sieving or by removal from tubes. Several of the larger specimens, including one of the paratypes, have eggs in the abdominal cavity, suggesting that 11 mm represents the length of an adult specimen.

Etymology.—The generic name combines *Para* (Greek like or resembling) with *Eupolymnia* Verrill, 1900. The specific name is given in honor of David K. Young, husband of the senior author, in appreciation of his having introduced her to the polychaetes (David, Hebrew, beloved = *carus,* Latin).

Remarks.—Using Fauchald's (1977:128) key to the genera of the Terebellidae, these specimens would invariably key out to *Eupolymnia* Verrill, 1900, were it not for the number of gills. Although the dental formula of the thoracic uncini closely resembles that of *E. nesidensis* (Delle Chiaje, 1828) and *E.* sp. B. Kritzler, 1984, other significant differences also rule out identification of these specimens with *Eupolymnia.* These are: a, the first appearance of notopodia and setae on the third segment and uncini on the fourth; b, the virtual absence of lateral lappets on segments 3 and 4; c, the absence of ventral glandular scutes, all of which are at variance with the diagnosis of *Eupolymnia.* Some authors hold that a genus of terebellids may contain species with one, two, or three pairs of gills, a position which makes difficult, not to say impossible, the erection of a key such as Fauchald's (1977) and creates a state of confusion for ecologists and other field workers attempting to identify the specimens in their collections.

The large number of specimens in an excellent state of preservation makes it clear that the consistent number of branchiae is indeed a key character setting *Paraeupolymnia* apart from *Eupolymnia* and other terebellid genera. All of the specimens that have been examined by us had to be removed from their tubes, a process that may have caused the loss of one or more gills from very small specimens, but definitely assured us that none had more than two pairs of branchiae. The character does not vary nor does that of having three pairs of gills in *Eupolymnia,* thereby giving us confidence in erecting the new genus *Paraeupolymnia.*

Acknowledgments

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NICOYA TUBERCULATA, A NEW GENUS AND SPECIES OF SPIDER CRAB FROM PACIFIC COSTA RICA (MAJIDAE: PISINAE)

Mary K. Wicksten

Abstract.—A new genus and species of spider crab (Majidae: Pisinae) has been collected in the Gulf of Nicoya, Costa Rica. The small crab resembles species of the genus *Pelia,* but differs in having a highly tuberculate carapace, broad meri of the walking legs, and a third maxilliped without a deep notch at the anteroexternal angle of the merus.

While sorting collections of crabs taken off El Salvador and Costa Rica, Dennis Moran of the Unviersity of Costa Rica found a specimen of an unidentified majid spider crab. The specimen was sent to me for identification. The crab, which does not quite match the description of any known genus or species, is described herein.

Nicoya, new genus

Description.—Carapace pyriform, convex, with pronounced tubercles. Rostrum well developed, with 2 rostral horns, united at their base, more or less parallel. Basal antennal article with tuberculate external margin, forming incomplete flooring to orbit, protruding beyond orbital margin and appearing at sides of rostrum. Movable flagellum long. Eye retractile into hollow fossette at base of tubercle limiting hepatic region in front. Merus of external maxilliped barely indented at anterointernal angle to receive palp.

Chelipeds feeble in female, fingers closing tightly, arm without crest. First pair of ambulatory legs slightly longer than following legs, fifth short; second–fourth walking legs robust and with broad meri.

Abdomen of female of 7 well-defined segments.

Remarks.—The new genus differs from species of *Pelia* in having a highly tuberculate carapace, lacking a notch in the external maxilliped in the region of the insertion of the palp, and having broad meri of the posterior walking legs. Unlike many common species of *Pelia,* the new species of crab lacked a coating of encrusting sponge. Having eyes with commencing orbits, short eyestalks, a broad basal antennal article and external maxillipeds with broad meri, the new genus readily fits into the subfamily Pisinae as defined by Garth (1958).

Etymology.—The name of the genus refers to the Gulf of Nicoya, Costa Rica, where the sole specimen was collected. Gender feminine.

Nicoya tuberculata, new species
Fig. 1

Description.—Carapace pyriform, convex, regions separated by shallow depressions; with pronounced tubercules: series running along anterior midline from rostrum to gastric region, patches on gastric, cardiac and intestinal regions, and extensive series on branchial regions and lateral margins. Rostrum about 0.1 × carapace length, horizontal with sides slightly sinuous, teeth denticulate and bearing hooked setae, intervening sinus sharply V-shaped. No preorbital tooth. Postorbital tooth broad, set off from orbital margin by narrow fissure, anterior margin slightly convex and

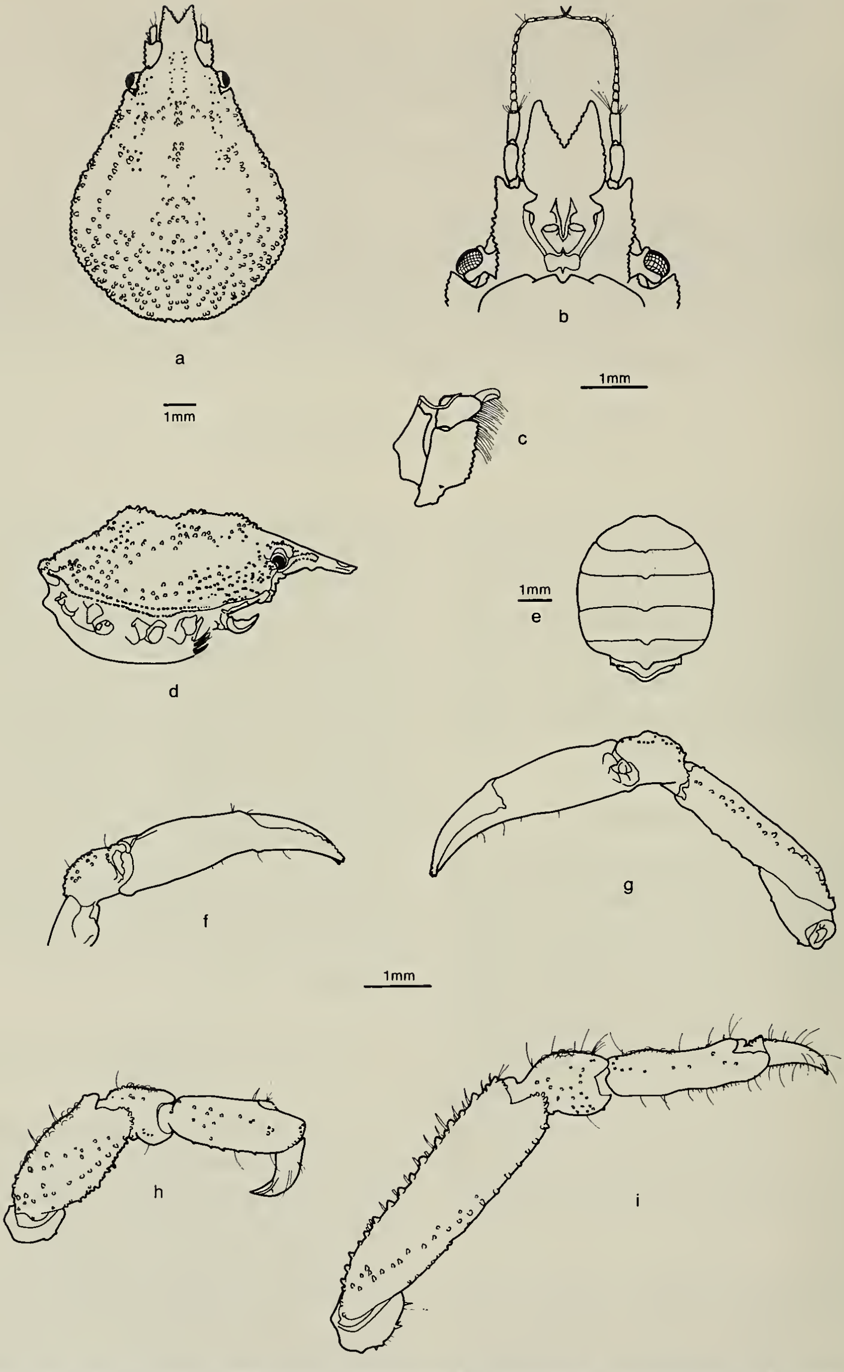

Fig. 1. *Nicoya tuberculata*: a, Carapace in dorsal view; b, Frontal region; c, External maxilliped; d, Body in lateral view; e, Abdomen; f, Chela; g, Cheliped; h, Fifth walking leg; i, First walking leg.

smooth, lateral margin denticulate. Patches of tubercles on gastric, cardiac, hepatic, intestinal, and branchial regions as well as on posterior margin, becoming most dense posteriorly. No posterolateral marginal ridge.

Basal antennal article smooth, mesial margin concave, with terminal knob; external margin tuberculate and ending in tooth, entire article just reaching beyond base of rostrum. Antennal flagellum long, greatly exceeding end of rostrum.

Eyes with commencing orbits. Small tubercles on eyestalk near cornea.

Ischium of third maxilliped somewhat rectangular, notched at anterior end, mesial margin serrate. Merus somewhat triangular, mesial margin serrate. Setose palp present. Pterygostomian regions with rows of tubercles.

Cheliped slender, fingers of chela closing tightly, with teeth. Carpus and merus tuberculate. Ischium with few spinules. Walking legs with strongly hooked dactyls; propodi, carpi, and meri tuberculate, carinate, with pile and scattered coarse setae and hooked setae. First walking leg longest, with merus 4 × long as broad. Posterior walking legs shorter, with meri 2 × long as wide.

Female abdomen with raised mesial ridge, without spines or tubercles, with 7 well-defined segments.

Holotype.—Female, ovigerous. Carapace length 7.4 mm, width 5.8 mm, chela 3.2 mm. Gulf of Nicoya (about 10°N, 85°W), 48 m, 23 Apr 1981, University of Costa Rica catalogue number 1043.

Remarks.—Species of the closely related genus *Pelia* are common on hard bottoms, ranging from California to Peru in the eastern Pacific and Massachusetts to Patagonia in the Atlantic (Garth 1958). *Nicoya tuberculata* seems to be closely related to *Pelia*, perhaps diverging from a common pisinine ancestor. The specific epithet refers to the tubercles of the carapace, which distinguish the new species from species of *Pelia*.

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ATTHEYELLA (*MRAZEKIELLA*) *SPINIPES*, A NEW HARPACTICOID COPEPOD (CRUSTACEA) FROM ROCK CREEK REGIONAL PARK, MARYLAND

Janet W. Reid

Abstract.—A collection from a spring in Rock Creek Regional Park, Maryland, near the boundary of the District of Columbia yielded the cyclopoid copepods *Macrocyclops albidus* (Jurine) and *Eucyclops agilis* (Koch), and the harpacticoid copepods *Attheyella* (*Mrazekiella*) *illinoisensis* (S. A. Forbes) and *A.* (*M.*) *spinipes,* new species. *Attheyella spinipes* is described and some comments made on morphological features of *A. illinoisensis.*

In a collection of aquatic invertebrates made by Mr. William B. Yeaman and Mr. Stephen W. Syphax of the National Park Service from a spring in Rock Creek Regional Park and brought for determination to Dr. Thomas E. Bowman, Department of Invertebrate Zoology, National Museum of Natural History, were four species of copepods (Crustacea). In order of abundance these were the cyclopoids *Eucyclops agilis* (Koch) and *Macrocyclops albidus* (Jurine), and the harpacticoids *Attheyella* (*Mrazekiella*) *spinipes,* new species, and *A.* (*M.*) *illinoisensis* (S. A. Forbes). *Attheyella spinipes* is described below, together with some comments on the morphology of *A. illinoisensis.*

This collection doubles the number of species of Copepoda recorded from the drainage basin of Rock Creek, an affluent of the Potomac River. The creek and part of its basin are included in Rock Creek National Park in the District of Columbia and its extension, Rock Creek Regional Park in Montgomery County, Maryland. Bowman (1967) recorded the cyclopoids *Cyclops exilis* Coker and *Paracyclops fimbriatus* (Fischer) and the harpacticoid *Bryocamptus zschokkei alleganensis* Coker from a spring-fed pool in the District of Columbia portion of the park. The eurytopic harpacticoid *Phyllognathopus viguieri* (Maupas) was reported by Reid (1985) from a compost heap at T. E. Bowman's residence, located near Turkey Branch in the Montgomery County section.

Attheyella (*Mrazekiella*) *spinipes,* new species
Figs. 1–22

Material.—Holotype: ♀, alcohol-preserved, National Museum of Natural History, USNM 232035. Allotype: ♂, alcohol-preserved, USNM 232036. Paratypes: 2 ♀ and 1 ♂, dissected on slides; and 3 ♀, 2 ♂ and 1 copepodite, alcohol-preserved, USNM 232037. All collected 8 Aug 1986 by W. B. Yeaman and S. W. Syphax from covered perennial spring at southeast corner of Maryland Maintenance Facility, Rock Creek Regional Park, Montgomery County, Maryland, approximately 100 m west of boundary with Washington, D.C., 38°59′16″N, 77°03′18″W. Spring is located on approximate border of 100-year flood plain, about 60 m north of Rock Creek.

Description.—Female: Length of holotype excluding caudal setae 0.73 mm; range of lengths of paratypes 0.54–0.66 mm. (Description is a composite of several specimens.) All somites except anal somite with serrate posterior margins (Figs. 1–4); cephalosome with oval nuchal organ. Genital segment and succeeding 2 somites each with row of spinules near posteroventral margin, this row discontinuous on somite 2. Genital field (Figs. 3, 5) extending to anterior third of segment. Anal somite (Figs. 1, 3, 4) with small spinules on posteroventral border and 1 larger spinule anterior to each caudal ramus on ventral surface; and with crescentic row of short hairs on dorsal surface anterior to each ramus. Anal operculum convex, margin with many spinules. Caudal rami (Figs. 1, 3, 4) slightly divergent, 2.4 × broader than long, each with dorsal keel on anterior ¼ which ends in dorsally directed seta. Posterior ¼ of dorsal surface of ramus with group of irregularly arranged spinules. Lateral surface of ramus with 2 setae inserted slightly anterior to midlength and in some specimens, also with few spinules anterior and dorsal to these setae; seta also at distolateral corner. Anterior half of medial surface of ramus with hairs and spinules, arranged irregularly (Fig. 3) or in groups (Fig. 4), some hairs extending to middle of ventral surface (Fig. 3). Outer terminal seta stout, ¾ length of ramus; inner terminal seta very fine, half length of outer terminal seta. Middle terminal seta about ⅔ length of body.

Rostrum (Fig. 2) indistinctly separated from cephalosome, blunt, shorter than antennule article 1. Antennule (Fig. 6) of 8 articles, articles 4 and 8 each with long slender esthetasc. Antenna (Fig. 7) with allobasis; single article of exopod with 4 setae. Mandible, maxillula and maxilla as in Figs. 8–10; maxilliped (Fig. 11) prehensile.

Swimming legs 1–4 (Figs. 12–15) each with exopod and endopod of 3 articles, except endopod of leg 4 which is of 2 articles. Setation formula for major armament as follows:

Leg 1	basis 1-1	exp 0-1; 1-1; 0,2,1
		enp 1-0; 1-0; 1,2,0
Leg 2	basis 0-1	exp 0-1; 1-1; 1,2,3
		enp 1-0; 1-0; 2,1,1
Leg 3	basis 0-1	exp 0-1; 1-1; 2,2,3
		enp 1-0; 1-0; 2,2,1
Leg 4	basis 0-1	exp 0-1; 1-1; 2,2,3
		enp 1-0; 3,2,0

Setae of basipods of legs 1 and 2 and all setae of exopods and endopods of legs 2–4 spiniform; some having heteronomous setules and spinules.

Leg 5 (Fig. 16) with inner expansion of basipod reaching about ¼ length of exopod and bearing 5 spines of which middle spine very short; few hairs on medial and anterior surfaces. Exopod about 3 × longer than broad, with groups of hairs on medial and lateral margins, and bearing 5 spines of which next innermost longest. Leg 6 (Fig. 5) consisting of 2 slender plumose setae.

Male: Length of holotype excluding caudal setae 0.44 mm; range of lengths of paratypes 0.45–0.46 mm. Nuchal organ and urosomal armament as in female, except ventral spine rows on urosomites 2–4 continuous. Caudal ramus (Fig. 17) much as in female, except with fewer spinules dorsally. Antennule (Fig. 18) of 8 articles, geniculate, with spines on articles 4 and 5 and slender esthetascs on articles 4 and 8. Antenna, mouthparts, and legs 1 and 2 as in female. Leg 3, exopod as in female with lateral spines not greatly enlarged; endopod (Fig. 19) of 3 articles, article 1 with stout inner seta, article 2 with slender apophysis lacking terminal barb, article 3 ending in 2 slender setae. Leg 4, exopod as in female, endopod article 2 (Fig. 20) with 3 spines and 2 slender terminal setae.

Leg 5 (Fig. 21), basipods fused, inner portion of each basipod little expanded, with stout inner and small outer spine; exopod much as in female except spines, particularly innermost spine, relatively stouter. One specimen with 2 spines on one basipod and 1 spine on other. Leg 6 (Fig. 22) consisting of 1 stout medial spine, 1 small middle spine and 1 slender lateral seta.

Etymology.—From L. "spiny-foot," referring to the spiniform setae of the swimming legs; proposed as a noun in apposition.

Relationships.—*Attheyella spinipes* keys


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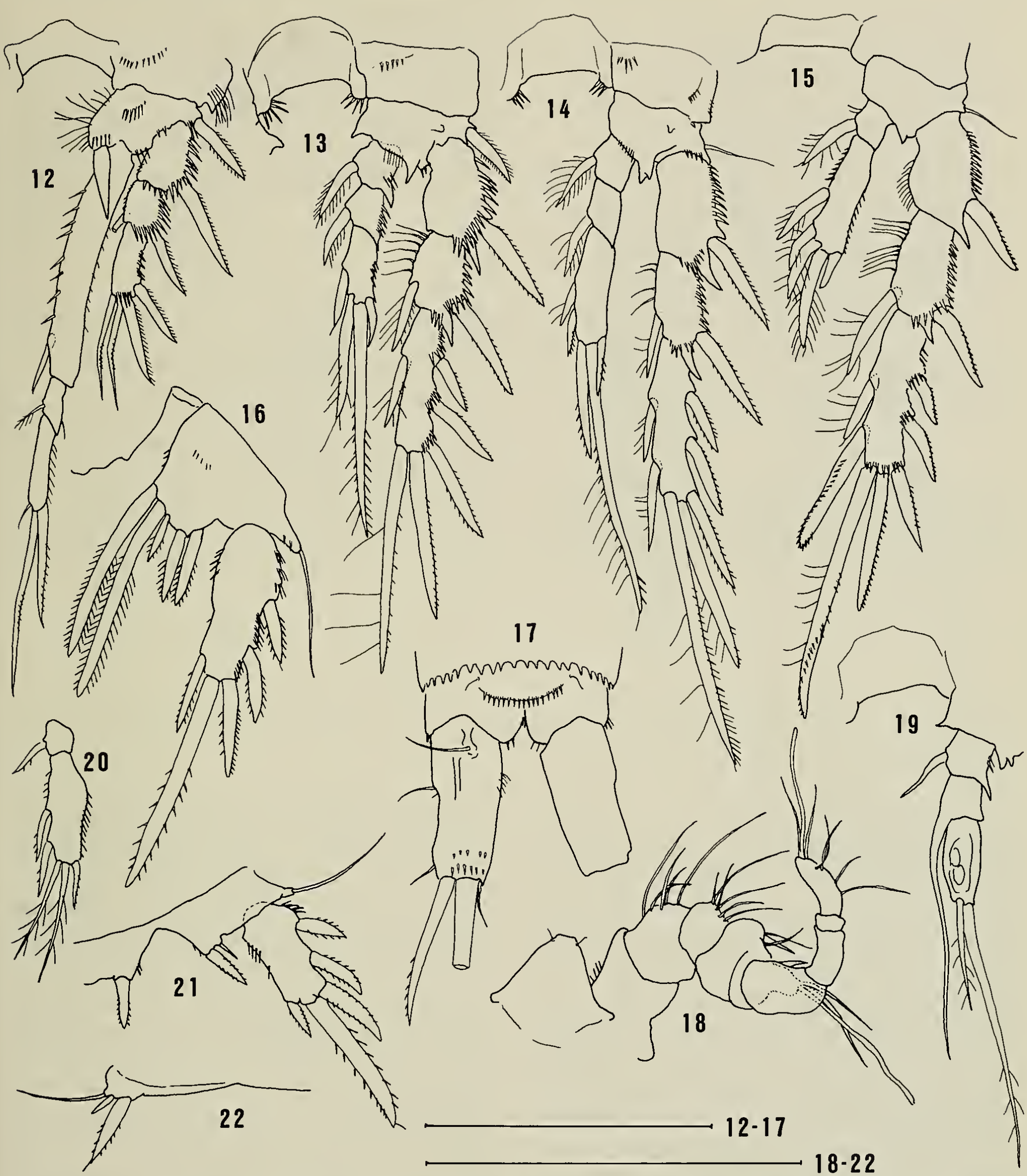

Figs. 12–22. *Attheyella* (*Mrazekiella*) *spinipes*, new species. 12–16, Female: 12, Leg 1; 13, Leg 2; 14, Leg 3; 15, Leg 4; 16, Leg 5. 17–22, Male: 17, Caudal rami and anal somite, dorsal; 18, Rostrum and antennule; 19, Leg 3, endopod; 20, Leg 4, endopod; 21, Leg 5; 22, Leg 6. Scales = 100 μm.

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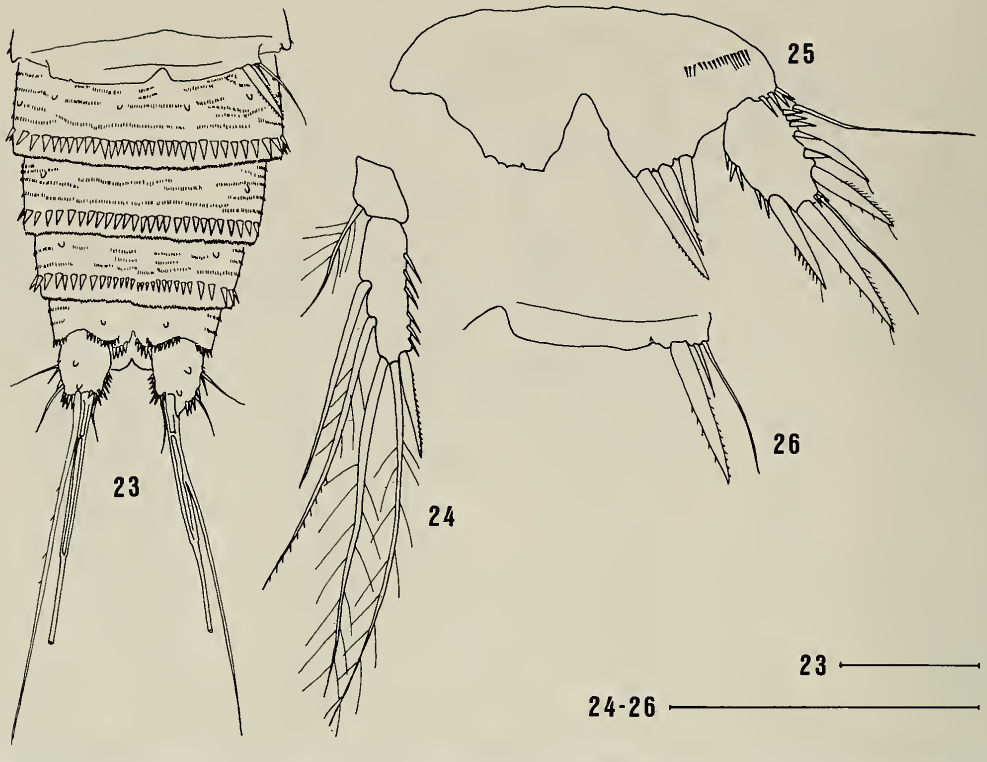
Figs. 1–11. *Attheyella* (*Mrazekiella*) *spinipes*, new species, female: 1, Habitus, lateral; 2, Cephalosome, dorsal, showing nuchal organ; 3, Urosome, ventral; 4, Caudal ramus and anal somite of a second female, dorsal; 5, Genital field and leg 6; 6, Antennule; 7, Antenna; 8, Mandible; 9, Maxillula; 10, Maxilla; 11, Maxilliped. Scales = 100 μm.



Figs. 23–26. *Attheyella* (*Mrazekiella*) *illinoisensis* (S. A. Forbes), male: 23, Urosome, ventral; 24, Leg 4, endopod; 25, Leg 5; 26, Leg 6. Scales = 100 μm.

to the *A. pilosa*/*A. carolinensis* couplet in Wilson and Yeatman's key to North American Harpacticoida (1958). It is similar to these two species, redescribed and compared by Bowman et al. (1968), in having caudal rami about 2.5–3× longer than broad. *Attheyella spinipes* differs most obviously in having fewer hairs and spinules on the somites and caudal rami; endopods of legs 2 and 3 of 3, not 2 articles; and in the spiniform setae of legs 2–4. In addition, the female of *A. carolinensis* has 4, not 5 setae on the basipod of leg 5. Neither *A. carolinensis* nor *A. pilosa* has been recorded from Maryland nor from the Virginia piedmont (Bowman et al. 1968).

Attheyella (*Mrazekiella*) *illinoisensis*
(S. A. Forbes, 1882)
Figs. 23–26

Inspection of the single male of this species in the collection revealed some slight morphological differences from Coker's redescription (1934) as well as some possible errors in Coker's figures. Coker did not mention rounded papillae on the ventral surface of the urosome, though his Text-Fig. 4 shows 2 on the female anal somite and 2 on each caudal ramus. The male from Rock Creek has 2–6 papillae on each urosomite and 2 on each caudal ramus (Fig. 23). Coker's figure for article 2 of the endopod of leg 4 of the male shows 4 setae and a short outer subterminal spinule; the Rock Creek male has 4 setae and a moderately long subterminal spine (Fig. 24), and therefore the correct spine formula for the endopod is probably 1–0; 221. There is a row of spinules on the anterior surface of the basipod of leg 5 (Fig. 25), a feature not mentioned by Coker. Finally, Coker's figure for leg 6 shows only 2 long setae. Since the Rock Creek specimen has 1 long and 1 short seta and a stout inner spine (Fig. 26), and Pearse (1905) figured a leg 6 with 2 setae and a stout inner spine, all of equal length, it is probable that Coker's specimen was simply missing the inner spine. None of these variations has significance at the species level; Coker (1934) particularly called attention to morphological variability in this widespread and common species.

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ANTARCTIC RECORDS OF ASTEROID-INFESTING ASCOTHORACIDA (CRUSTACEA), INCLUDING A NEW GENUS OF CTENOSCULIDAE

Mark J. Grygier

Abstract.—The following Ascothoracida parasitizing Antarctic asteroids are described and illustrated: an immature female *Dendrogaster* sp. cf. *antarctica* Grygier, and females and brooded offspring of *Gongylophysema asetosum,* new genus and species, all parasitic in *Odontaster validus* Koehler; several females and males of *D. usarporum,* new species, from *Porania antarctica glabra* Sladen. Females of both species of *Dendrogaster* have setose thoracopods, a new morphological feature for this genus. *Gongylophysema* is the most apomorphic genus of the Ctenosculidae and has numerous similarities witih the dendrogastrid genus *Ulophysema.* Its embryological development omits the nauplius, and the ascothoracid larva's medial penis originates as paired embryonic limb buds, a finding with implications for the entire Ascothoracida and Cirripedia. The sexes are separate by ascothoracid larva I. The opportunity is also taken to identify tentatively an historically enigmatic parasite of a Canadian brisingid asteroid as a ctenosculid ascothoracidan.

Ascothoracidans of the order Dendrogastrida are all crustaceans that parasitize echinoderms. Two members of this group have been described from Antarctica, *Dendrogaster antarctica* Grygier, 1980, a coelomic parasite of the asteroid *Acodontaster conspicuus* Koehler in McMurdo Sound, and *Ascothorax gigas* Wagin, 1968, a bursal parasite of the large ophiuroid *Ophionotus victoriae* Bell along the Antarctic Peninsula (and in the South Sandwich Islands) (Grygier 1981b, Grygier and Fratt 1984). Also, A. M. Clark (1962, 1977) mentioned an ascothoracidan, apparently a member of the family Ctenosculidae, in the asteroid *Acodontaster hodgsoni* forma *stellatus* (Koehler) from off MacRobertson Land. New records of *Dendrogaster* from two Antarctic asteroids are given in the present report as well as a new dendrogastridan genus, here assigned to the Ctenosculidae, from one of these same asteroids.

Class Maxillopoda Dahl, 1956
Subclass Thecostraca Gruvel, 1905
Superorder Ascothoracida
Lacaze-Duthiers, 1880
Order Dendrogastrida Grygier, 1987b
Family Dendrogastridae Gruvel, 1905
Dendrogaster Knipovich, 1890

Dendrogaster sp. cf. *antarctica* Grygier, 1980

(nom. correct. pro *D. antarcticus*)
Fig. 1

Material.—Non-brooding ♀ (USNM 228260) from coelom of *Odontaster validus* Koehler also infested with *Gongylophysema asetosum,* new genus and species (see below), coll. G. Hendler, 25 Mar 1982, *Hero* Cr 824, Sta 30-1, 64°14.15′S, 62°33.60′W, 90–135 m.

Description.—Transverse span of mantle 21.4 mm (Fig. 1A, B). Middle piece distorted, but longer than wide and tapered

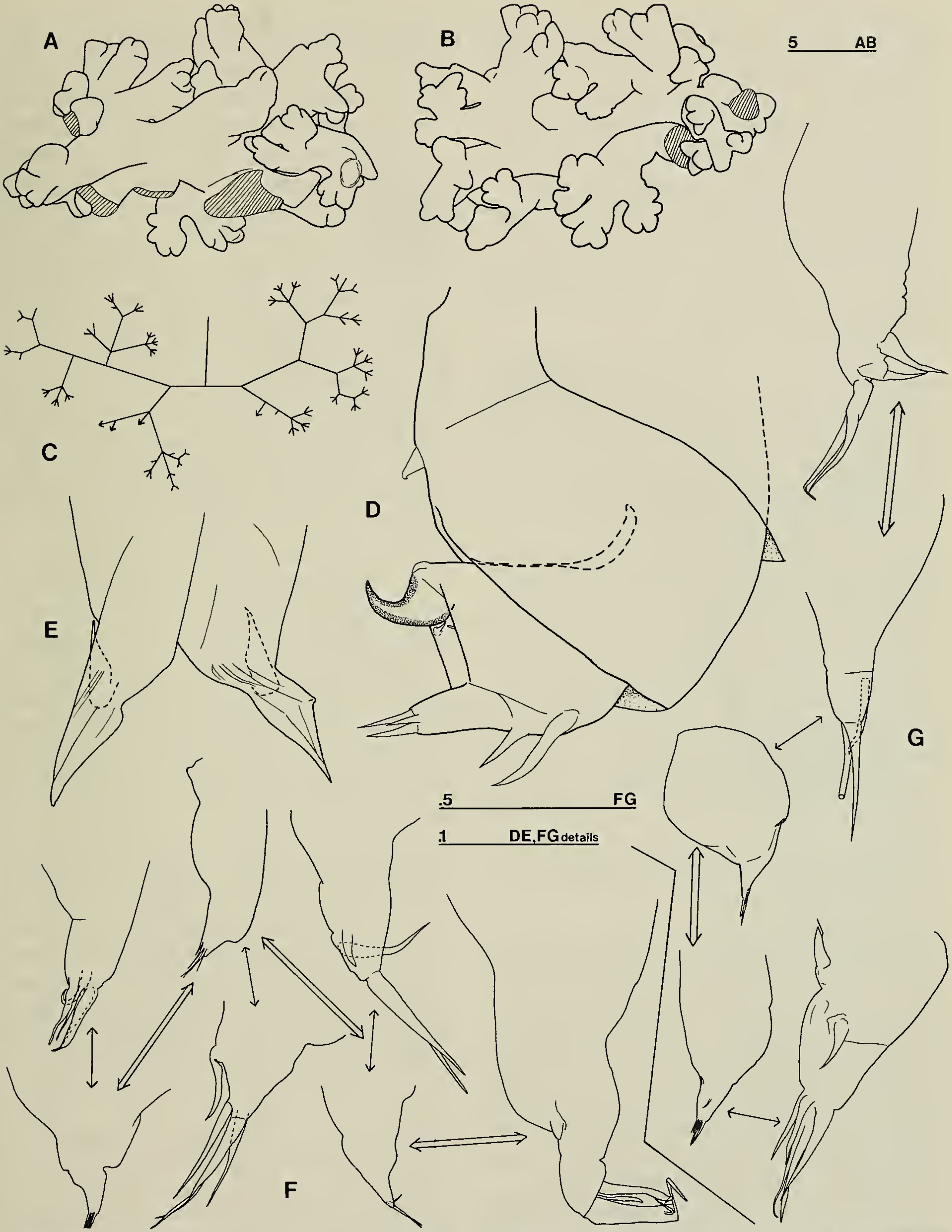

Fig. 1. *Dendrogaster* sp. cf. *antarctica* Grygier, 1980 (USNM 228260): A, B, Female, habitus, dorsal and ventral views, respectively, sites of missing branches hatched; C, Schematic diagram of mantle branching pattern (cf. A); D, Distal part of antennule, lateral view; E, Distal part of maxillae, posterior hooks dashed; F, G, 4 right and 3 left thoracopods, respectively, in order indicated by thick arrows (front and rear end of each series confused in dissection), fine arrows indicating details of thoracopodal tips, smallest limb in each series only shown in higher magnification. Scale bars in mm.

with distal slit. Tightly packed mantle branches short, stout, with lobular tips. Branching pattern shown in Fig. 1C: short main branch on each side dividing into anterior and posterior primary branches, these branching laterally or dichotomously up to as much as 5th-order terminal branches, last 2 orders of branching sometimes trichotomous; posterior branching possibly less well developed than anterior, but some posterior branches torn off. No ♂♂ found in middle piece or in main branches.

Antennules 4-segmented, subchelate, normal for genus (Fig. 1D). [Grygier (1981b) misdescribed the antennular segmentation in *D. antarctica*; segments 1–3 are arranged, and the third is armed, normally for the genus.] Segment 3 with fusion seam, its anterobasal muscle visible in 1 antennule only; small seta on anterior edge. Segment 4 much smaller than 3, with movable claw and fixed, slightly tapered claw guard; setation including: seta below claw (seen in 1 antennule); 2 setae on ridges between claw and claw guard, tiny lateral one on ridge edge (seen in 1 antennule), larger medial one on inside face of ridge, directed transversely; variably 2–3 apical setae on claw guard, another at its rear base; longer seta on ventral side of segment.

Maxillae bifid, with basally directed posterior hooks (Fig. 1E).

Thorax sac-like, with at least 7 setose, uniramous thoracopods, 4 on right (Fig. 1F), 3 on left (Fig. 1G). Order preserved in dissection, but anterior and posterior became confused. Legs typically consisting of broad, unarmed base and narrow, tapered distal part witih 3–5 terminal and 0–2 subterminal setae, all setae short and simple or occasionally bifid. One leg on each side, either first or last, much smaller than others.

Remarks.—The compact array of mantle branches, their stoutness, and the mixture of mantle branching geometries are characteristic of *D. antarctica*; no other *Dendrogaster* species is similar (Grygier 1981b). However, *D. antarctica* was originally described from *Acodontaster conspicuus* and its type specimens are at least twice as large as the present one and have a distally swollen middle piece and up to 9th-order branching. The present antennules differ from those of the type lot in having one small seta instead of two on segment 3, and two setae behind the claw guard instead of none. Since the present specimen is immature (not brooding), these differences may not be significant. Antennular setation is ontogenetically unstable in *Dendrogaster* and is not always a good taxonomic character compared with the mantle branching pattern (Karande and Oguro 1981a, b). More specimens from *O. validus* are necessary before a firm identification can be made.

The thoracopods are the most surprising feature of this specimen. Although Knipowitsch (1892) interpreted small, unarmed lobes as thoracopods in *D. astericola* Knipovich, 1890, females of *Dendrogaster* have generally been considered legless. The present exception, though spectacular, is not unique (also *D. usarporum,* new species, herein), and it may be that other females of this genus and of the closely related *Bifurgaster* Stone & Moyse, 1985, will prove to have similar legs if dissected properly. These reduced, uniramous, setose legs corroborate the supposedly close relationship of *Dendrogaster* to the third genus of Dendrogastridae, *Ulophysema* Brattström, 1936 (Wagin 1950, 1976; Grygier, 1987b), which is also so equipped (cf. Brattström 1948).

Dendrogaster usarporum, new species
Fig. 2

Diagnosis.—Middle piece about twice as long as wide; mantle branches very thick, anterior and posterior branching complex-

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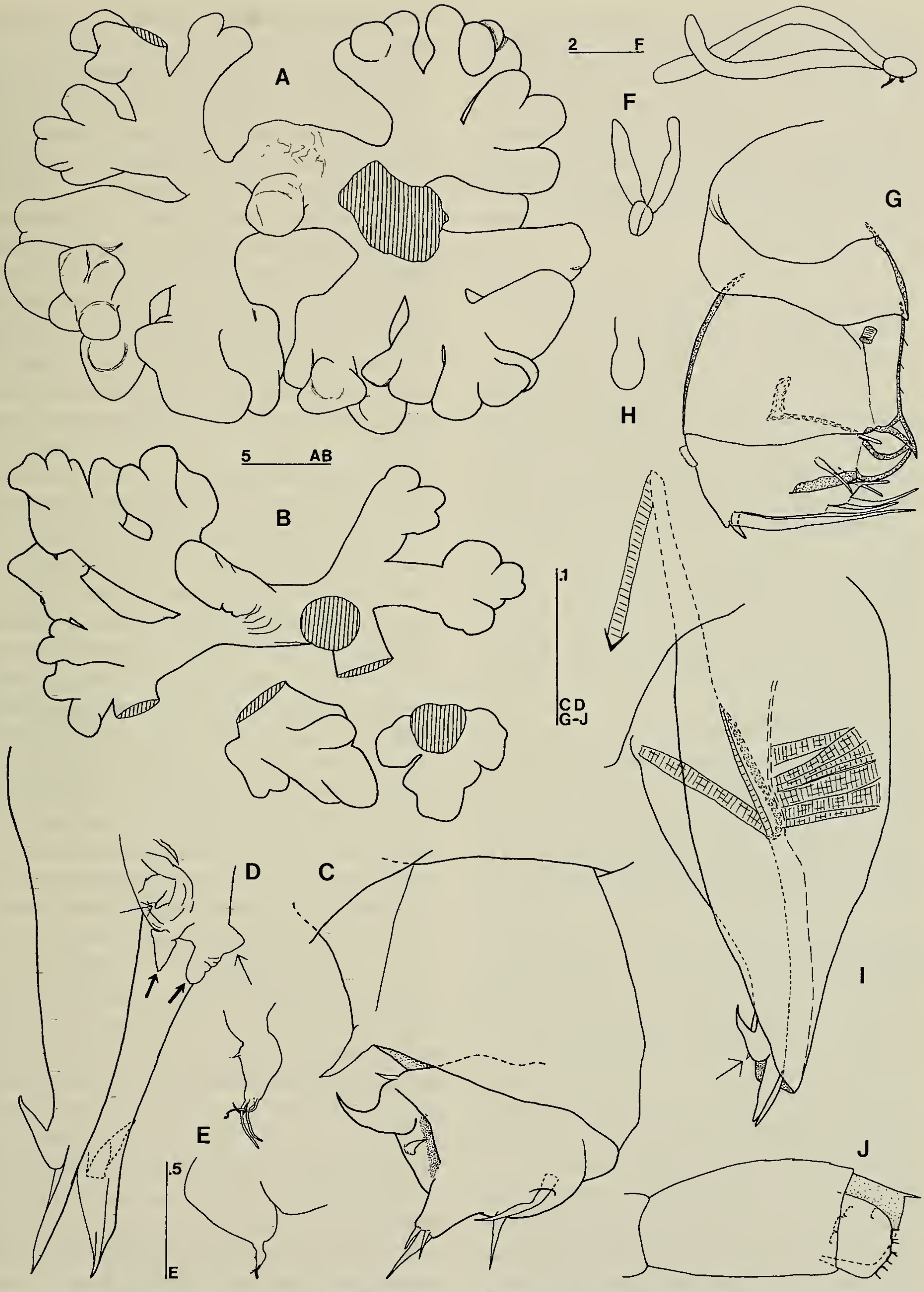
Fig. 2. *Dendrogaster usarporum,* new species: A–E, Females: A, Holotype (USNM 228256), habitus, wounds and missing branch sites hatched; B, Paratype and broken branches from it (USNM 228257); C, Distal part of paratype antennule, lateral view; D, Holotype maxillae, oblique lateral view, with vestigial mandibles (thin



arrows) and maxillules (thick arrows) at base; E, Holotype thoracopod (below) with detail of tip (above); F–J, Male paratypes (USNM 228257): F, Two males, habitus, lateral and dorsal views; G, Antennule, lateral view; H, Frontal filament; I, Oral cone, including some musculature (mostly of pharyngeal pump) and extra point on maxilla (arrow); J, Fifth abdominal segment and furcal rami, showing bases of 8 setae on near ramus. Scale bars in mm.

ity about equal; terminal branches generally tertiary, very large and rounded. Single large, spine-like seta on ♀ antennule segment 3; no muscle in anterobasal part of this segment. Males with cylindrical posterior processes, pad instead of aesthetasc on antennular segment 4, often small spines on seta-bearing prominance behind claw guard, small extra points on maxillae.

Etymology.—Named for the men and women of the United States Antarctic Research Program (USARP).

Material.—3 ♀♀ (holotype USNM 228256; paratypes USNM 228257) in coelom of 3 *Porania antarctica glabra* Sladen; coll. G. Hendler, 29 Mar 1982, *Hero* Cr 824, Sta 39-1, 64°47.51′S, 64°11.66′W, 226–265 m. Holotype and 1 paratype dissected. Holotype brooding round, 0.42 mm diameter eggs, 7 ♂ paratypes (USNM 228257) removed from middle piece, 1 left in main branch; dissected ♀ paratype with ripe ovaries but no brood or ♂♂; second paratype ♀ in poor condition, lacking tip of middle piece with appendages.

Description.—Females: Holotype mantle span 33 mm, paratypes 28–30 mm (Fig. 2A, B). Middle piece torn in holotype, 5.6 mm and 8.0 mm long in paratypes, about twice as long as wide, shape variable. Span of main branches about as long as middle piece, thicker than middle piece. Thick anterior and posterior primary branch on each side quickly dividing into 2–3 thick secondary branches, these breaking up into several round terminal branches from half to nearly as large as distal end of middle piece.

Antennule 4-segmented, subchelate (Fig. 2C). Segment 3 with 1 large, anterior, spine-like seta, a faint anterobasal fusion seam laterally, no muscle visible in cut-off corner. Segment 4 rounded, with movable claw and truncately conical claw guard; medial ridge between claw and claw guard more prominent than lateral one; small seta at base of claw; large lateral and tiny medial seta behind claw, former directed either upwards or transversely; 2–3 distal setae on claw guard, 1 longer than others; 2 setae arising separately behind claw guard, proximal one longer.

Holotype with vestigial mandibles and maxillules, maxillae well developed, bifid, with elongate posterior hooks directed basally, elongate distal prongs either straight or splayed outwards (Fig. 2D).

Post-cephalic part of body in dissected paratype segmented: first a wide zone with vestigial left thoracopod (massive base and appendix with 5 setae) and lobe medial to it (Fig. 2E), 2 unequal lobes on right; then a narrow, transverse ridge; then 3 progressively less broad, diaphanous bulges, the first possibly paired; then an unsegmented portion.

Males: Segmented, appendage-bearing main body between 2 oval valves about 0.8 mm long and 0.4 mm high, each with cylindrical, slightly curved or bent posterior process 1.9–6.2 mm long (Fig. 2F). Processes containing gut diverticulum and testes with typical bullet-headed sperm (Grygier 1981a). Body consisting of head, 6-segmented thorax (suture between first thoracomere and head clearly visible dorsally), and 5-segmented abdomen. Antennules 4-segmented, subchelate (Fig. 2G). Segment 3 with tiny hairs anteriorly, 2 anterodistal spines, lateral fusion seam, and small transverse muscle in delimited anterobasal region. Segment 4 with movable claw and tapered claw guard; seta at base of claw; longer one to each side behind claw; 1 short apical and 2 long, subterminal setae on claw guard; long seta (bifid in 1 case) behind claw guard arising from prominence with up to 2 short spines; small proximal pad corresponding to ventral aesthetasc of other *Dendrogaster* ♂♂. Pair of small, club-shaped frontal filaments present posterolateral to antennules (Fig. 2H). Oral cone normal, with conical labrum around bifid maxillae (Fig. 2I), rear hooks of latter pointing basally or distally, minute extra points medial to them.

Thoracomeres less high posteriorly; no long gap between oral cone and thoracopods; no epaulets on thoracomere 6; no limbs on thoracomere 1. Other 5 limb pairs (thoracopods 2–6) of normal construction: coxa, basis, 2-segmented exopod, 3-segmented endopod except 2-segmented in thoracopod 6. Limb setation examined in 3 ♂♂: lateral coxal seta on thoracopods 2–3, longer on 2; medial basal seta not visible on any leg in whole mount; 4 long terminal exopod setae (3 on exopod 6), apparently 3 long terminal endopod setae (one-half as long as others) plus 1 seta on second endopod segment (2 terminal setae only on thoracopod 6). Abdominal segments 2 and 5 longest, 4 shortest. Penis not visible in whole mounts. Furcal rami, as seen clearly in 1 specimen (Fig. 2J), square with normal setation: 3 basomedial, 1 mediodorsal, and 4 terminal setae, ventral one shortest; dorsal terminal spine present or not. Natatory setae of limbs and furca setulate.

Remarks.—The robustness of the branches suggests an affinity with *D. antarctica,* but the branching pattern is simpler and the terminal branches much larger relative to the middle piece. The dissected paratype, which has rather long secondary branches, superficially resembles *D. rimskykorsakowi* Wagin, 1950, but its branches are thicker and the clusters of terminal branches much larger. A single large spine on antennule segment 3 also occurs in *D. sagittaria* Grygier, 1985b, *D. arbusculus* Fisher, 1911, *D. punctata* Grygier, 1982, *D.* sp. cf. *antarctica,* and sporadically in *D. fisheri* Grygier, 1982 (Grygier 1982, 1985b, herein). In the present case, the apparent lack of an anterobasal muscle in this segment is probably real, since it could not be found in four antennules examined. The single reduced thoracopod has implications discussed above.

The males are entirely typical of the genus except for the minute extra point on each maxilla; a larger such point has been described in specimens attributed to *D. beringensis* Wagin, 1957 (Grygier 1985b), but not in any other species. The posterior hooks on the maxillae are clearly movable, being found in more than one position, so their directionality cannot be used as a taxonomic character (e.g., by Wagin 1950). The anteriorly bounded first thoracomere is noteworthy since it is usually described as fused to the head in this genus.

Finding vestigial mouthparts in either sex probably depends on luck in dissection, so their reported presence or absence should not be used as taxonomic criteria in this genus.

Family Ctenosculidae Thiele, 1925

Gongylophysema, new genus

Diagnosis.—Female carapace spherical or subspherical with thin cuticle; small, protruding, ventral aperture guarded by spines and hooked setae. Cephalic attachment zone semi-inverted. Antennules apparently absent. Labrum short, its edges well separated; mandibles absent; maxillules present as rounded lobes; maxillae large, mostly fused except for short, bifid tips. Thorax enlarged, especially anteriorly, with long medial dorsal horns on segments 2–5 and 6 pairs of uniramous, asetose limbs, sixth much smaller than rest. Short filamentary appendages present. Seminal receptacles in legs 2–5. Penis absent. Abdomen 4-segmented. Furcal rami pointing ventrally, tapered with very few or no setae. Sexes separate by ascothoracid larva, adult males unknown. Inhabiting internal integumental cysts in asteroids.

Etymology.—From Greek *gongylos* (ball) and *physema* (bubble), referring to the shape of the carapace; gender neuter.

Type species.—*Gongylophysema asetosum,* new species.

Gongylophysema asetosum, new species

Figs. 3, 4

Diagnosis.—As for genus.

Etymology.—Referring to the basically asetose thoracopods and furca.

Material.—11 ♀♀ (holotype USNM 228254, 10 paratypes USNM 228255) inhabiting internal cysts in 3 *Odontaster validus,* 9 in specimen shared with *Dendrogaster* sp. (see above), 1 immature and 2

Fig. 3. *Gongylophysema asetosum*, new genus and species, paratype females (USNM 228255): A, Armament of carapace aperture; B, Main body, thoracomeres 2–6 and abdominal segments numbered, s, seminal receptacles; C, Oral cone showing maxillules (mx) flanking pointed maxillae, e, esophagus; D, Set of thoracopods, numbered,

mature paratypes dissected, carapace opened in holotype and another paratype. Coll. G. Hendler, 25 Mar 1982, *Hero* Cr 824, Sta 30-1, 64°14.15′S, 62°33.60′W, 90–135 m.

Host-parasite relations.—Each parasite lies within the host's disc or arm in a thin, tough pocket of host tissue (invaginated integument?) which separates it from the coelom. Access to the external medium is maintained through a minute slit in the host's aboral wall at the site of the carapace aperture (i.e., the parasite is normally upside down). This is nearly the same relationship as *Endaster hamatosculum* Grygier, 1985c, has with its zoroasterid starfish hosts (Grygier 1985c), but the cyst wall here lacks calcareous elements. Large cysts may be evident externally as bumps. The dermal ossicles of *O. validus* are normally ornamented with many small spinules, but in the vicinity of many cysts only bare knobs remain, and there are no papular openings around the slit. Cysts are roughly spherical or slightly wider than thick, mostly 3–7 mm across, but down to 1.5 mm. Some cysts from host arms bear imprints of the ambulacral plates against which they have grown.

Description.—Carapace roughly spherical, usually slightly wider than high or long, nearly same size as enclosing cyst (holotype 6.7 × 6.4 mm, a dissected paratype 7 × 6.5 × 6.0 mm). Short aperture on small ventral prominence, cuticle thickest there, with pores. Narrow zone of spines and hooked setae along aperture lips (Fig. 3A), then wider zone of hooked setae, most of surface smooth, unarmed. Diverticula of ovaries and midgut ramifying extensively within carapace.

Body attached by partly inverted head to anteroventral side of carapace, thorax curved so abdomen points ventrally toward aperture (Fig. 3B). Head bearing oral cone; no antennules, antennae, or frontal filaments found. Thorax 6-segmented, no boundary discerned between first segment and head. Thoracomeres 1–5 enlarged dorsally, but not greatly widened. Front and rear borders of first segment indistinct. Thoracic segments 2–5 each with a hirsute, forwardly curved, presumably movable (internal muscles present), dorsal protrusion or "horn," first one much shorter than others; horns relatively much shorter in smallest, immature, dissected individual. Dorsum of thoracomere 1 (region anterior of base of first horn) of variable length, short in holotype, quite long in illustrated paratype (Fig. 3B), intermediate in other examined paratypes. Filamentary appendages and 6 pairs of thoracopods present. Abdomen 4-segmented, tapered and ending with furcal rami, segment 1 larger than other 3 combined.

Labrum relatively short, its edges far apart, exposing most of maxillae (Fig. 3C). Mandibles apparently absent. Maxillules reduced to pair of round lobes (identity judged on basis of extrinsic musculature [Grygier 1984]). Maxillae large, basal region projecting ventroposteriorly, medially fused for most of length; tips bifid, immovable, barely projecting from fused portion. Prominent pair of maxillary gland swellings between oral cone and thoracopods 1, this the widest part of main body. Thoracopods 1–5 elongate, uniramous (Fig. 3D), lacking true setae but bearing short, fine hairs, leg 2 longest, then 1 and 3, 4 and 5 somewhat shorter. Leg 1 attached higher on body than others, with ♀ genital opening anteriorly at base and filamentary appendage with numerous short projections anterodorsal to that (Fig. 3D, E). Cluster of short, tubular seminal receptacles basolaterally within legs 2–5. Thoracopod 6 uniramous, naked, much smaller than other legs (Fig. 3D). No penis observed on first abdominal segment. Furcal rami ta-

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←

with filamentary appendage (f) and sites of seminal receptacles (s) indicated, latter only drawn in leg 2; E, Detail of a filamentary appendage; F, Furcal ramus of different specimen from B. Scale bars in mm.

pered or bluntly triangular, longer than high, surfaces heavily hirsute, but only 0–2 short distal setae (Fig. 3B, F).

Developmental stages.—Holotype brooding about 275 embryos and hatched ascothoracid larvae I. One dissected paratype with 314 ascothoracid larvae I ready to molt to ascothoracid larva II, 2 other large paratypes with about 450 embryos and about 400 eggs, respectively. Embryological development proceeding directly to ascothoracid larva, no naupliar stage.

Eggs: Oval, 0.51 × 0.42 mm.

Early embryos (Fig. 4A): Helmet-shaped, 0.73 mm long, 0.56 mm wide, 0.54 mm high, filled with yolk or oil gobules, ventrolateral rim produced into small anteroventral flaps and larger posterior protrusions. Unarmed antennules extending beyond rim, state of other appendages unclear.

Late embryos (Fig. 4B, C): Dome-shaped, yolk- or oil-filled shield over cephalic appendages and posteriorly protruding thoraco-abdomen. Shield 0.46 mm long, 0.41 mm wide, 0.36 mm high, total length 0.66 mm. Appendages present as unarmed anlagen: antennules longest, with or without distal notch; labrum rounded; antennae and mandibles absent; maxillules smaller than maxillae, both uniramous; 6 pairs of biramous thoracopods, endopod more narrow than exopod; pair of lobes behind them, presumably representing genital limbs; short furcal lobes.

Ascothoracid larva I: Carapace bivalved, oval, averaging 0.84 mm long. Sexes separate, some specimens with bundles of elongate sperm in carapace valves, others with immature ovaries. Body with head, 6-segmented thorax (first segment not distinct from head), and 4-segmented abdomen (Fig. 4D). Head bearing large, approximately 4-segmented antennules, small frontal filaments, labrum and maxillae (maxillules not seen, probably present). Antennules Z-shaped (Fig. 4D); penultimate segment with about 4 anterodistal setae; distal segment with large, probably immovable claw with 3 short basal setae, short cylindrical claw guard with 2 setae, long seta behind claw guard, and protrusion with tiny sensillum. Frontal filament short with 2 unequal, short processes (Fig. 4E). Labrum a flat shield in front of and shorter than maxillae, edges folded back, hiding any other mouthparts (Fig. 4D, F). Maxillae separate for much of length, tips with 1–3 small points (Fig. 4D, F). Six pairs of biramous thoracopods with long setae (half as long on first pair) (Fig. 4D, G, H). Legs divided into coxa, basis, 2-segmented exopod, and 3-segmented endopod (2-segmented in legs 1 and 6, first segment very short in leg 1). Exopods with 3 terminal and 1 slightly subterminal setae, just 3 terminal setae on leg 6. Endopods with 1 short seta on second segment (none on proximal segment of leg 1), 2 long setae on terminal segment. Abdominal segment 4 longest, others approximately equal (Fig. 4D). Penis of segment 1 sexually dimorphic, in males longer than legs, with 2 distal setae (Fig. 4I), in females less than half as long and unarmed (Fig. 4J). Furcal rami rectangular, just under twice as long as high, usually with 4 terminal and 3 mediodistal setae (Fig. 4D), but slightly variable.

Ascothoracid larva II: Some features of this stage could be made out beneath cuticle of older ascothoracid larvae I preparing to molt. Antennular claws sexually dimorphic, females with 10 ± 2 triangular teeth along inner curve (Fig. 4K), males with comb-like row of about twice as many, finer teeth (Fig. 4L). Impossible to determine number of antennular segments or whether strap-like aesthetasc present. Frontal filaments with relatively much longer aesthetasc than before. Sharp, pointed maxillules and apparently distally undivided maxillae present (Fig. 4F).

Remarks.—Systematic position: *Gongylophysema asetosum* has features characteristic of the Petrarcidae (Petrarcinae), the Dendrogastridae (Ulophysematinae), and the Ctenosculidae. The *Petrarca*-like fea-

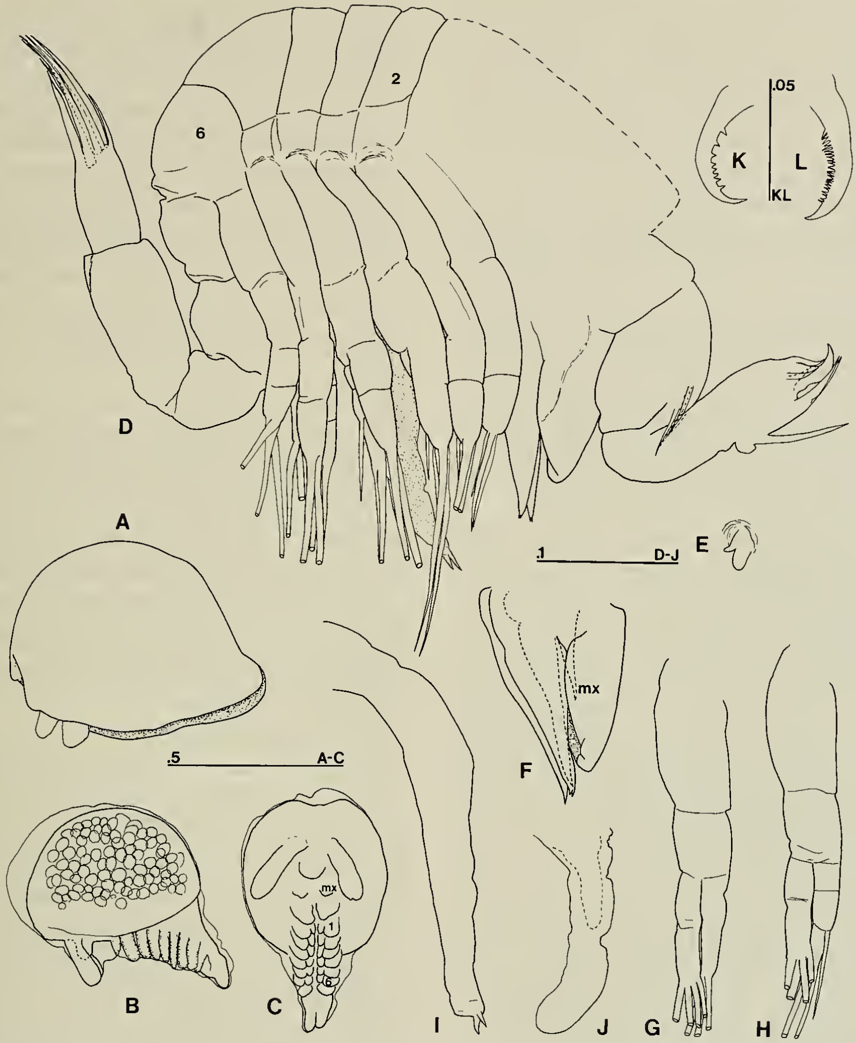

Fig. 4. *Gongylophysema asetosum,* new genus and species, developmental stages: A, Embryo, lateral view, front end left; B, C, Late embryos, lateral and ventral views respectively, latter showing appendage anlagen (e.g., mx, maxillule, thoracopods 1 and 6); D–J, Ascothoracid larva I; D, Main body, lateral view, some thoracomeres numbered, setae only shown complete on legs 1 and 3, penis stippled; E, Frontal filament; F, Oral cone, maxillules (mx) and longer maxillae of ascothoracid larva II dashed within; G, Thoracopod 1; H, Thoracopod 2; I, Male penis; J, Female penis with anlage of ascothoracid larva II penis dashed within; K, L, Female and male antennular claws, respectively, of ascothoracid larva II. Scale bars in mm.

tures include the oral cone—the short labrum with widely separated lateral margins and the labium-like, nearly fused maxillae (most similar to *Petrarca morula* Grygier, 1985a)—and the asetose, unsegmented limbs. The Petrarcidae infest scleractinian corals, and these resemblances must be convergent simplifications. Adult characters in common with *Ulophysema* include an at least partly inverted cephalic attachment zone, anteriorly curled, muscular thoracic horns on 4 thoracomeres (segments 1–4 in *Ulophysema*), uniramous thoracopods, loss of some mouthparts (all but labrum in *Ulophysema*), a ventrally pointed abdomen, and nearly asetose furcal rami (asetose or absent in *Ulophysema*). The sexual dimorphism of the ascothoracid larva II antennular claw is the same as in *U. oeresundense* Brattström, 1936 (Grygier, 1987a), and that species also exhibits sexual differences in penis development at this stage. *Ulophysema,* however, shares so many advanced features with the dendrogastrine genera *Bifurgaster* and *Dendrogaster*—nearly identical, subchelate, larval antennules; loss of first thoracopod at all stages; loss of seminal receptacles; reduction of mandibles and maxillules; reduction of abdomen to 2 segments or less; great enlargement of carapace into lobes; complete or nearly complete endoparasitism—that these three dendrogastrid genera together must form a monophyletic set (Grygier, 1987b).

Gongylophysema shares a mode of life within an integumentary cyst of an asteroid with the ctenosculid genera *Ctenosculum* Heath, 1910 (see Grygier 1983a) and *Endaster* Grygier, 1985c. All three genera have vestigial or absent antennules, apparently no mandibles, a partly or wholly inverted cephalic attachment zone, large but simplified thoracopods (mostly biramous in *Ctenosculum* and *Endaster*) with small, tubular seminal receptacles in legs 2–5, no discernable penis in adult females, filamentary appendages, and an array of spines and hooked setae near the carapace aperture (last 2 features previously overlooked in *Ctenosculum*). *Gongylophysema* is assigned to the Ctenosculidae on the basis of these mostly apomorphic features. *Ctenosculum* has 4 dorsal horns on segments 1–4 or 2–5 and tapered filamentary appendages (based on new, Australian specimens and reexamination of Grygier's 1983a specimen); unlike *Gongylophysema* it has a large, toothed, posteroventral carapace aperture, setose legs and furca, and 2-segmented antennules. *Endaster* is similar to *G. asetosum* in carapace form aside from being more oval, and its abdomen points ventrally, but it has setose thoracopods and furcal rami, very long, conical filamentary appendages, and a completely different thoracic armament with no long dorsal horns. In both *Ctenosculum* and *Endaster* the oral cone is more generalized than in *Gongylophysema*; the rear edges of the labrum meet behind the other mouthparts. *Endaster* shows sexual dimorphism at ascothoracid larva I, involving penis development as well as gonads (Grygier 1985c). In sum, *G. asetosum* appears to be the most apomorphic (i.e., reduced) member of the Ctenosculidae in terms of mouthparts, thoracopods, and furcal setation; the thoracic horns suggest a close affinity to *Ctenosculum.*

Embryology: The seventh pair of trunk limb buds in this species can only reasonably be interpreted as rudimentary genitalia, yet the fully developed ascothoracid larva has a medial penis, as do adult ascothoracidans in general. This seems to confirm the assumption (e.g., Grygier 1983b) that the penis is the Ascothoracida (and Cirripedia) represented fused appendages of trunk segment 7.

Although retention of the brood to the ascothoracid larva is quite usual in the Ascothoracida, there normally are brooded naupliar instars. Direct development from the embryo to the ascothoracid larva, as seen here, only otherwise occurs in a few species of *Dendrogaster* (Wagin 1948, 1954; Grygier 1981b) as one end of a spectrum of ontogenetic patterns.

Notes on an unidentified ctenosculid.—H. L. Clark (1902) described a 15 mm long, bilobed structure (USNM 19899) collected at *Albatross* Sta 3342 (off Queen Charlotte Islands, Canada, 2900 m) as a monstrous possible holothurian. A. H. Clark (1916) reexamined the specimen and determined it to be a piece of a *Brisinga* (Asteroidea) arm with an external cyst induced by a "curious type of degenerate mollusc." Although this specimen is not Antarctic, it is worth treating in the present context because after examining the specimen, I have concluded that the parasite was most likely a ctenosculid ascothoracidan, of which only a portion of the carapace remains. Typically branched ascothoracidan ovaries are present in the carapace. Among the Ctenosculidae, *Ctenosculum hawaiiense* Heath, 1910, infests a deep-water brisingid, so this parasite may possibly belong to that genus. A. H. Clark (1916) noted more cysts on *Brisinga* from the same station, but these specimens were not found at the Smithsonian in 1985, so the precise identity of the parasite cannot be determined.

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IDENTITY OF *CROCODILUS MEXICANUS* BOCOURT, 1869 (REPTILIA: CROCODYLIDAE)

Charles A. Ross and Franklin D. Ross

Abstract.—Examination of type material and analysis of Central American crocodile neck squamation indicate that *Crocodilus mexicanus* is a synonym of *Crocodylus moreletii.*

Crocodilus mexicanus Bocourt, 1869 was recognized for less than twenty years (Sumichrast 1880, 1882, 1884; Cope 1887, as a subspecies of *C. americanus*) until Günther (1885) synonymized it with *Crocodylus moreletii* Duméril and Bibron, 1851 (as *C. americanus* var. *moreletii*). In 1889 Boulenger transferred *C. mexicanus* to the synonymy of *Crocodilus americanus* Laurenti, 1768 (=*Crocodylus acutus* Cuvier, 1807) as suggested by Gray (1872). Since Boulenger's action, the specific allocation of this taxon has been uncertain and most subsequent authors have merely followed Boulenger uncritically.

Crocodilus mexicanus was described from two specimens: an adult received at the Muséum National d'Histoire Naturelle, Paris (MNHN 7579), from Tampico in 1845 and referred to as "variété à dix écussons cervicaux" of *C. acutus* by Duméril and Duméril (1851), and Duméril (1852); along with a juvenile.

Crocodilus mexicanus was said to differ from *C. acutus* by head shape, color, and neck squamation, but was not compared to *C. moreletii.* The figure of the adult syntype (Bocourt 1873, pl. 8, fig. 3) showed a large crocodile with ten neck shield or nuchal scales, and dark coloration. This plate also showed regular tail squamation, and a distinct preorbital hump, two character states associated with *C. acutus.*

Analysis of the number of neck scales in *C. acutus* and *C. moreletii,* based on museum specimens and material examined in Mexico and Central America, and a re-examination of MNHN 7579, the adult syntype of *C. mexicanus,* now permit a more definitive specific allocation of this taxon and confirms Smith and Smith's (1977) tentative allocation of *C. mexicanus* to the synonymy of *C. moreletii.*

Analysis of variation in neck squamation used data from 170 crocodiles from Mexico and Central America north of Panama. Our criteria for distinguishing between *C. acutus* and *C. moreletii* are many, but most are subtle and some vary individually. Two reliable characters were found: the presence or absence of basicaudal scale row irregularity (Ross and Ross 1974), and the shape of the premaxillary-maxillary suture (Schmidt 1924). These characters are used by us to identify this sample as containing 70 *C. acutus,* and 100 *C. moreletii* (as shown in Table 1).

Nape scales (PC 25 + 26; terminology of Ross and Mayer 1983 = post-occipital scales of Deraniyagala 1939; King and Brazaitis 1971; Brazaitis 1974; Ross and Roberts 1979) and neck shield scales (PC 20 + 21, 22 + 23 and rarely PC 19 and 24 = nuchal scales as above) were counted. The most common condition in both *C. acutus* and *C. moreletii* is 4 nape scales (60% *C. acutus,* 64% *C. moreletii*) and 6 neck shield scales (60% *C. acutus,* 85% *C. moreletii*). How-

Table 1.—Frequency distribution of number of neck scales in crocodiles from Mexico and Central America north of Panama. Analysis of neck shield scales and nape scutes utilized data from 70 *C. acutus*, and 98 (neck shield) and 100 (nape scutes) *C. moreletii*. Neck shield, Chi square = 38.99, 5 d.f., $P < 0.01$. Nape scutes, Chi square = 63.81, 5 d.f., $P < 0.01$.

	Number of scales					
Neck shield (PC 19–24)	3	4	5	6	7	8
C. acutus	4	18	4	43	1	0
C. moreletii	0	1	1	87	5	4
Nape scutes (PC 25–26)	2	3	4	5	6	7
C. acutus	13	14	43	0	0	0
C. moreletii	0	0	64	15	20	1

ever, the distribution of these traits is significant and helps to distinguish *C. acutus* (fewer neck scales) from *C. moreletii* (Table 1). Only one *C. acutus* (FMNH 23147 from Isla Cozumel, Mexico), had more than 6 neck shield scales and two *C. moreletii* (FMNH 123668 and MCZ 8047 from northeastern Mexico and Quintana Roo, Mexico, respectively) had less than 4 nape scales or 6 neck shield scales.

A discriminant analysis (BMDP7M; Dixon 1975) of these data was performed. The adult syntype of *C. mexicanus*, MNHN 7579, which has 4 nape and 10 neck shield scales, was entered without species identity. It was assigned to *C. moreletii* with a 99% probability.

Examination of MNHN 7579 showed that this specimen also exhibits basicaudal scale row irregularity, a distinctive characteristic of *C. moreletii* (Ross and Ross 1974). This characteristic was not mentioned in the original description, or later redescription, and the figure of MNHN 7579 (Bocourt 1873, pl. 8, fig. 3), which is accurate in most details, was inaccurate for this trait as it clearly shows regular basicaudal scale rows, a condition found in *C. acutus* in Mexico and Central America (Ross and Ross 1974).

The juvenile syntype of *C. mexicanus* has not been located. Bocourt (1869) stated that it originated in the same locality as the adult, i.e., Tampico, but later (1873) gave the locality only as "Mexique." Bocourt (1869) described this specimen, the juvenile syntype, as being no larger than 79 cm and possessing 8 neck shield scales. Owing to the number of neck shield scales it is likely to be referable to *C. moreletii* for the reason outlined above. Because the juvenile is missing, has questionable locality data, and since the nature of its basicaudal tail squamation and shape of the premaxillary-maxillary suture cannot be determined, we designate MNHN 7579, the mounted, ca. 2 m long adult, as lectotype of *C. mexicanus.*

Crocodilus mexicanus Bocourt, 1869

Crocodilus mexicanus Bocourt, 1869:20, 1873:34.—Sumichrast, 1880:171, 1882:276, 1884:34.

Crocodilus americanus var. *moreletii* (part.): Günther, 1885:21.

Crocodilus americanus mexicanus: Cope, 1887:20.

Crocodilus americanus (part.): Boulenger, 1889:281.—Cope, 1900:173.

Crocodylus moreletii (part.): Schmidt, 1924:84.—Smith and Smith, 1977:95.

Champsa acuta (part.): Werner, 1933:17.

Crocodylus acutus acutus (part.): Smith and Taylor, 1950:211.

Crocodylus acutus (part.): Wermuth, 1953:476.—Mertens and Wermuth, 1955:408.—Wermuth and Mertens, 1961:359, 1977:141.—Steel, 1973:62.—Alvarez del Toro, 1974:13.—Smith and Smith, 1976:Cr-10.

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MICROPROSTHEMA EMMILTUM, NEW SPECIES, AND OTHER RECORDS OF STENOPODIDEAN SHRIMPS FROM THE EASTERN PACIFIC (CRUSTACEA: DECAPODA)

Joseph W. Goy

Abstract.—A new species of shrimp in the genus *Microprosthema* from the eastern Pacific is described and figured. Specimens have been collected from the Galapagos Islands, Panama, and the Gulf of California. The new species, *Microprosthema emmiltum,* represents a geminate or cognate species for it is closely related to the western Atlantic *M. semilaeve. Microprosthema emmiltum* is distinguished from *M. semilaeve* by slight morphological differences in abdomen, uropods, and spination of the pereiopods as well as by coloration. A specimen of *Stenopus hispidus* is recorded from Taboga Island, Panama, bringing the total to five for species of stenopodidean shrimps found in the eastern Pacific.

While examining some unidentified stenopodid material from the National Museum of Natural History, Washington, D.C., I found two specimens of an undescribed *Microprosthema,* collected by the *Velero III* off Isla Santa Maria, Galapagos. Dr. M. K. Wicksten, while sorting specimens at the Allan Hancock Foundation, University of Southern California, found another specimen of the new species from off Taboga Island, Panama. Alex Kerstitch, an underwater photographer, sent Dr. Wicksten another specimen of this stenopodid with photographs of the animal in life.

While examining some stenopodid material in the collection of the Copenhagen University Zoological Museum, I found a male specimen of *Stenopus hispidus* collected by Mortensen in 1916 from Taboga Island, Panama. The banded coral shrimp, *Stenopus hispidus,* is widespread in tropical waters of the western Atlantic, Indian and western Pacific Oceans. The present record extends its known range into the eastern Pacific.

Microprosthema emmiltum, new species
Figs. 1–4

Material examined.—GALAPAGOS ISLANDS: ISLA SANTA MARIA (Floreana or Charles Island), off Black Beach, 1°16′36″S, 90°29′42″W, *Velero III* sta 33-33, rocky shores, 27 Jan 1933, USNM 231363, female (holotype).—1°17′38″S, 90°29′55″W, *Velero III* sta 199-34, 30 Jan 1934, USNM 231364, ovigerous female (paratype).

PANAMA: TABOGA ISLAND, 8°47′35″N, 79°33′15″W, T. Mortensen, Apr 1916, AHF 161, ovigerous female (paratype).

MEXICO: BAJA CALIFORNIA, Los Friales, north of Cabo San Lucas, 23°23′N, 109°24′W, 9.1 m, rock and sand, hand net, under rock. Alex Kerstitch coll., 8 Jul 1981, AHF 8110, ovigerous female (paratype).

Diagnosis.—Moderately small stenopodidean shrimp with subcylindrical, depressed body, with few spinous processes; carapace covered with some small spines; third pereiopod with minutely pitted surface giving

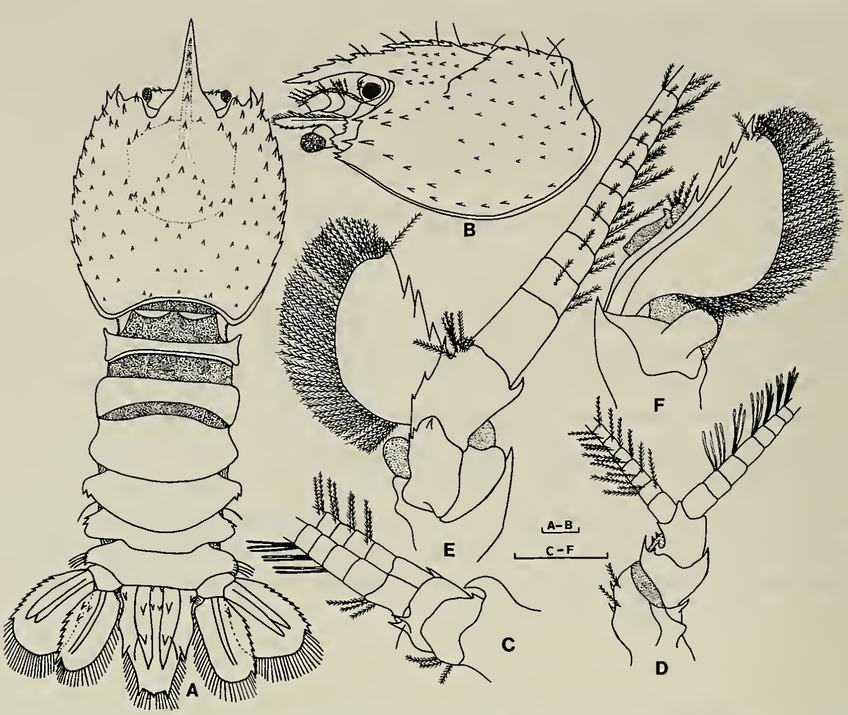

Fig. 1. *Microprosthema emmiltum,* holotype, female: A, Dorsal view; B, Carapace, lateral view; C, Antennule, dorsal view; D, Antennule, ventral view; E, Antenna and scaphocerite, ventral view; F, Antennal peduncle and scaphocerite, dorsal view. Scale bars represent 1.0 mm. Setules not shown on all setae for clarity.

scaly appearance, propodus with dorsal crista, numerous small spines dorsally and ventrally; dorsal surface of abdominal somites glabrous, pleura of last 3 abdominal somites ending in small spines; 1–3 spinules on dorsal surface of uropodal endopodite outside median ridge; scaphocerite lobate with 4–5 very strong teeth on outer margin; first maxilliped with 3-segmented endopodite; antennular and antennal flagella, fourth and fifth pereiopods red; rest of shrimp white with appendages, carapace, and abdomen tinged with red.

Description.—Holotype (female, USNM). Rostrum (Fig. 1A, B) long, deflexed, nearly reaching level of distal end of scaphocerite. Dorsal margin with 5 strong spines, ventrally small spine, laterally without spines.

Carapace (Fig. 1A, B) covered with few long setae, scattered spinules, directed forward, placed in more or less longitudinal rows. Spinules most strongly developed anterodorsally, smallest posterodorsally. Three rows of 3–4 spinules in median region of carapace from base of rostrum to cervical groove. Cervical groove distinct with 4 spinules along each lateral margin. Large supraorbital, antennal, brachiostegal, and hepatic spines present. Two small pterygostomian spines present. Ventrolateral carapacial angle and posterior margin of branchiostegite rounded.

Abdomen (Fig. 1A) broad, depressed, dorsally glabrous, without transverse carinae or rows of tubercles. First 3 abdominal somites with posterior margin near base of pleura rounded. Pleura of fourth somite ending in 2 sharp teeth; bearing long seta laterally. Pleura of fifth somite ending in 1 blunt, 2 sharp teeth. Pleura of sixth somite ending in blunt tooth; 4 long setae laterally.

Telson (Fig. 1A) longer than uropods, truncately triangular. Dorsal surface with 2 longitudinal ridges, ending considerable distance before posterior margin, bearing 3 strong teeth; middle teeth provided with long seta at outer part of base. Two pairs of spinules anteriorly in median groove; 2 small anterior submarginal spines present at telson base. Lateral margin at each side provided with large median lateral spine; posterior margin with 3 small spines; posterior ½ of telson fringed with plumose setae.

Uropods (Fig. 1A) well developed, almost reaching tip of telson. Exopodite with outer margin slightly rounded, bearing 9–10 teeth; inner margin semicircular, fringed with plumose setae. Dorsal surface with 2 distinct longitudinal ridges without spinules. Endopodite subovate, outer margin with 7–8 teeth; inner margin fringed with plumose setae; dorsal surface with distinct unarmed median longitudinal ridge with 1–3 spinules outside ridge.

Eyes (Fig. 1A) well developed, cornea smaller, narrower than peduncle. Facets, pigment distinct in cornea. Ophthalmic peduncle dorsally with 2 spinules.

Basal segment of antennular peduncle (Fig. 1C, D) with distinct, sharply pointed, curved stylocerite. Basal, middle segments with some spinules. Both flagella short, provided with numerous plumose setae; upper flagellum with 63 aesthetascs, 2 on articles 2–3, 3 on articles 4–12, and 4 on articles 13–20.

Antenna (Fig. 1E, F) with strong basal segment; outer margin ending in acute spine; inner margin with distinct laminate process. Other segments of antennal peduncle with some spinules. Scaphocerite reaching slightly beyond tip of rostrum; lobate, rather narrow at base; outer margin slightly concave with 5 sharp, strong teeth; inner margin strongly convex, fringed with long plumose setae. Dorsal surface with distinct longitudinal carina, ventral surface glabrous. Antennal flagellum well developed, extending slightly beyond abdominal somites, covered with numerous short plumose setae.

Epistome (Fig. 2A) triangular anteriorly with 2 stout submedian spines, 1 small median spine at end of median carina. Labrum normally developed. Paragnath bilobed with lobes separated by median fissure. Thoracic sternites broadening from front to back with 2 submedian blunt spinules on segments 5–6, none on segments 4, 7–8.

Mandible (Fig. 2B, C) robust with short, fused molar and incisor processes. Molar surface with few irregular teeth; incisor thickened with 6 small median teeth. Palp well developed, 3-segmented. Proximal segment without setae; middle segment with 4 small lateral plumose setae, 5 distal plumose setae, plumose seta at distordorsal extremity; distal segment broad, fringed with plumose setae.

Maxillule (Fig. 2D) with slender undivided endopodite bearing 2 lateral, 4 distal plumose setae. Proximal endite moderately broad, somewhat truncate distally with 4 plumose setae laterally; 10 compound spinose setae, 8 simple setae distally. Distal endite slightly broader, rounded distally, bearing 8 compound spinose setae, numerous simple setae.

Maxilla (Fig. 2E) with setose coxal and basal endites. Endopodite long, slender, exceeding anterior margin of scaphognathite, 29 long plumose setae laterally and distally. Scaphognathite long, narrow, fringed with numerous plumose setae.

First maxilliped (Fig. 2F) with 3-segmented endopodite; proximal segment long with 8 long plumose setae laterally; middle segment rounded, about 0.5 length of proximal segment, with 12 long plumose lateral setae, short plumose distomesial seta; distal segment small with minute simple terminal seta. Basipodite large, rounded anteriorly, with straight outer border bearing dense fringe of short plumose setae; coxopodite bilobed, with each lobe bearing numerous short plumose setae. Exopodite well developed, bearing 3 proximal and 32 distal long plumose setae. Large epipod with moderately slender proximal and distal lobes.

Second maxilliped (Fig. 2G) with 4-segmented endopodite. Dactylus suboval with

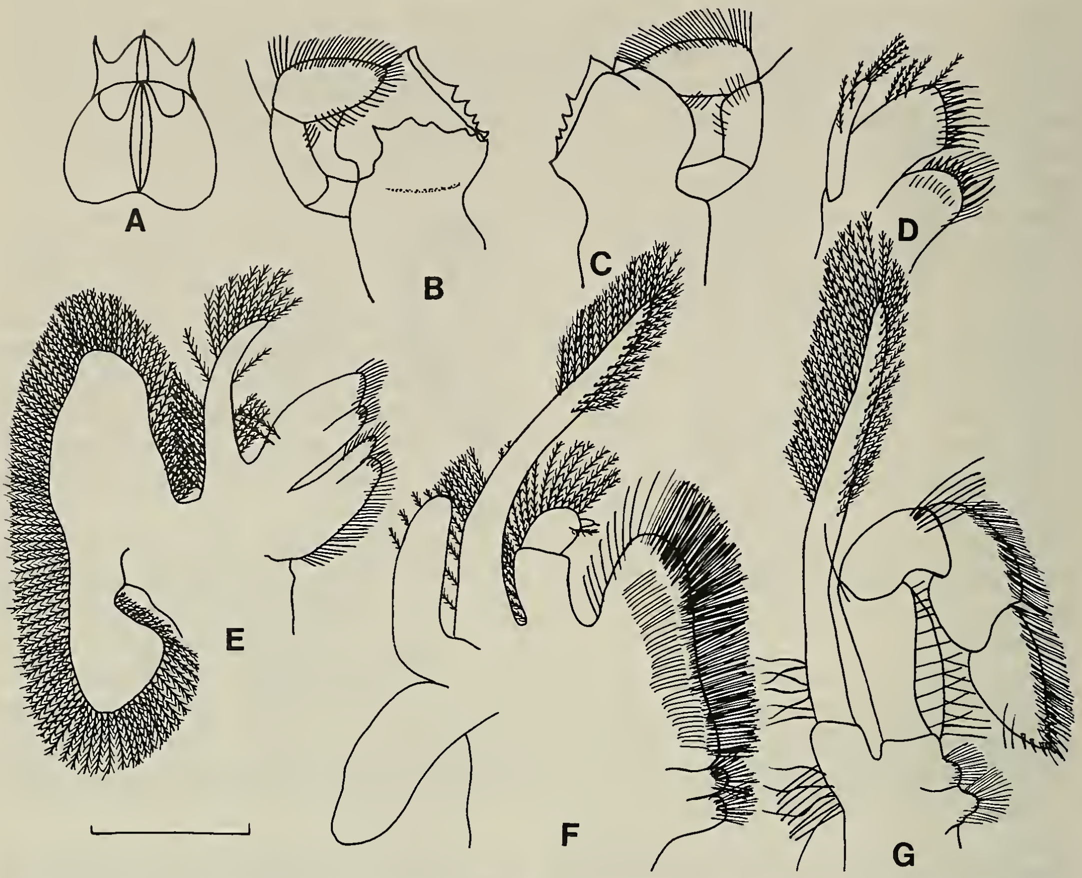

Fig. 2. *Microprosthema emmiltum,* holotype, female: A, Epistome and labrum, ventral view; B, Mandible, ventral view; C, Mandible, dorsal view; D, Maxillule; E, Maxilla; F, First maxilliped; G, Second maxilliped. Scale bar represents 1.0 mm. Setules not shown on all setae for clarity.

dense fringe of setae along distodorsal margin, 8 compound spinose setae, few simple setae on distal margin. Propodus rounded, about equal in length to dactylus, densely setose on dorsal margin. Carpus short, slightly longer than propodus, with 6 long simple setae at distodorsal angle. Merus 2.0 times length of dactylus, with straight inner border bearing long simple seta distally; outer border convex with numerous long simple setae. Ischium and basis fused into setose lobes; coxa lobate with dense fringe of setae. Exopodite long, slender, undivided with distal ½ bearing 44 long plumose setae, 7 long simple proximal setae. Basipodite with 12 long simple setae.

Third maxilliped (Fig. 3A) endopodite strongly developed, 5-segmented. Dactylus slender with dense fringe of setae. Propodus slightly longer than dactylus, with numerous simple setae, setiferous organ distally on inner margin. Carpus equal to dactylar length, with numerous simple setae. Merus almost 2.0 times carpal length, robust, with 4 sharp spines, few simple setae on outer margin; inner margin with numerous simple setae. Ischium robust, almost 2.0 times meral length, with 7 sharp spines on outer margin; 3 spines, numerous simple setae on inner margin. Coxa short, rounded, with dense fringe of simple setae. Exopodite long, slender, extending past carpus, with distal ½ bearing 34 long plumose setae.

First pereiopod (Fig. 3B) small, slender,

Fig. 3. *Microprosthema emmiltum*, holotype, female: A, Third maxilliped; B, First pereiopod; C, Second pereiopod; D, Third pereiopod; E, Fourth pereiopod; F, Fifth pereiopod; G, First pleopod; H, Second pleopod. Scale bar represents 1.0 mm. Setules not shown on all setae for clarity.

reaching past scaphocerite, all segments without spines. Fingers slightly compressed, with hooked tips, cutting edges provided with 8 minute peg-like teeth separated by rectangular chitinous lamellae. Fingers and distodorsal extremity of palm bearing small tufts of long setae. Distoventral part of carpus and proximoventral part of propodus provided with setiferous organ, 2 long setae extending over carpal part of organ. Carpus longest segment, about 2.0 times propodal length, merus about 0.7 times carpal length, ischium about 0.5 times carpal length. These segments all bearing few simple setae.

Second pereiopod (Fig. 3C) similarly built as first, including setation, but longer. No setiferous organ present. Carpus longest segment, about 2.0 times longer than propodus, merus slightly longer than propodus, ischium about 0.8 propodal length.

Third pereiopod (Fig. 3D) robust, largest, strongest, reaching with entire carpus beyond scaphocerite, covered with minute pits giving surface scaly appearance. Palm of chela longest segment with dorsal crista bearing 25 small spines, numerous simple setae; ventral margin with 23 small spines, numerous simple setae. Fingers elongate, with sharp hooked crossing tips, distally bearing small tufts of long setae. Dactylar cutting edge with large triangular tooth dividing chitinous ridge, fitting into 2 dorsal teeth on propodal cutting edge. Cutting edge of propodus with chitinous ridge bearing sharp tooth, blunt tooth about midlength. Carpus almost as long as propodus, narrowing proximally; dorsal margin with 10 spines; 2 large rounded tubercles, 3 spines at distal margin; ventral margin with 11 spines; few long simple setae on margins. Merus same length as carpus; dorsal margin with 3 small proximal spines, few long simple setae; ventral margin with 3 small proximal spines, 3 long distal spines, few long simple setae.

Ischium short, unarmed except for 2 long simple setae at distodorsal extremity. Basis and coxa short with few long simple setae.

Fourth and fifth pereiopods (Fig. 3E, F) long, slender, propodus and carpus undivided. Dactyli biunguiculate with unguis long, slightly curved, separated from dactylar corpus; accessory spine straight, more than 0.5 times length of unguis. Propodi with ventral row of 13–14 movable spines, dorsally with few long simple setae. Carpi longest segments, with 3–4 ventral movable spines, few long simple setae dorsally. Ischia, bases, coxae short, unarmed except for few long simple setae.

First pleopod (Fig. 3G) uniramous, second (Fig. 3H) biramous, all lacking appendices. First pleopod smallest, with exopodite about 2.0 times length of basipodite, margins with dense fringe of plumose setae. Rami of second pleopod 1.5 times length of basipodite, 2 plumose setae on basipodite, margins of rami fringed with plumose setae. Third to fifth pleopods generally similar, third largest of all pleopods, decreasing in size posteriorly.

Branchial formula:

	Maxil-lipeds			Pereiopods				
	I	II	III	I	II	III	IV	V
Pleurobranchs	–	–	1	1	1	1	1	1
Arthrobranchs	1	1	2	2	2	2	2	–
Podobranchs	–	1	–	–	–	–	–	–
Epipods	1	1	1	1	1	1	1	–
Exopods	1	1	1	–	–	–	–	–

Measurements (in mm): The measurements are given for the holotype first followed by the paratypes from smallest to largest in parentheses. Postorbital carapace length, 5.6 (2.8, 4.5, 5.0). Rostral carapace length, 7.3 (4.3, 6.4, 6.7). Total length, approx., 17.5 (11.1, 14.0, 14.3). Length of third pereiopod, 17.2 (9.9, –, 14.1).

Coloration: "Few red spots laterally, for greater part colorless. Antennular and antennal flagella also red. Dactyl and propodi of last 2 pairs of legs red but proximal and distal ends of joints white. Merus of chelipeds red, a longitudinal splash of red on outer side of either palm. Narrower, bar-like on smaller chela." (W. L. Schmitt. unpublished color notes accompanying holotype.) Coloration of the Baja California paratype is based on color photographs of the shrimp immediately after capture. The overall body color is white with carapacial spines, rostrum, abdominal somites, telson, and uropods having a reddish outline. Antennular and antennal flagella and carpi of last 2 pairs of pereiopods are deep red. Dactyli, propodi, and meri of fourth and fifth pereiopods outlined in red. Third pereiopods with seashell pink meri and lower half of palms. First 2 pereiopods and mouthparts whitish with pink outlines. Eggs are emerald green.

Paratypes: The new species is slightly variable in the number of body and appendage spines. For example, the smallest specimen (Fig. 4A) has more spines on the carapace and abdominal pleura, but fewer teeth on the uropodal endopodite than the holotype. There are fewer spines on the third pereiopod (Fig. 4B) and more spines on the inner ischial margin of the third maxilliped (Fig. 4C) than those of the holotype. Two paratypes have only 4 teeth on the outer margin of the scaphocerite and 2–3 external meral spines on the third maxilliped. All three paratypes were ovigerous with eggs 0.49–0.53 mm in diameter. Eggs early in embryonic development (Fig. 4D) were rounded and yolky, while eggs later in development (Fig. 4E) were elongated with eyed embryos. The egg masses were not large, with the specimens from Taboga having 37 eggs, Baja California 80 eggs and the Galapagos 82 eggs. Some of the morphological differences probably reflect allometric growth changes and normal variation in the species.

Type-localities.—Galapagos Islands, Isla Santa Maria (Floreana), off Black Beach; Taboga Island, Panama; Baja California, Mexico.

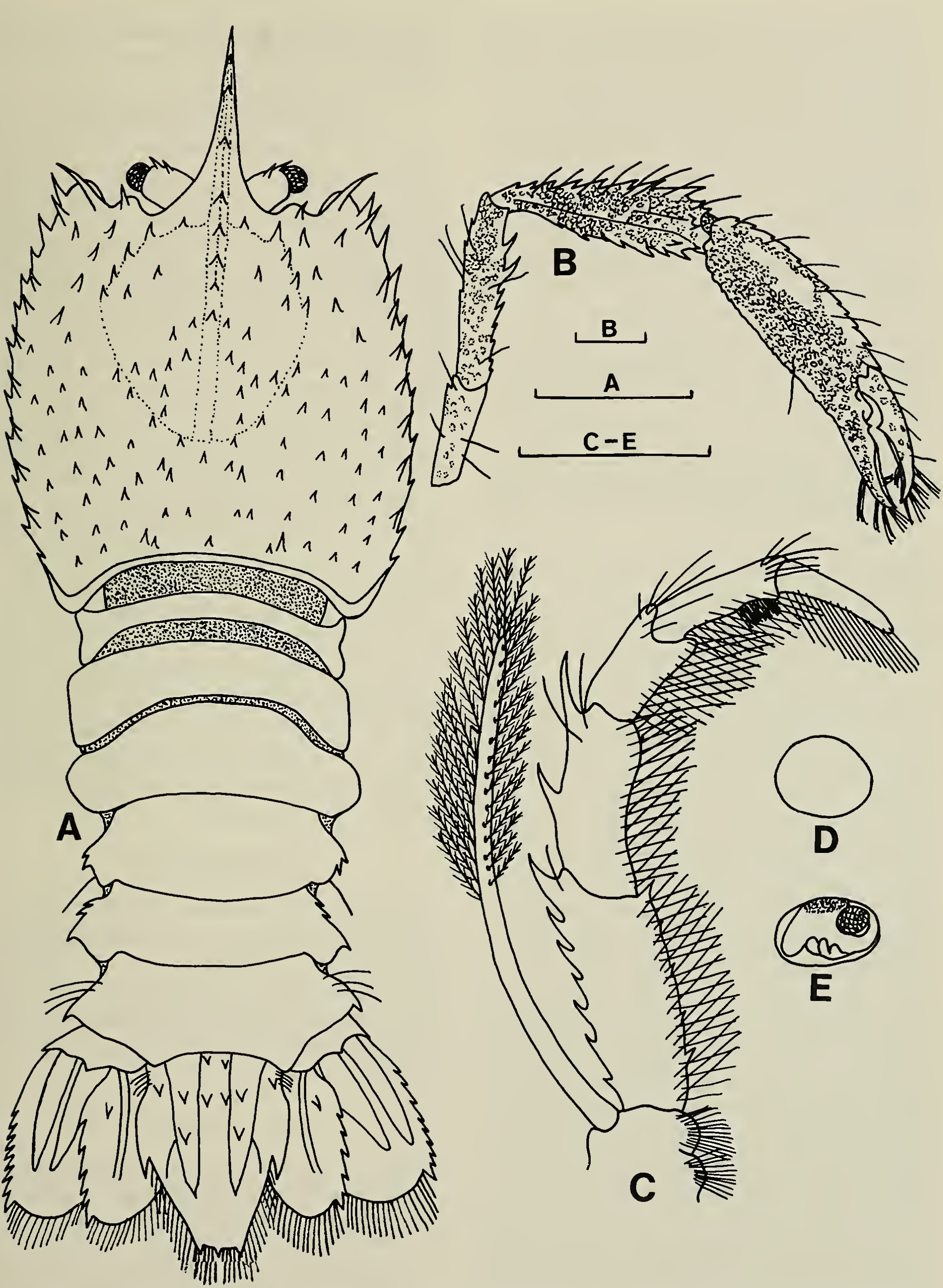

Fig. 4. *Microprosthema emmiltum,* paratypes, Gulf of California: A, Dorsal view; B, Third pereiopod; C, Third maxilliped; D, Early egg, Galapagos; E, Egg with eyed embryo. Scale bars represent 1.0 mm. Setules not shown on all setae for clarity.

Habitat.—All the specimens were taken in rocky shores with one captured under a rock in sand and rubble substrate. This specimen was collected at a relatively shallow depth of less than 10 m, which is consistent for other members of the genus (Holthuis 1946).

Etymology.—The specific name is derived from the Greek "emmiltos" meaning "red-tinged"; it is given in reference to the coloration of the living animal.

Remarks.—The new species, *Microprosthema emmiltum,* closely follows the definition of the genus *Microprosthema* Stimpson given by Holthuis (1946). It represents another example of a geminate species of decapod crustacean from the eastern Pacific (Abele 1972, 1974). It is most closely related to the western Atlantic *M. semilaeve,* but differs in color, abdomen, uropods, and spination of the pereiopods. A complete color description of *M. semilaeve* was given by Manning (1961) and comparison with the new species shows that *M. emmiltum* has both a different overall body color and pattern. In all specimens of *M. semilaeve* (77) examined from the western Atlantic by the author, the second pereiopods bear 1–2 meral spines; the third pereiopods have numerous spinules on the surfaces of the meri, carpi, propodi and dactyli; the first and second abdominal somites have transverse ridges dorsally; and the dorsal longitudinal ridge of the uropodal endopodite bears 1–2 medial spinules and ends in a spinule. *Microprosthema emmiltum* also resembles the Indo-West Pacific *M. validum* but differs in abdomen, uropods, and body and appendage spination. Several authors have recently identified *Microprosthema* from India and Pakistan coasts as either *M. validum* (Pillai 1962, Tirmizi and Kazmi 1979) or *M. semilaeve* (Mahadevan et al. 1962, Raje and Ranade 1978). I agree with de Saint Laurent and Cleva (1981) that all of these above-mentioned Indian and Pakistan specimens are not *M. validum* or *M. semilaeve* but represent an undescribed species of *Microprosthema.*

Other Stenopodids from the Eastern Pacific

A male *Stenopus hispidus* taken from off Taboga Island, Panama (8°47′35″N, 79°33′15″W) was examined by the author. This specimen closely resembles the description and illustrations of *S. hispidus* (Holthuis 1946). However, the telson is abnormally forked with 8–11 spines on each fork. This may have been due to improper healing of an injury, since in all other morphological characters the specimen fits the description of *S. hispidus.* Three other stenopodidean shrimps have so far been collected in the eastern Pacific. *Spongicoloides galapagensis* was found off the Galapagos Islands at 717 m depth (Goy 1980). *Odontozona rubra* was collected in shallow waters of the Gulf of California and *O. spongicola* was found off Santa Catalina Island at 609 m depth (Wicksten 1982). The present records of *Microprosthema emmiltum* and *Stenopus hispidus* brings the total to five species of stenopodidean shrimps known from the eastern Pacific.

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TWO NEW SPECIES OF *PAGURISTES* (DECAPODA: ANOMURA: DIOGENIDAE) FROM SOUTHWESTERN AUSTRALIA

Gary J. Morgan

Abstract.—Two new species of *Paguristes* from southwestern Australia are diagnosed and described. A key to known Australian species of *Paguristes* is presented.

The genus *Paguristes* Dana has a worldwide distribution, occurring in waters ranging in depth from the intertidal to greater than 200 m. Very little is known of *Paguristes* species in Australian waters. The described Australian species are *P. aciculus* Grant, 1905, *P. brevirostris* Baker, 1905, *P. frontalis* (H. Milne Edwards, 1836), *P. pugil* McCulloch, 1913, *P. squamosus* McCulloch, 1913, *P. sulcatus* Baker, 1905 and *P. tuberculatus* Whitelegge, 1900. *Paguristes barbatus* (Heller, 1862) possibly occurs in Australia as noted by Alcock (1905) though this was disputed by McCulloch (1913). *Paguristes setosus* (H. Milne Edwards, 1848) has been recorded from New Guinea and New Zealand (Stimpson 1859, Alcock 1905) and hence might be expected to occur in Australia.

Recent collection by hand, snorkelling, and SCUBA of hermit crabs from littoral and shallow sublittoral waters of southwestern Australia from Esperance (33°52′S, 121°53′E) in the east to Dongara (29°15′S, 114°56′E) in the north and west yielded specimens of *Paguristes frontalis* and *P. sulcatus,* and of two undescribed species. The new species are described in this paper. A key is provided for the known species of *Paguristes* in Australia.

Western Australian Museum registration numbers are prefixed by WAM. Shield length is abbreviated as SL, carapace length as CL and Western Australia as W.A.

Paguristes longisetosus, new species
Fig. 1A–G

Material examined.—Holotype ♂, SL 7.3 mm, CL 11.8 mm, Two Mile Beach, east of Hopetoun, 33°57′S, 120°07′E, W.A.; shallow sublittoral rocky platform, in shell of *Thais orbita* (Gmelin, 1791); 28 Nov 1985, G. J. Morgan, WAM 1441-86. Paratypes 2 ♂♂, SL 7.3 mm and 5.0 mm, 1 juvenile in shell, type locality, from *Phasianella ventricosa* Swainson, 1822, *Nerita atramentosa* Reeve, 1855, and *Cominella eburnea* (Reeve, 1846) shells respectively; 28 Nov 1985, G. J. Morgan, WAM 1442-86. 2 ♂♂, SL 4.9 mm and 2.4 mm, 2 ♀♀, SL 4.3 mm (ovigerous) and 2.3 mm, 1 juvenile, Frenchmans Bay, 35°05′S, 117°56′E, near Albany, W.A.; shallow sublittoral rocks and sand, in shells of *Thalotia conica* (Gray, 1827); 19 Apr 1986, G. J. Morgan, WAM 1443-86.

Diagnosis.—Rostrum narrow and exceeding lateral projections. Ocular acicles multispinous. Antennular peduncles slightly shorter than or similar in length to ocular peduncles. Antennal flagella much shorter than carapace. Chelipeds subequal and spinose. Posterior lobes of telson with marginal spines. Long setae on chelipeds, pereopods and tailfan, but not obscuring spines. Coloration generally brown with cream or white spines and scattered red patches.

Description.—Shield (Fig. 1A) slightly

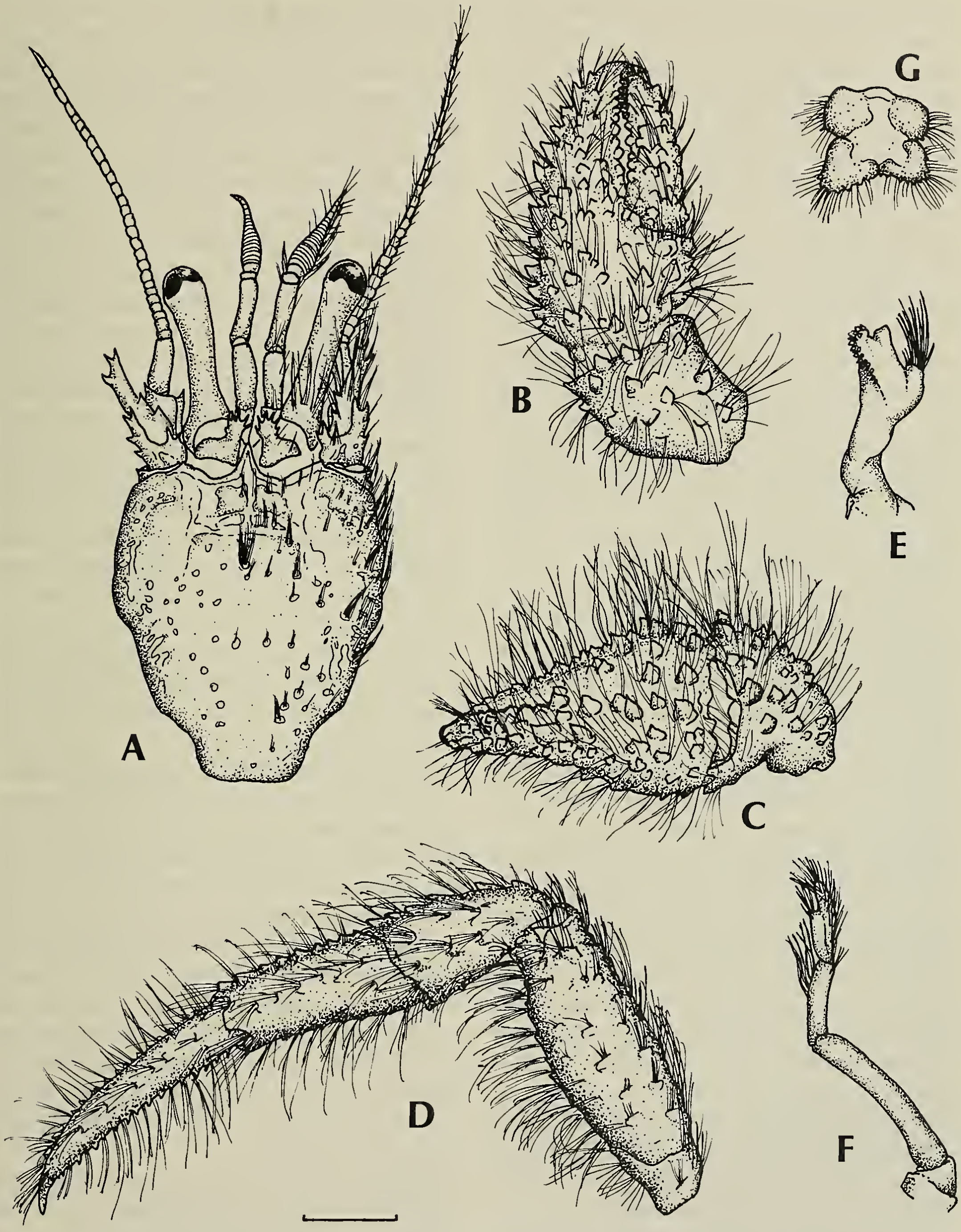

Fig. 1. *Paguristes longisetosus,* holotype ♂: A, Shield and cephalic appendages (dorsal view) (setae omitted left side); B, Left cheliped (dorsal); C, Left cheliped (lateral); D, Left second pereopod (lateral); E, Left first pleopod (lateral); F, Left second pleopod (ventral); G, Telson (dorsal). Scale = 2.0 mm (A–D, G); 1.2 mm (E, F).

longer than broad. Anterior margin between rostrum and lateral projections concave; rostrum narrow, very produced and exceeding lateral projections; lateral projections usually with small terminal spinule. Dorsal surface of shield punctate and sculptured, with coarse setae scattered dorsally, denser laterally.

Ocular peduncles long and generally cylindrical, approximately same length as width of anterior margin of shield; peduncles slightly inflated proximally and nearly naked except for long setae on proximodorsal surface. Ocular acicles multispinous, with 5 large and 1 small distal spines on holotype, 3–5 spines on paratypes; mesial margins slightly concave, lateral margins approximately right angular; acicles separated basally by slightly less than ½ basal width of one acicle.

Antennular peduncles slightly shorter than or similar in length to ocular peduncles. Ultimate and penultimate segments unarmed, proximal segment with 4 distolateral and 1 distomesial spines. Peduncular setation sparse.

Antennal peduncles reaching to distal third of ocular peduncles. Fifth (ultimate) segment unarmed; fourth segment with dorsolateral spine; third with distal apical spine; second with bifid distolateral spine, 1–2 lateral spines and 1–2 spines at distomesial angle; first segment with 1–2 lateral spines. Antennal acicle reaching to or very nearly to distal end of ultimate peduncular segment; acicle terminating in bifid spine, distolateral margin with 1–2 spines, proximomesial edge with 1–3 spines. Antennal flagella much shorter than carapace. Long sparse setae on peduncular segments, longer and denser on acicle; flagellar articles each with about 10 moderately long setae.

Chelipeds (Fig. 1B, C) subequal, very spinose and hirsute; no distinct sexual dimorphism. Dactyl slightly longer than half length of propodus; cutting edge with irregularly-sized teeth, row of about 10 corneous teeth distally and large terminal corneous tooth; dorsal and mesial surfaces with irregularly distributed spines and tubercles, larger dorsally, some corneous tipped. Dactyl slightly overlapped by fixed finger distally, small but distinct gap between fingers proximally. Fixed finger with irregularly sized cutting teeth, generally larger than those on dactyl, and large corneous terminal tooth; irregularly-sized and distributed spines and tubercles on dorsal and lateral surfaces, also on palm; spines on ventrolateral surface of propodus and ventral surface posterior to dactyl. Palm slightly broader than long. Carpus almost as broad as long, subtriangular, shorter than merus; spines on dorsal and lateral surfaces, some corneous tipped; small spine at distoventral margin. Merus compressed laterally; low tubercles on dorsomesial and lateral faces, small spines and denticles along distal, ventromesial and ventrolateral edges. Setation heavy on dactyl, propodus and carpus; setae long, mostly in clumps around base of spines but not obscuring spines, especially on dorsal surfaces; merus less hirsute, most setae along distal margin and ventral surface.

Second pereopod (Fig. 1D) slightly longer than cheliped. Dactyl longer than propodus, terminating in strong corneous claw; 18–21 and 22–25 corneous spines along ventral and dorsomesial edges respectively, ventral spines longer. Propodus with dorsal row of 8–9 spines, ventrally some small spinules at setal bases. Carpus shorter than merus, several spines on dorsal surface, tubercles at setal bases. Merus laterally compressed, unarmed except for row of spinules along ventral and dorsal margins. Tufts of long simple setae on all segments, especially on dorsal and ventral margins.

Third pereopod similar to second.

Sternite of third pereopod with anterior lobe subrectangular, gradual concavity posteriorly, abruptly concave anteriorly.

First and second pleopods of male paired, illustrated in Fig. 1E, F. Females with paired gonopores and first pleopods; brood pouch subquadrate.

Tailfan very asymmetrical, left uropods much larger than right. Telson (Fig. 1G) with left posterior lobe larger than right; left lobe with 9 spines along posterior margin, right lobe with 9–10 posterior spines also distributed along lateral margin. Anterior lobes of telson each with 1–2 lateral spinules. Telson and uropods fringed with long setae.

Coloration (in life).—Shield pale brown with setal pores cream or white and darker red/brown patches, especially along midline and midlaterally. Ocular peduncles and acicles pale brown, darker proximally; corneas black. Antennular and antennal peduncles and flagella red/brown. Chelipeds pale brown with white spines and tubercles; some red patches on carpi and meri. Pereopods red or red/brown, with white patches at setal bases forming irregular dorsal, lateral and ventral rows. Setae pale yellow or yellow/brown.

Eggs.—Ovigerous female with 15 relatively large (maximum diameter 1.2–1.3 mm) subspherical orange eggs.

Etymology.—From the Latin for "long bristles."

Remarks.—This species is readily recognizable in southern Australia by the long setae and acute spines on the chelipeds. Unlike *Paguristes sulcatus* which also occurs along southwestern Australian shores, the setae do not obscure spination of the chelipeds. In *P. squamous* McCulloch and *P. pugil* McCulloch from southeast Australia, the palm of the chelipeds bears crenulate squamiform tubercles (McCulloch 1913).

Paguristes longisetosus is presently known only from the Hopetoun and Albany regions of Western Australia.

Paguristes purpureantennatus, new species

Figs. 2A–I, 3A

Material examined.—Holotype ♂, SL 21.2 mm, CL 33.3 mm, Cosy Corner, 35°06′S, 117°37′E, near Migo Island, Torbay, west of Albany, W.A.; 3 m, rocks and sand near *Amphibolis* and *Posidonia* seagrasses, in shell of *Campanile symbolicum* Iredale, 1917; 1 Dec 1985, G. J. Morgan, WAM 1438-86. Paratypes ♂, SL 22.2 mm, 3 ♀♀, SL 19.0 mm (ovigerous), 15.6 mm, 15.6 mm, near Dyer Island, Rottnest Island, 32°00′S, 115°30′E, W.A.; 3–4 m, rock and sand, in *C. symbolicum* shells; 19 Dec 1985, G. J. Morgan, WAM 493-86.—2 ♀♀, SL 14.8 mm, 12.9 mm (both ovigerous), Geordie Bay, Rottnest Island, W.A.; 6 m, rock and sand, in *C. symbolicum* shells; 18 Dec 1985, G. J. Morgan, WAM 405-86.—2 ♂♂, SL 10.9 mm, 10.2 mm, offshore from Rottnest Island hotel, W.A.; 6 m, rock and sand; 19 Dec 1985, G. J. Morgan, WAM 403-86.—♀, SL 18.2 mm (ovigerous), Parker Point, Rottnest Island, W.A.; 3 m, sand, rock and *Pocillopora* coral; 19 Dec 1985, G. J. Morgan, WAM 500-86.—2 ♂♂, SL 9.5 mm and 3.8 mm, 1 juvenile, Cliff Head, 29°32′S, 114°59′E, south of Dongara, W.A.; 2–3 m, sand and rock near seagrasses; 23 Apr 1986, G. J. Morgan, WAM 1440-86.—♀, SL 4.5 mm, 4 juveniles, Seven Mile Beach, 29°11′S, 114°53′E, north of Dongara, W.A.; 1–3 m, sand and rock, in *Rhinoclavis bituberculatum* (Sowerby, 1855) shells; 22 Apr 1986, G. J. Morgan, WAM 1439-86.

Diagnosis.—Rostrum narrow, exceeding lateral projections. Ocular acicles simple, approximate distally. Antennular peduncles slightly shorter than or similar in length to ocular peduncles. Antennal flagella shorter than carapace. Chelipeds very unequal, left much larger than right; dactyls and propodi densely covered with small tubercles, dactyl of right cheliped with similarly sized tubercles. Lateral surfaces of propodi of chelipeds with distinct longitudinal ridge. Dactyls of pereopods 2 and 3 much longer than propodi. Shield red; pereopods covered with fine, short longitudinal red flecks; antennules and antennae lilac or purple.

Description.—Shield (Fig. 2A) approximately 1.5 times longer than broad. Anterior margin between rostrum and lateral projections concave; rostrum narrow, very produced and much exceeding lateral pro-

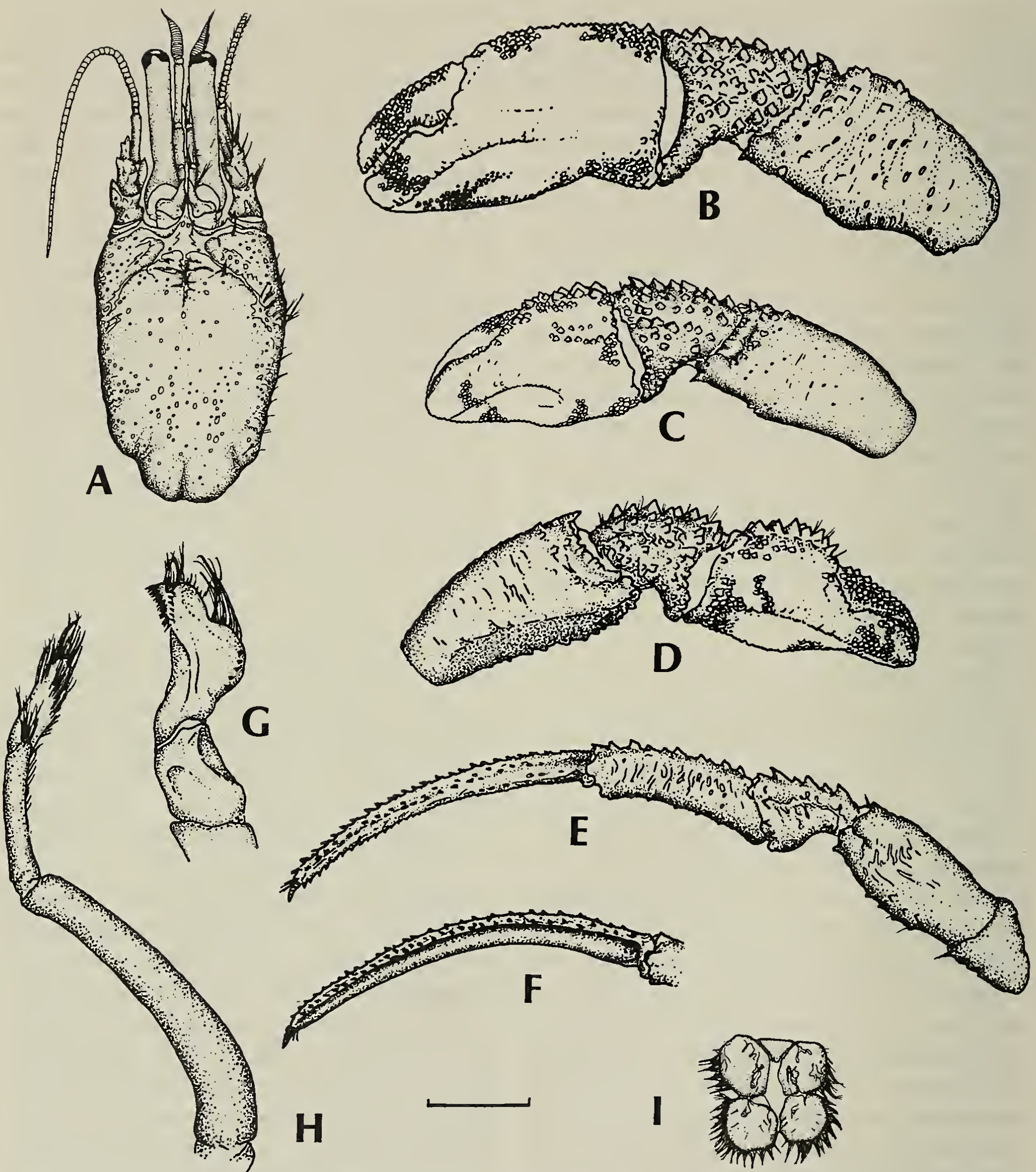

Fig. 2. *Paguristes purpureantennatus,* A, B, D–I, holotype ♂; C, paratype ♀, SL 19.0 mm: A, Shield and cephalic appendages (dorsal view) (setae omitted left side); B, Left cheliped male (lateral); C, Left cheliped female (lateral); D, Right cheliped male (lateral); E, Left second pereopod (lateral); F, Dactyl of left third pereopod (lateral); G, First pleopod male (lateral); H, Second pleopod male (ventral); I, Telson (dorsal). Scale = 10.0 mm (B, D–F); 8.0 mm (A, C, I); 2.6 mm (G, H).

jections; lateral projections with terminal spinule. Dorsal surface of shield punctate and anteriorly sculptured, with very light setation. Some spinules laterally.

Ocular peduncles long and cylindrical, approximately same length as width of anterior margin of shield; peduncles slightly inflated proximally and almost naked. Ocular acicles simple, mesial margins convex, lateral margins almost right angular; acicles approximate at tips, separated basally by less than half basal width of one acicle.

Antennular peduncles slightly shorter than or similar in length to ocular peduncles; peduncular segments unarmed and sparsely setose.

Antennal peduncles reaching to or slightly beyond half length of ocular peduncles. Fifth (ultimate) segment unarmed; fourth with small dorsolateral spine; third with distal apical spine; second with distolateral (often bifid) and distomesial spines; first segment unarmed. Antennal acicle reaching to proximal third or half length of ultimate peduncular segment; acicle with terminal spine, 2 distolateral spines and 1–2 proximomesial spines. Antennal flagella shorter than carapace (sometimes similar length on small specimens). Antennal setation sparse, densest on third peduncular segment and on acicle; flagella with very short setae.

Left cheliped of males (Fig. 2B) much larger than right. Dactyl half length or slightly shorter than half length of propodus; cutting edge with small, rounded cutting teeth, recessed proximally, and about 11-12 small distal corneous teeth; all surfaces of dactyl densely tuberculate. Dactyl touching fixed finger distally, narrow gap between fingers proximally. Fixed finger with small cutting teeth, protruding into proximal dactylar recess; finger with distinct broad lateral ridge curving from distal apex to lateral surface of palm, ventrolateral surface of finger and distal palm shallowly concave; sharper ventral ridge from apex of finger to distal palm, flattening on proximoventral surface of palm; blunt dorsal ridge on palm. Fixed finger and palm densely covered by small blunt tubercles, largest dorsally and very small and flattened on ventrolateral surface. Palm slightly longer than broad. Carpus longer than broad, subtriangular, much shorter than merus; carpus spinose, spines smallest laterally and mesially, larger dorsally. Merus slightly compressed laterally; dorsal and ventromesial edges with small blunt spines, elsewhere with small scattered tubercles. Setae extremely sparse on all segments.

Left cheliped of females (Fig. 2C) smaller and less robust than that of males, but still larger than right cheliped. Propodus and dactyl densely tuberculate, larger tubercles dorsally, midlaterally and ventrally on propodus.

Right cheliped of males (Fig. 2D) more elongate than left, right propodus about ¾ length of left propodus. Dactyl approximately half length of propodus; small cutting teeth, recessed proximally, and numerous small corneous distal teeth fusing into large apical tooth; dactyl densely tuberculate, most tubercles similarly-sized though sharper dorsomesially and slightly larger proximally. Fixed finger with small cutting teeth, cutting edge produced into recess of dactyl, distal tip only slightly corneous; distinct broad lateral ridge and sharp ventral ridge on fixed finger and propodal palm, ventrolateral surface of propodus flattened. Propodus densely tuberculate, tubercles very small on ventrolateral and mesial surfaces; 1–2 irregular rows of blunt spines on dorsal ridge of palm. Carpus laterally compressed, much shorter than merus; dorsal margin with large broad-based spines, lateral and dorsomesial surfaces with spaced tubercles and small spines, ventromesial surface quite smooth. Merus with small distal spines; scattered tubercles on dorsal and lateral surfaces, small denticles along ventral edge; mesially smooth. Setation light, most setae on dorsomesial surfaces of propodus and carpus. Right cheliped of females similar to that of males, though tubercles usually slightly larger on proximodorsal surface of dactyl and lateral surface of propodus. Propodus and carpus less setose than on males.

Second pereopod (Fig. 2E) distinctly longer than left cheliped. Dactyl much longer than propodus, terminating in corneous claw; ventral row of corneous spines, largest distally, proximally very small; dense clumps of short, very thick setae in irregular rows on dorsal surface. Propodus with 8–

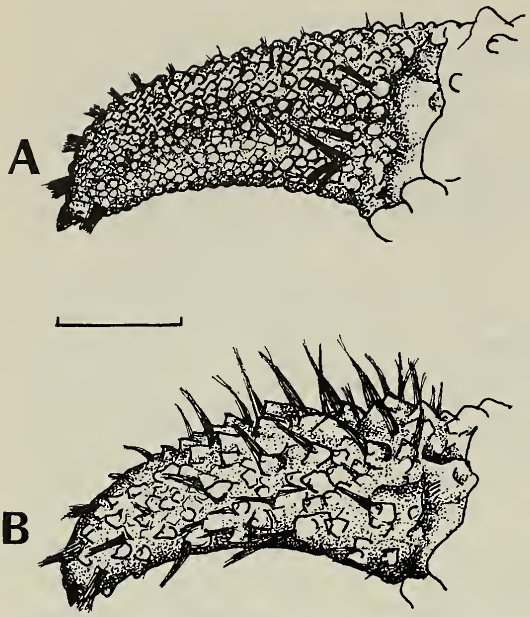

Fig. 3. Dactyl, right cheliped (mesial view): A, *Paguristes purpureantennatus*, holotype; B, *P. frontalis*, SL 24.0 mm. Scale = 4.0 mm.

11 dorsal spines, and several small scattered dorsomesial spines; small spinules ventrally. Carpus laterally compressed and with longitudinal sulcus, much shorter than merus; about 5 dorsal spines, 1–2 distolateral spines and often distolateral spinules. Merus laterally compressed, with row of small ventral spines and some dorsal spinules; 1–2 spines at distolateral angle.

Third pereopod slightly longer than second; dactyl and propodus longer, and merus shorter and less compressed, than those segments of second pereopods. Right third pereopod longer than left. Dactyl (Fig. 2F) with sharp dorsolateral longitudinal ridge; terminating in corneous spine but lacking ventral spines; clumps of short, thick setae in irregular dorsal rows. Propodal and carpal spines smaller than on second peropod. Pereopods 2 and 3 sparsely setose; pereopods 4 and 5 with denser dorsal and ventral setation.

Sternite of third pereopod with abrupt posterior indentation and gradually concave, converging lateral sides.

First and second pleopods of male paired, illustrated in Fig. 2G, H. Females with paired gonopores and first pleopods; brood pouch very elongate, subtriangular.

Tailfan very asymmetrical, left uropods much larger than right. Telson (Fig. 2I) with posterior lobes subquadrate, left lobe slightly larger than right; margins of both lobes unarmed, fringed with long setae.

Coloration (in life).—Shield bright red or red/brown, thorax slightly paler. Ocular peduncles orange or red, corneas black, ocular acicles orange or red. Antennular and antennal peduncles and flagella lilac or purple. Dactyls of chelipeds cream or white, sometimes tinged with pink, sometimes with pale small orange dots; propodi of chelipeds similar to dactyls, often tinged red/orange proximally; carpi and meri red/orange with white spines and tubercles. Pereopods cream or orange with numerous red or deep pink short longitudinal flecks. Very small individuals paler, pereopods cream with orange flecks.

Eggs.—Eggs subspherical, maximum diameter 1.5–1.8 mm, orange.

Etymology.—From the Latin "purpureus," purple, and "antenna."

Remarks.—This large species closely resembles *Paguristes frontalis* which occurs in Victoria (Phillips et al. 1984) and South Australia (Hale 1927) and ranges into Western Australia at least as far west and north as Cape Naturaliste, 180 km south of Perth. *Paguristes purpureantennatus* has been less frequently collected, though probably often confused with *P. frontalis,* and is presently known only from Western Australia from the Albany region west and north to Dongara, including Rottnest Island. The ranges of the two species therefore overlap considerably but I am not aware of their occurrence at the same locality. Microhabitat preferences of the species are not known though both inhabit broadly similar environments of shallow subtidal waters, usually in association with rocky reefs, and both frequently utilize the large *Campanile symbolicum* shells.

The two species differ in several small but distinct morphological characters. The lateral surfaces of left and right chelipeds of *P. purpureantennatus* are more distinctly ridged than on *P. frontalis.* The dactyl of the right cheliped of *P. purpureantennatus* is ornamented dorsomesially with closely packed similarly-sized tubercles, while the dactyl of *P. frontalis* bears more widely spaced, irregularly sized spines and tubercles (Fig. 3). The dactyl, propodus and carpus of the right cheliped of male *P. purpureantennatus* are less setose than those of *P. frontalis.* Dactyls of pereopods 2 and 3 are relatively longer on *P. purpureantennatus.*

The most obvious difference between the species is their respective coloration. *Paguristes purpureantennatus* is predominantly bright red on the shield with pereopods 2–5 cream or orange and densely flecked with red or deep pink. The antennules and antennae are lilac or purple and ocular peduncles uniformly orange or red. *Paguristes frontalis* is deep salmon on the shield, with pereopods similarly colored and only sparsely dotted with deep red/brown spots at setal pores. Antennules and antennae are salmon/brown and ocular peduncles salmon with an orange band proximal to corneas. The species can be distinguished readily by coloration while alive.

There was some difficulty in deciding which of the two species was originally described as *P. frontalis.* Milne Edwards's (1836) description is insufficiently detailed to permit certain identification, but the illustration (pl. 14, fig. 1) supports the present designation in that the dactyl of the right cheliped appears to bear irregularly sized tubercles and the dactyls of pereopods 2 and 3 are not as long as those of *P. purpureantennatus.* The redescription of *P. frontalis* by Baker (1905) is more detailed though similarly inconclusive, but examination of South Australian specimens described by Baker and other material labelled *P. frontalis* in the South Australian Museum collection confirmed the present designation. The specimen illustrated in Hale (1927) as *P. frontalis* would appear to bear only scattered dark spots on pereopods, again supporting the present decision.

Key to Australian Species of *Paguristes*

1\. Chelipeds subequal 2
– Left cheliped obviously larger than right 7
2\. Rostrum broad, only slightly exceeding lateral projections 3
– Rostrum acute, much exceeding lateral projections 4
3\. Ocular acicles simple .... *P. aciculus* Grant
– Ocular acicles multispinous .... *P. brevirostris* Baker
4\. Setae on chelipeds very long, but not obscuring spines *P. longisetosus,* n. sp.
– Setae on chelipeds moderately long, very dense and obscuring spines .. 5
5\. Dorsal surface of propodus of chelipeds with acute spines .... *P. sulcatus* Baker
– Dorsal surface of propodus of chelipeds with crenulate squamiform tubercles 6
6\. Carpus of chelipeds with anterodorsal rounded boss .... *P. pugil* McCulloch
– Carpus of chelipeds lacking boss . ... *P. squamosus* McCulloch
7\. Rostrum short, not exceeding lateral projections; left cheliped spinose .... *P. tuberculatus* Whitelegge
– Rostrum long, much exceeding lateral projections; left cheliped finely tuberculate 8
8\. Dactyl of right cheliped with irregularly-sized tubercles and spines; pereopods salmon with scattered red spots, antennae red/orange .... *P. frontalis* (H. Milne Edwards)
– Dactyl of right cheliped with dense, similarly-sized tubercles; pereopods cream/orange with dense red speckling, antennae purple .... *P. purpureantennatus,* n. sp.

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REVISION OF THE GENUS *GOLFINGIA* (SIPUNCULA: GOLFINGIIDAE)

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Abstract.—The species in the sipunculan genus *Golfingia* (*Golfingia*) are reviewed and evaluated in light of 13 historically used morphological characters. Whenever possible type material was examined. The monograph of Stephen and Edmonds (1972) was used as a starting point and changes made in the intervening years are reiterated here. Of the 40 putative species listed in that work or described since then, 12 remain valid species (two moved to other genera), three are reduced to subspecific rank, four are considered either *species inquirendum* or *incertae sedis,* and the remainder (21) are considered junior synonyms. One new monotypic subgenus (*Spinata*) is described. The known distribution of each species is summarized and a key is provided.

This is the last in a series of revisionary articles (begun in Cutler and Murina 1977) addressing those taxa previously treated as subgenera of the sipunculan genus *Golfingia.* Earlier papers dealt with *Mitosiphon, Fisherana,* and *Apionsoma* (Cutler 1979), *Golfingiella* and *Siphonoides* (Cutler, Cutler and Gibbs 1983), *Thysanocardia* (Gibbs, Cutler and Cutler 1983), and *Nephasoma* = *Phascoloides* (Cutler and Cutler 1986). The starting point for this paper is the monograph of Stephen and Edmonds (1972) and includes all 35 names listed as valid species in that work, one from another genus, plus the four named since that time. Table 1 lists those names and their current status.

This taxon traces its origins back to an "outing on the greens" of 19th century St. Andrews, Scotland: ". . . and I have accordingly ventured to dedicate the new genus of Sipunculid worms indicated by this specimen to the local goddess whose cult is historically associated with the most ancient of Scottish seats of learning" (Lankester 1885:469). There was subsequent confusion about the proper use of this name and the generic name *Phascolosoma* until Fisher clarified the matter in 1950.

Whenever possible we have obtained type material to verify the original descriptions. In several cases we have made detailed observations on series of recently collected individuals to evaluate better the traditionally used morphological characters. Much of the material for this analysis of variation within populations came from collections near the Kerguelen Islands.

We first discuss the morphological characters in light of our recent analyses. This is followed by a section where each of the species we consider to be valid is discussed; this includes a synonomy and discussion of newly added junior synonyms. The two species previously transferred to other genera and the four species considered to be *incertae sedis* or *species inquirendum* are discussed separately. A key to all the valid species and a summary of their distribution is presented.

The following abbreviations are used in this text for the museums from which we borrowed material: Australian Museum, South Sydney (AMSS); British Museum (Natural History) (BMNH); Irish National Museum, Dublin (INMD); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum für Naturkunde der Humboldt-Universitat zu Berlin (MNHU); Musée

Table 1.—Original and proposed names of species of *Golfingia.*

Original name	Proposed name
Golfingia anderssoni (Théel, 1911)	no change
Golfingia anguinea (Sluiter, 1902)	species inquirendum
Golfingia appendiculata (Sato, 1934)	*Golfingia muricaudata*
Golfingia birsteini Murina, 1973	no change
Golfingia cantabriensis Edmonds, 1960	*Golfingia margaritacea*
Golfingia capensis (Teuscher, 1874)	no change
Golfingia charcoti (Hérubel, 1906)	*Golfingia elongata*
Golfingia cylindrata (Keferstein, 1865)	*Golfingia elongata*
Golfingia derjugini (Gadd, 1911)	*Golfingia elongata*
Golfingia elongata (Keferstein, 1863)	no change
Golfingia glossipapillosa (Sato, 1934)	*Golfingia margaritacea*
Golfingia herdmani (Shipley, 1903)	*Golfingia vulgaris herdmani*
Golfingia hudsoniana (Chamberlin, 1920)	*Golfingia muricaudata*
Golfingia ikedai Fisher, 1950	*Golfingia margaritacea*
Golfingia iniqua (Sluiter, 1912)	no change
Golfingia kolensis (Gadd, 1911)	*Golfingia vulgaris*
Golfingia lagensis (Fischer, 1895)	incertae sedis
Golfingia liochros Cutler & Cutler, 1979	*Golfingia vulgaris herdmani*
Golfingia margaritacea (Sars, 1851)	no change
Golfingia mawsoni (Benham, 1922)	*Golfingia margaritacea ohlini*
Golfingia mirabilis Murina, 1969	no change
Golfingia muricaudata (Southern, 1913)	no change
Golfingia mutabilis (Southern, 1913)	*Golfingia iniqua*
Golfingia nordenskjoldi (Théel, 1911)	*Golfingia margaritacea*
Golfingia nota (Sato, 1934)	*Golfingia margaritacea*
Golfingia ohlini (Théel, 1911)	*Golfingia margaritacea ohlini*
Golfingia okinoseana (Ikeda, 1904)	*Golfingia margaritacea*
Golfingia owstoni (Ikeda, 1904)	*Golfingia vulgaris*
Golfingia pectinatoida Cutler & Cutler, 1979	*G.* (*Spinata*) *pectinatoides*
Golfingia profunda (Roule, 1898)	*Golfingia margaritacea*
Golfingia pudica (Selenka, 1885) (partim)	*Golfingia margaritacea ohlini*
Golfingia recondita (Sluiter, 1900)	*Apionsoma recondita*
Golfingia reticulata (Hérubel, 1925)	incertae sedis
Golfingia rugosa (Southern, 1913)	*Golfingia iniqua*
Golfingia scutiger (Roule, 1906)	incertae sedis
Golfingia signa (Sato, 1934)	*Golfingia margaritacea*
Golfingia solitaria (Sluiter, 1912)	*Golfingia vulgaris*
Golfingia soya (Sato, 1934)	*Golfingia margaritacea*
Golfingia trichocephala (Sluiter, 1902)	*Apionsoma trichocephala*
Golfingia vulgaris (de Blainville, 1827)	no change

Océanographique, Monaco (MOMV); Naturhistoriska Riksmuseet, Stockholm (NHRS); National Museum of Canada, Ottawa (NMCO); National Science Museum, Tokyo (NSMT); Royal Scottish Museum, Edinburgh (RSME); University Museum, Oxford (UMOU); United States National Museum (USNM); Zoologisk Museum, Copenhagen (UZMK); Zoological Institute, Leningrad (ZIAS); Zoological Institute, Tohoku University, Sendai (ZITU); Zoologisch Museum, Universiteit van Amsterdam (ZMUA); Zoological Museum, Bergen (ZMUB); Zoological Museum, Hamburg (ZMUH).

Morphological Characters

The following section includes comments on those features which have historically been used by systematists to describe and differentiate species within this genus. These descriptions were legitimate attempts but not always based on a good understanding of possible variation within a population (species). These characters are the same as those used in *Nephasoma.* In Cutler and Cutler (1986) parallel observations are presented for that genus. There are striking parallels between these two genera and obvious "species pairs" exist. For example, there is one species in each genus with large bulbous inflated papillae and distinct tails on the posterior end of the trunk (*G. anderssoni* and *N. flagriferum*) and one species in each with hooks in rings (*G. elongata* and *N. rimicola*). *Golfingia margaritacea* and *N. eremita* are twins except for the lack of dorsal retractors in the latter.

1. *Introvert hooks.*—Several species are known to have deciduous hooks and we suspect this is true for most species. Those few putative species reported as lacking hooks are based on individuals over 10 mm long and hooks may have been present in earlier ontogenetic stages. The only "hookless" species remaining after this work is *G. anderssoni* for which the smallest animal recorded to date has a 25 mm trunk. Most species in the genus have small (20–40 μm), scattered, pale hooks. Two species have large (150–300 μm), slender, spinelike hooks (*G. birsteini* and *G. mirabilis*). Between these two extremes are *G. muricaudata* (50–150 μm in small worms) and *G. vulgaris* with dark hooks generally 50–120 μm tall (Saiz-Salinas 1986 reported 20–275 μm hooks and Edmonds 1956 reported 120–200 μm hooks in his var. *queenslandensis* = *G. vulgaris herdmani*).

Two species that have hooks in rings are *G. elongata* (45–100 μm) and *G.* (*Spinata*) *pectinatoides* (25–30 μm). These latter ones are unique as they have a small comb of basal spinelets like several of the *Apionsoma* species.

2. *Tentacles.*—The standard pattern is a series of digitate circumoral tentacles whose number and complexity increases with age (Fig. 1; see also Théel 1905, pl. 14, figs. 192–195 or Gibbs 1977). Adult specimens commonly have 16–40 units but the number may exceed this in large worms (over 10 cm). The array in *G. nordenskjoldi* was alleged to consist of only two tentacles but what was seen is only the tips of the two larger, dorsal tentacles in an incompletely expanded specimen of *G. margaritacea.* A few species have been reported to have fewer than 16 but most of these were based on small individuals and may not be meaningful. *Golfingia birsteini* with 8–10 very short ones may be one real exception. The tentacular crown in *G.* (*Spinata*) *pectinatoides* may be unique, being neither the standard array nor nuchal tentacles. The small diameter and partially retracted state of the specimens precludes a definitive statement.

3. *Caudal appendage.*—The posterior end of the trunk in most species comes to a blunt, rounded terminus but may form a "pencil point" due to contraction of the circular muscle layer (Fig. 2). There are two species (*G. anderssoni* and *G. muricaudata*) which do exhibit a distinct caudal appendage (tail) of variable length being rudimentary in small individuals. This can be a useful character unless the worm is damaged or less than 5 mm long when its apparent absence could be misleading.

4. *Trunk length to width ratio.*—Most species have cylindrical trunks with the length exceeding the diameter by 5–10 times. Since these are very elastic muscular sacs, selective contraction and relaxation of muscle layers can greatly modify these proportions in a single individual and therefore these measurements should not be used in a precise or strict way. There is only one species which is very elongate—*G. birsteini* has a trunk 15–20 times longer than wide. *Golfingia elongata* has been reported as having similar proportions but most individuals are less elongate. One species is consistently at the other end of the spectrum—*G. iniqua* almost always has a length only about three times the diameter, i.e., plump and stout.

5. *Introvert length.*—This measurement is

usually presented as a proportion of the trunk length and there are three problems here: A. As has been demonstrated in other genera the relative length of these two body parts changes with age, the introvert being a larger part of the whole in younger animals and appearing to decrease in relative size due to allometric growth. B. The second problem results from the very plastic form of these animals and extreme elasticity of the introvert in particular. When the introvert is measured in the withdrawn condition the value obtained will be much shorter than in the same worm with a fully extended introvert. C. The third problem results from different ways of determining where the introvert/trunk junction is, i.e., where does the introvert start? We have defined this as being just anterior to the nephridiopores (or anus in those taxa where this is anterior). With this understanding it can be asserted that most species have introverts 0.7–1 times the trunk length. *Golfingia* (*Spinata*) *pectinatoides* has a significantly longer one (up to 2×). One other apparent anomaly is in *G. rugosa* = *iniqua.* The worm Southern (1913) described was 5 mm long: "The proboscis is invaginated for a distance of 2 mm, and its total length from the anus to the tentacular crown is 8.5 mm." This was changed in Stephen and Edmonds (1972: 107) to read "Introvert up to about 10.5 mm . . . ." This could be read as having an introvert twice the trunk length but in Southern's one worm it should read 1.7× and, more importantly note the small trunk size which reaffirms point A above. Another confusing situation occurs with *G. muricaudata.* Southern (1913) gives measurements which include total length (introvert, trunk and tail) and says that there is "thus considerable variation in the relative proportions." If one discounts the tail, since it is not part of the trunk but only an appendage, the introvert lengths range from 62–89% of the trunk length. Sato's (1934) data were misinterpreted by Stephen and Edmonds (1972:109) to suggest a short introvert (less than 50%) in *G. soya.* Some of his measurements are of incompletely extended introverts and the actual range is 65–75%. In summary, except for *G.* (*Spinata*) *pectinatoides,* the introvert is from 65–100% of the trunk length in *Golfingia* species and is not a useful character for differentiating species.

6. *Anus/nephridiopores relationship.*—In this genus the anus is either at the same anterior/posterior level of the nephridiopores or slightly posterior to them. In the latter case the distance is rarely more than 1–2 mm in larger worms.

7. *Papillae distribution/size/shape.*—The epidermis of sipunculans has a variety of glandular bodies capable of producing mucus and other products. The number and density of these structures, the degree to which these protrude above the surface to form papillae and the particular shape of these papillae is extremely variable. In almost all species these are more numerous in the anterior and posterior 10–20% of the trunk. These are especially distinct in *G. vulgaris* and large on the posterior end of *G. anderssoni,* but aside from these exceptions, the specificity of form and size ascribed to various species by earlier authors is misleading. Our observations suggest that the age (older worms have larger papillae), microhabitat (a close-fitting hard dwelling stimulates larger papillae) and postmortem chemical history of the worm (bleaching of pigment) has a significant impact on the morphology of these papillae.

8. *Shields.*—This term has caused some confusion within this phylum. The Aspidosiphonidae have a hardened epidermal structure (calcium carbonate or scleroprotein) at the anterior end of the trunk (sometimes posterior also) which is called a shield. This same term has been used to describe a different situation in this genus, i.e., an aggregation of close-packed papillae around the ends of the trunk giving it a dark, rugose appearance as in *G. vulgaris* and its subspecies (Edmonds 1980:19). This is not a shield

as the term is used in the Aspinosiphonidae and its use here should be avoided. A recent example of the problem is in Murina's (1969: 1732) description of *G. mirabilis* where she said "At both ends of the trunk papillae are distributed thickly enough and resemble a shield." Murina (1975) also used this term when creating her new subgenus *Dushana* (see below).

9. *Spindle muscle.*—In most sipunculans there is a thin thread-like muscle running through the gut coil and connecting to it at intervals. The origin of this muscle is either on the body wall anterior to the anus (as in *G.* (*Spinata*)), or from the wall of the rectum, wing muscle or a small flap of tissue just under it (as in *Golfingia* (*Golfingia*)). This muscle terminates posteriorly within the gut coil in this genus. In some other genera it extends out of the coil and attaches to the posterior end of the trunk. Whether this muscle is described as strong or weak can be a semantic issue depending on that author's experience and frame of reference. While it may not be equally developed, all *Golfingia* species do have one.

10. *Retractor muscles' point of origin.*—The two pairs of muscles which insert behind the 'head' and function to retract the introvert have their origins on the inner surface of the trunk wall. The position of these attachments along the anterior/posterior axis has been assumed to be meaningful by many authors (Benham 1922 is one exception). Our data from *Nephasoma* suggest that the relative position does change during growth, resulting in an apparent anteriad shift in the point of origin (Cutler and Cutler 1986). The data from this genus are less clear, perhaps because of fewer large worms. The most common condition is for the ventral pair to have its origin in the middle third (35–65% of the distance to the posterior end) and the dorsal pair more anteriorly (10–20%). Two apparent exceptions to this may be in some large *G. muricaudata* or the long, slender *G. birsteini* in which the *ventrals* are around 20%. The other exceptions to this rule are in *G. mirabilis* and *G.* (*Spinata*) *pectinatoides* where the dorsal origins are posterior to the ventrals, both in the anterior quarter.

11. *Intestinal coiling.*—As in other genera the number of gut coils increases with age and is not species specific. This number is commonly 20–30 but the reported range is from 10 to 90. Most species exhibits a tightly wound double helix but this can be disrupted and appear loose.

12. *Intestinal fixing muscles.*—The number of fine, thread-like muscles attaching the gut coil to the body wall varies from 0–4 according to published accounts. This has been alleged to be a species-specific character but our experience suggests that these are very fragile structures and can be easily broken, overlooked, and even if present not mentioned by certain authors. The number of muscles within one population also varies (our *G. margaritacea ohlini,* and Gibbs 1973:81 on *G. elongata*). The one species which appears to lack these is *G.* (*Spinata*) *pectinatoides.*

13. *Rectal caecum.*—As in *Nephasoma* this character is difficult to see in small individuals and not consistently present. Also, some authors simply do not mention whether or not it is present but this should not be interpreted as equivalent to being absent.

Summary.—Of these 13 characters six have some usefulness to the systematist (1, 2, 3, 4, 7, 10) while the remaining seven do not help differentiate species within *Golfingia* (*Golfingia*). We have been unable to discern any helpful new morphological characters.

Systematic Section

Genus *Golfingia,* Lankester, 1885

Type species.—*Sipunculus vulgaris* (de Blainville, 1827).

Diagnosis.—Species small to large sized; body wall with continuous muscle layers; oral disc carries tentacles arranged around mouth; four introvert retractor muscles;

contractile vessel without true villi; spindle muscle not attached posteriorly; two nephridia.

Key to *Golfingia* Species

1. Nephridia bilobed, both pair of retractors close to ventral nerve cord, hooks with basal spinelets, spindle muscle anterior to anus .... *G.* (*Spinata*) *pectinatoides*
– Nephridia unilobed, anterior retractors dorso-laterally displaced, hooks (if present) without basal spinelets, spindle muscle posterior to anus or on rectum subgenus *Golfingia* s.s. 2
2. Caudal appendage present 3
– Caudal appendage not present ... 4
3. Large bladderlike papillae at base of caudal appendage ...... *G. anderssoni*
– Base of caudal appendage without large bladderlike papillae .... *G. muricaudata*
4. Introvert hooks in rings .. *G. elongata*
– Introvert hooks scattered, if present 5
5. Anterior and posterior ends of trunk dark and coarsely papillated 6
– Ends of trunk not distinctly different color/texture 7
6. Ventral retractor muscles originate posterior to dorsal pair .... *G. vulgaris*
– Ventral retractor muscles originate anterior to dorsal pair .... *G. mirabilis*
7. Trunk length less than 3 times the width .... *G. iniqua*
– Trunk length more than 3 times the width 8
8. Reduced tentacles, large hooks (>150 μm) .... *G. birsteini*
– Normal tentacles, hooks, if present, small (<75 μm) 9
9. Contractile vessel simple, without bulbous swellings .... *G. margaritacea*
– Contractile vessel with bulbous swellings/vesicles, often orange colored, southern Africa .... *G. capensis*

Golfingia (*Spinata*), new subgenus

Type species.—*Golfingia pectinatoides* Cutler and Cutler, 1979.

Diagnosis.—Small to medium sized with introvert longer than trunk; small hooks with basal spinelets and arranged in rings; slender retractor muscles about equal in size and both pairs very close to ventral nerve cord; spindle muscle originates from the body wall just anterior to anus; nephridia bilobed.

Remarks.—This monotypic subgenus is an inhabitant of shallow warm waters. There is a suite of character states (retractors, hooks and nephridia) which this taxon shares with *Phascolosoma* (*Edmondsius*) *pectinata* and several *Apionsoma* species. This is most likely an example of convergent or parallel evolution. The decision to place this taxon in *Golfingia* is based on the arrangement of the tentacles which appear to be around the mouth (no individual has its introvert completely extended) and the spindle muscle not inserted posteriorly on the body wall. There is real need for closer analysis of these similar species using non-morphological characters. The subgeneric name refers to the presence of small basal spinelets on the hooks.

Golfingia pectinatoides
Cutler and Cutler, 1979

Golfingia pectinatoida Cutler and Cutler, 1979a:951–954, figs. 3–5.

Material examined.—Type material: MNHN and USNM.

This inhabitant of coral reefs is distinctive. The important characters are those of the subgenus. Additionally, the gut is in an irregular loose coil and there are no fixing musles.

Known distribution.—Coral reefs at Tulear, Madagascar, and Moorea Island, French Polynesia, at intertidal depths.

Subgenus *Golfingia* (sensu stricto) Lankester, 1885

Type species.—*Sipunculus vulgaris* (de Blainville, 1827).

Diagnosis.—Introvert equal to or shorter than trunk; simple hooks usually scattered if present (rings in *G. elongata*); anterior pair of retractor muscles with origins more dorsally placed than posterior ventral pair; spindle muscle originates from wall of rectum (sometimes under wing muscle); nephridia unilobed.

We first present a consideration of the most complex "superspecies" in this genus which will be followed by the remaining valid species in alphabetical order.

Comments on the "*margaritacea*" Section

As seems to be true in several genera there is here one very widespread and ill defined species (superspecies?) which has a long and complex history. This morph has retained most of those characters thought to be plesiomorphic (Cutler and Gibbs 1985) with no distinguishing traits other than the lack of anything unique. We here present a summary of those names which have been considered to be some kind of subset of *G. margaritacea* by previous authors. In a later section we propose additional changes.

Sars introduced the name *Sipunculus margaritaceus* in 1851. It consisted of four sentences in Norwegian, had no illustrations and was based on an unspecified number of individuals from Norwegian fjords. This was summarized in Latin in the same year by Diesing as a five phrase description.

In 1865 Keferstein introduced *Phascolosoma oerstedii* from Greenland, and Quatrefages used *Siponcle oerstedii* referring to Keferstein's material; this genus name was not used by subsequent authors. Koren and Danielssen (1875) treated *oerstedii* as a junior synonym of *G. margaritacea.* However, Théel (1875) and Horst (1882) continued to treat it a a species. Selenka et al. (1883) and J. Fischer (1914) both considered it to be a junior synonym.

The name *Phascolosoma capsiforme* was put forth by Baird in 1868 for some Falkland Island worms. Théel (1911) reduced this to be a junior synonym. It was continued as a variety by Fischer (1913) who in 1920 reconsidered and also treated it as a junior synonym. However, Leroy (1936) ignored them and listed it as a species. In 1965 Edmonds used it at the subspecific rank, but in Stephen and Edmonds (1972), it again was reduced to a junior synonym.

The next names appeared in 1875: *Phascolosoma albidum* and *P. fulgens* by Théel for far North Atlantic material. Selenka et al. (1883) and J. Fischer (1914) both reduced these names to junior synonyms.

In 1881 Danielssen and Koren named *Stephanostoma hanseni* for some Norwegian arctic worms. This was changed to *Phascolosoma hanseni* by Selenka et al. (1883). Théel (1905) first synonymized *Stephanostoma barentsei* (Horst, 1882) with *P. hanseni* and then divided this taxon into two "forms": occidentalis and orientalis. Sluiter (1912) used this name for one specimen. Fischer (1922a and 1924) considered this whole complex to be synonymous with *G. margaritacea.* In 1925 Wesenberg-Lund used *P. hanseni* as a species. Stephen (1941), Wesenberg-Lund (1955), and Stephen and Edmonds (1972) used it as a subspecies. In 1974, Gibbs demoted it again to the status of a junior synonym, and we concur.

Michaelsen in 1889, introduced three names for several Antarctic specimens: *Phascolosoma georgianum, P. fuscum,* and *P. antarcticum.* These names were repeated by Fischer (1895) and Hérubel used one in 1906 and another in 1908. In 1911, Théel synonymized all three names under *G. margaritacea,* and we concur. But, *antarcticum* has continued to appear as a subspecies or varietal name up to the present.

The next new name, *Phascolosoma japonicum,* was introduced by Ikeda in 1904 for Japanese material. In 1947, Chin mistakenly applied this name to something with only one pair of retractor muscles. Fisher (1950) changed this name to *Golfingia ikedai* (since *P. japonicum* was unavailable; see *P. japonicum* Grube). Cutler and Cutler (1981) reduced this to the rank of subspecies.

In 1905 Théel named *Phascolosoma trybomi* from Sweden, but in 1924 Fischer suggested that it should be treated as a variety of *G. margaritacea* and this was also the conclusion arrived at by Lindroth (1941). However, Stephen (1934) used it as a species and then (1941, 1948, 1960) treated it as a subspecies. This last choice was also followed by Wesenberg-Lund (1955), Murina (1957), and Stephen and Edmonds (1972). We do not concur but treat it as a junior synonym.

In the same year, Théel (1905) split the species into two forms, "siberica" and "finmarchica." These were transformed to subspecies in Stephen and Edmonds (1972). Gibbs (1974) asserted that "finmarchica" must be considered synonymous with the nominate subspecies. We treat both names as junior synonyms.

Roule (1906) erected the taxon *Phascolosoma profundum* off the Azores, but this name went unused until Stephen and Edmonds (1972). In 1977 Cutler and Murina placed it in the synonymy of *G. margaritacea.*

In 1908 Lanchester named *Phascolosoma socium* for Antarctic material which Fischer (1929) submerged as a junior synonym.

Sluiter (1912) introduced *Phascolosoma iniquum* from the NE Atlantic which also went unused until Stephen and Edmonds (1972). Cutler and Murina (1977) reduced this to the status of a junior synonym. Gibbs (1986) considered this a valid species and a senior synonym of *G. mutabilis* and *G. rugosa.*

In the same year, Sluiter (1912) erected *Phascolosoma pusillum* from the Cape Verde Islands. Wesenberg-Lund (1959a:209) "is inclined to regard" it as a junior synonym, but Stephen and Edmonds (1972) transferred the taxon to the subgenus *Golfingiella* and made no reference to Wesenberg-Lund's paper. In 1977 Cutler and Murina considered this entity to be a junior synonym of *Golfingia* (*Mitosiphon*) *trichocephala* (now *Apionsoma trichocephala* sensu Cutler 1979).

Gerould (1913) created the subspecies *Phascolosoma margaritacea meridionalis* for a population off North America. This was repeated in Stephen and Edmonds (1972), but the name has not been applied to any new material (see Cutler 1973). It was differentiated from the nominate form by being very elongate (length often 10–20 times the width). Its biological significance is doubtful.

In 1934 Sato named *Phascolosoma noto* and *P. soyo* from the Sea of Japan; they were not mentioned again until Stephen and Edmonds (1972). In Cutler and Cutler (1981) *G. soyo* was demoted to a subspecies with *G. noto* its junior synonym.

Fisher (1952) erected a subspecies, *Golfingia margaritacea californiensis,* which was maintained by Stephen and Edmonds (1972), Gibbs (1974), and Rice (1980) based only on Fisher's original material. The assertion that this form deserves subspecific rank is based on tentacle number and morphology, skin thickness/roughness and number of fixing muscles. As discussed in the Introduction these characters are too variable to be used in this way.

Four years later Edmonds (1956) established *Golfingia margaritacea adelaidensis* from Australia which was repeated in Stephen and Edmonds (1972) and Edmonds (1980). Murina (1977:230) listed it in the synonymy of *G. margaritacea margaritacea.* This subspecies has only been reported from Southern Australia but in many ways resembles both the shallow water *G. margaritacea* from Japan and the South African *G. capense.* This is only known from large (60–100 mm trunk) shallow water specimens. It supposedly differs from the nominate form on such characters as strength and attachment of spindle muscle, number of fixing muscles, color, and a more rudimentary caecum. While this may be a biologically distinct taxon our anatomical analysis makes the retention of this subspecific rank difficult to justify. Future analyses of this population should consider the possibility of a shallow water Indo-West Pacific taxon with a strong spindle muscle attaching under the wing muscle and a voluminous contractile vessel.

Edmonds (1960) also named a new species from New Zealand, *Golfingia cantabriensis,* which was later (Cutler and Murina 1977) synonymized with *G. margaritacea.*

Summary.—The reason that so many names have been used for a single species rests largely in the variability of the external form. The characters used by these authors to differentiate the taxa have included: overall size (few to several hundred millimeters long); color (e.g., yellowish to reddish brown, dirty pink, bluish white, straw, rust and the following shades of grey: reddish, whitish, brownish, yellowish, or bluish); ratio of introvert to trunk length (up to 1.2:1), thickness/texture of skin (thin to thick, smooth to corky, translucent to opaque, with or without reticulations); papillae shape, size, and distribution; shape of the posterior end (with or without "tail"); and the presence and distribution of introvert hooks. Perhaps the most elaborately described external feature has been the tentacular crown (from few to many tentacles). The relative position of the nephridiopore and anus has also been utilized by some authors.

The internal anatomy has been used but to a lesser extent, e.g., the number of gut coils (but without reference to the size of the individuals), the number of fixing muscles, and presence of a rectal caecum. As noted above many of these characters do vary with size of the worms, nature of the microhabitat, or the preservation methods.

Some of these biologists had limited experience with both the worms and the sipunculan literature. Also, they were working within the paradigm of a typological species concept. The kind of analysis we have engaged in suggests to us that these variations are all possible within one biological species but willingly acknowledge that we could be wrong and hope that different kinds of data can be generated to test this hypothesis.

Golfingia margaritacea margaritacea (Sars, 1851)

In Stephen and Edmonds (1972:94) there is a lengthy synonymy for this species and those taxa considered subspecies at that time, which we will not repeat here. What follows is only a partial synonymy including the original author and changes made since 1970.

Sipunculus margaritaceus Sars, 1851:196–197.

Golfingia margaritacea.—Murina, 1971:42; 1972:301; 1973:69; 1974:235; 1977:230–232; 1978:122.—Cutler, 1973:136–138; 1977a:139–140.—Gibbs, 1974:871–876; 1977:12–13.—Cutler and Murina, 1977: 176–177.—Cutler and Cutler, 1979b:104; 1980b:197–198.—Frank, 1983:12–13.—Cutler, Cutler and Nishikawa, 1984: 263–264.—Saiz-Salinas, 1984:180–182; 1986:21–22.

**Golfingia margaritacea adelaidensis* Edmonds, 1956:302–303, pl. 2, fig. 2; 1980: 21.—Stephen and Edmonds, 1972:97.—Murina, 1977:230.

**Golfingia margaritaceum californiensis* Fisher, 1952:392–393.—Stephen and Edmonds, 1972:97–98.—Rice, 1980:494.

Phascolosoma margaritacea finmarchica Théel, 1905:63–64.

**Golfingia margaritacea finmarchica.*—Stephen and Edmonds, 1972:98.

Phascolosoma margaritaceum forma *sibirica* Théel, 1905:64–65.

**Golfingia margaritacea sibirica.*—Stephen and Edmonds, 1972:99.

Phascolosoma antarcticum Michaelsen, 1889:73–84.

Phascolosoma margaritaceum var. *antarcticum.*—Fischer, 1929:481.

**Golfingia margaritacea antarctica.*—Stephen and Edmonds, 1972:97.—Cutler, Cutler and Nishikawa, 1984:265.

Golfingia cantabriensis Edmonds, 1960: 163–164, text-fig. 4.—Stephen and Edmonds, 1972:86–87.

Phascolosoma glossipapillosum Sato, 1934: 10–12, pl. 1, fig. 5.

Golfingia glossipapillosa.—Stephen and Edmonds, 1972:91.—Murina, 1977:229.—Cutler and Cutler, 1981:61–62.

Phascolosoma hanseni Danielssen and Koren, 1881:9–13.

Phascolosoma margaritaceum hanseni.—Stephen, 1941:253.

**Golfingia margaritacea hanseni.*—Wesenberg-Lund, 1955:9.

Phascolosoma japonicum Ikeda, 1904:5–7, figs. 2, 28, 29.—Chin, 1947:100.

Golfingia ikedai.—Fisher (nom. nov. pro *Phascolosoma japonicum* Ikeda, 1904, non *Physcosoma japonicum* Grube, 1877), 1950:550; 1952:390.—Stephen and Edmonds, 1972:92.—Murina, 1977:228–229.—Nishikawa, 1977:11.

Golfingia margaritacea ikedai.—Cutler and Cutler, 1981:63.—Cutler, Cutler and Nishikawa, 1984:264–265.

**Phascolosoma margaritaceum* var. *meridionalis* Gerould, 1913:382.

Golfingia margaritacea meridionalis.—Stephen and Edmonds, 1972:98–99.

Golfingia mawsoni.—sensu Murina, 1964: 230–233.

Phascolosoma nordenskjoldi Théel, 1911: 30–31, pl. 3, figs. 35–41.—Fischer, 1920: 416; 1922b:34; 1929:483.—Stephen, 1941:253–254; 1948:217.

Golfingia nordenskjoldi.—Wesenberg-Lund, 1955:9–11.—Murina, 1964:237–238; 1978:122.

Phascolosoma noto Sato, 1934:14–16, pl. 1, fig. 7, text-fig. 17.

Golfingia nota.—Stephen and Edmonds, 1972:102.—Murina, 1977:234.—Cutler and Cutler, 1981:63.

Phascolosoma okinoseanum Ikeda, 1904:9–12, text-figs. 4, 34–38.

Golfingia okinoseana.—Stephen and Edmonds, 1972:103.—Murina, 1977:223.—Cutler and Cutler, 1981:64.—Cutler, Cutler, and Nishikawa, 1984:263.

Phascolosoma profundum Roule, 1898:385; 1906:74–77.

Golfingia profunda.—Stephen and Edmonds, 1972:104.—Cutler and Murina, 1977:176–177.

Phascolosoma signum Sato, 1934:16–17, pl. 1, fig. 8, text-fig. 18.

Golfingia signa.—Stephen and Edmonds, 1972:108.—Murina, 1977:233.—Cutler and Cutler, 1981:65.—Cutler, Cutler and Nishikawa, 1984:266.

Phascolosoma soyo Sato, 1934:17–20, fig. 9, text-figs. 19–21.

Golfingia soya.—Stephen and Edmonds, 1972:109.—Murina, 1977:233–234.

Golfingia margaritacea soyo.—Cutler and Cutler, 1981:66.—Cutler, Cutler and Nishikawa, 1984:265.

Phascolosoma trybomi Théel, 1905:69–70.

Phascolosoma margaritaceum trybomi.—Fischer, 1924:72.

**Golfingia margaritacea trybomi.*—Wesenberg-Lund, 1955:8.—Murina, 1971:42; 1977:232–233.

Material examined.—Types: AMSS, *G. margaritacea adelaidensis* Edmonds; BMNH, *P. capsiforme* Baird; NHRS, *P. nordenskjoldi* Théel; USNM, *G. margaritaceum californiensis* Fisher and *G. m. meridionalis* Gerould; ZITU, *P. soyo* Sato; ZMUB, *P. hanseni* Danielssen and Koren; ZMUH, Michaelsen's three species, *P. antarcticum, P. fuscum, P. georgianum*; ZMUT, *P. japonicum* Ikeda (=*G. ikedai*). Also: recently collected specimens of *G. ikedai* from near the type locality; *G. soya* from the Japan Sea (*G. nota* cannot be located); some *G. margaritacea* from the East Atlantic Ocean at UZMK and NHRS identified by

Wesenberg-Lund, and at NHRS some identified by Théel.

There are eight names used as subspecies in Stephen and Edmonds (1972) which we regard as undeserving of that rank/status. These are marked with an * in the above synonymy and are discussed in the preceding, "Comments on the '*margaritacea*' Section." The following nine names were presented as valid species in Stephen and Edmonds (1972). We conclude that these should be treated as junior synonyms of *G. margaritacea.* Following that is the single taxon we present as a subspecies.

Cutler and Murina (1977) reduced *G. cantabriensis* to the status of a junior synonym. Subsequent analysis of the single specimen showed it to be in very poor condition and complete examination is prohibited. There are only some subtle external differences.

Golfingia glossipapillosa was discussed in Cutler and Cutler (1981) where they raised questions about its biological validity but did not change its status. However, in Cutler, Cutler, and Niskikawa (1984) this was reduced to the status of a junior synonym.

Cutler and Cutler (1981) determined *G. ikedai* to be a subspecies of *G. margaritacea.* The putative difference at that time was the bulbous and vesicular contractile vessel in larger worms. In Cutler, Cutler, and Nishikawa (1984) it was noted that some individuals from a particular population (trunks less than 20 mm) bore scattered small hooks. It is now apparent that these differences are not unique.

Golfingia okinoseana was discussed in Cutler and Cutler (1981), and at that time it was left unchanged despite a very weak foundation (one specimen). Cutler, Cutler, and Nishikawa (1984), after finding no new material in their collections of over 3200 worms, reduced this to a junior synonym.

Cutler and Cutler (1981) determined *G. nota* and *G. soya* to be conspecific and reduced this combined taxon to subspecific rank. They did not consider it conspecific with the nominate form based on the large, cone- or pear-shaped papillae on the proximal portion of the introvert. This is not a clear distinction, and since no additional specimens have been located for comparative studies, we now further reduce the rank of this taxon.

The type material of *G. nordenskjoldi* at NHRS consists of three vials. No. 218 has only an introvert with many tentacles. No. 219 has three specimens, one of which is missing its introvert. No. 220 has three specimens, the largest has a 5 mm trunk which is rough. One does appear to have only two tentacles, but the introvert is not completely extended. Fischer did not have new material but merely repeated Théel's record. It is now clear that these worms are merely a few young animals.

Golfingia profunda was determined to be a junior synonym in Cutler and Murina (1977).

Golfingia signa (Sato 1934) was discussed in Cutler and Cutler (1981). Cutler, Cutler, and Nishikawa (1984) concurred by retaining the name but expressed reservations. Its putative differences from *G. margaritacea* are only external, mostly the wavy, zig-zag ridges on the posterior end of the body. We have found this condition in other material from different parts of the world and we can no longer justify specific rank for this name.

The variations in the morphology of this taxon have been commented on above. It is therefore a very difficult species to describe with precision. Aside from the generic and subgeneric characters and the above comments on the variations one can add very little.

Known distribution.—*Golfingia margaritacea margaritacea* is a very widely distributed taxon living in all sectors of the Atlantic, Arctic and Antarctic Oceans (80°N–78°S); the North, Southeast and Southwest Pacific (over 30°N and S) with a few exceptions at lower latitudes but in deep water (over 2000 m). The depth range is 1–5300 m but most specimens have been col-

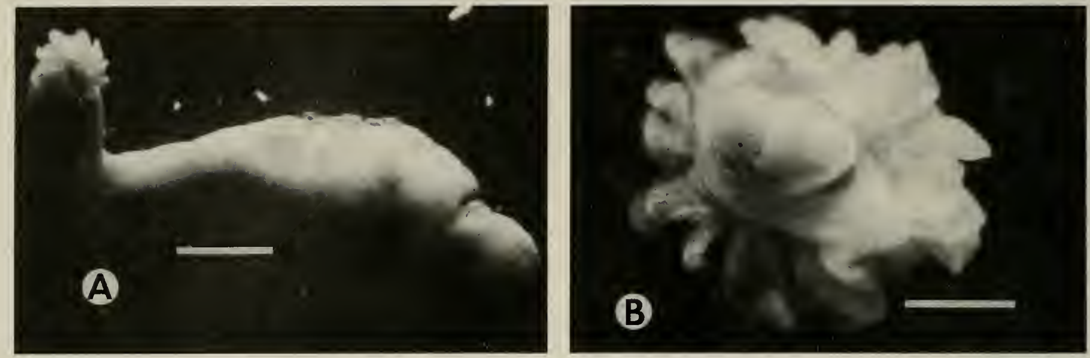

Fig. 1. *Golfingia margaritacea ohlini,* the generalized golfingiid morph: A, Whole animal; B, Tentacular crown. (Scale lines are 2 and 0.5 mm.)

lected from depths less than 300 m. It is unknown from the Indian Ocean and Mediterranean Sea.

Golfingia margaritacea ohlini (Théel, 1911)
Figs. 1, 2

Phascolosoma ohlini Théel, 1911:29–30, pl. 2, figs. 21–23, pl. 3, figs. 24–27, pl. 5, figs. 69–70.—Fischer, 1920:413; 1929:484.—Stephen, 1941:254–255.

Golfingia ohlini.—Wesenberg-Lund, 1955: 10; 1963:106–107.—Edmonds, 1965: 31.—Stephen and Edmonds, 1972:102.—Murina, 1972:301–302; 1974:235; 1978: 122.—Cutler and Cutler, 1980b:199.

Not *Golfingia ohlini.*—Wesenberg-Lund, 1959b:61 (see *G. elongata*).

Phascolosoma mawsoni Benham, 1922:13–17.—Fischer, 1929:482–483.—Stephen, 1948:218.

Golfingia mawsoni.—Edmonds, 1972:84–85.—Murina, 1972:301; 1977:225–227.—Stephen and Edmonds, 1972:99–100. Not Murina, 1964:230–233.

Phascolosoma pudicum Selenka, 1885:11–12.—Fischer, 1929:484.—Stephen, 1948: 217–218.

Golfingia pudica.—Stephen and Edmonds, 1972:104–105.—Cutler, Cutler and Gibbs, 1983:671–672.

Golfingia vulgarls [sic] var. *antarctica* Murina, 1957:996–997.

Golfingia vulgaris murinae.—Stephen and Edmonds, 1972:111.

Material examined.—Types: NHRS, *G. ohlini*; AMSS, *G. mawsoni*; additional recently collected specimens from subantarctic waters near the Kerguelen Islands. *G. pudica*: BMNH, Type material; UMOU, one specimen which we believe to be part of the original collection; UZMK, a specimen of Wesenberg-Lund's from Mauritius; ZIAS, a specimen of Murina's from the East China Sea.

The following is a chronologically-arranged, historical review of this taxon.

In 1911 Théel named this species from five specimens collected at 24–95 m off South Georgia. The total body length was 6–17 mm with a pointed posterior extremity having crowded cylindrical papillae. The anus was "in the middle of the body" with the nephridia at the same level; therefore, as currently defined, the trunks were 3–9 mm long with introverts of equal length. There were 10–16 tentacles. He compared these worms to *G. cylindrata* but the hooks and papillae separated them. Our examination of this material showed the following: Vial no. 215 is the very small one which is listed as holotype in Stephen and Edmonds (1972). This worm had never been opened and proved to have only two retractor muscles; therefore it is a *Nephasoma,* not a *Golfingia* species. No. 216 has

Fig. 2. Posterior ends of some *Golfingia margaritacea ohlini* from the Kerguelen Islands showing possible variation in form within one population. (Scale line is 1 mm.)

two large worms with eggs in the coelom, a "pencil point" posterior end, and no visible hooks. No. 217 has two worms packed with sperm and has small introvert hooks. These also had never been dissected but do have four retractor muscles. They are very similar to the small Japanese *G. margaritacea* reported by Cutler, Cutler, and Nishikawa (1984).

In 1920 Fischer recorded one *G. ohlini* from 385 m off Australia with hooks and 12 tentacles (therefore a small worm?). He apparently repeated this record in 1929.

When Benham described *G. mawsoni* in 1922 he had 50 worms with total length ranging from 8–42 mm. He had some interesting comments about how one "cannot put much reliance on proportions of length of various regions or upon such features as the exact position of the origin of the introvert retractor muscles." He also discussed how contractions of the circular and longitudinal muscle layers could modify the shape of the posterior end. His assertion that this species was clearly distinct from *G. margaritacea* was less than convincing since he based that distinction on the color and texture of the skin plus the presence of a "distinct cone" at the posterior tip. He also mentioned the "longer introvert" and other unspecified differences. Our examination of the type collection served to confirm the accuracy of his description and figures. Only our conclusions were different. Seven years later Fischer (1929) repeated Benham's record from Commonwealth Bay. He had no new material.

In 1941, Stephen reported 24 *G. ohlini* from the Falklands at 130–720 m. Our examination of this material showed it to agree well with Théel's animals but not all of them have hooks, they have more tentacles, and come from deeper water. The vial from station WS-33 also contains some *Nephasoma* species.

The next record of *G. mawsoni* was Stephen (1948:218) where he recorded about 200 worms (size not mentioned) from near the type locality at depths of 163–300 m. His one morphological observation of interest was that the posterior cone was hardly ever sunk into a "pit" as many of Benham's were.

In 1955 Wesenberg-Lund reported a single, 8 mm *G. ohlini* from 270 m off Chile. We could not examine the tentacles or hooks, and this could have been almost any member of the genus. Her comment ". . . rather long, cylindrical papillae crowded at the posterior extremity of the body and characteristic of this species were distinct under the microscope" reflects a dependency on one of the most labile characters.

In 1957 Murina described the new variety *G. vulgaris* var. *antarctica* but on the copy sent to us had drawn a line through that name and written in *G. ohlini* (see 1972).

In 1959b Wesenberg-Lund recorded one *G. ohlini* from intertidal water on Mauritius. Our examination of this worm showed it to be a member of this genus with hooks but with no posterior point. According to Wesenberg-Lund, it has 24 tentacles and 15 rings of hooks with 30 hooks per ring. This habitat makes the record very suspect and, given hooks in rings and slender proportions, this worm should be considered a *G. elongata.*

In 1963 Wesenberg-Lund recorded five specimens of *G. ohlini* from 12–13 m in False Bay, South Africa. These measure 5–19 mm, and the largest one has 30 tentacles. In her discussion of the tentacles and nuchal organ, she has the dorsal and ventral sides reversed. Hooks are present and scattered.

After a gap of sixteen years, *G. mawsoni* was used again by Murina (1964:230–233) where she gave a detailed account of two specimens from 3990 m in the Bering Sea. These worms had trunks 35 and 40 mm long and introverts shorter than the trunks. She felt these fit Benham's species despite a few differences such as the introvert length and anterior position of the retractor muscles. She accounted for this by ontogenetic changes which she discussed at some length including an interesting quote from Gerould (1913) about these problems. The drastically different depth and far northern latitude of these two worms raises our doubts about these belonging to the same gene pool as the shallow Antarctic populations. Therefore, we have moved these two worms to *G. margaritacea margaritacea.*

In 1965 Edmonds reported five *G. ohlini* from 5–432 m in the Ross Sea. These were 8–22 mm long with introverts a little shorter than the trunks and 14–16 tentacles. Hooks were in irregular rows. He identified these on the bases of size, shape, number of tentacles, retractors, and hooks.

Murina (1972) recorded two smaller *G. mawsoni* from the South Atlantic (South Africa, 318 m and Argentina, 75 m) which seem to fit more closely Benham's species. In this same article, she also has *G. ohlini* with *G. vulgaris* var. *antarctica* as a junior synonym. This latter record was based on 17 specimens from 59–1900 m in the Antarctic Ocean. Their trunks are 3–14 mm and posterior ends range from blunt to pointed with obvious tail-like appendage. This paper also contained *G. margaritacea.*

In that same year, Edmonds (1972) published on a collection of 47 *G. mawsoni* from the Antarctic with introverts shorter than the trunk (maximum length 30 mm, most between 18 and 24 mm) and other "minor" differences from Benham's description. Some had short, sharp pointed posterior ends.

Also in 1972, Stephen and Edmonds differentiate *G. mawsoni* from *G. margaritacea* in their key to this genus by the presence or absence of a rectal caecum, and from *G. nota/soya* by the number of fixing muscles

(3 vs. 2). *Golfingia mawsoni* has not been used since.

In 1974 Murina reported five *G. ohlini* from 932–1435 m off the Falklands. The largest trunk is 3.5 mm, but she said that the color of the body and the form of the papillae allowed her to identify them. This assertion is difficult to accept. She went on to compare it to the "closely related" *G. vulgaris* from which it differs, according to her, by the form of the nuchal organ and posterior papillae.

In 1978 Murina added two *G. ohlini* from 710–850 m south of New Zealand. Then Cutler and Cutler (1980b) recorded 96 specimens of *G. ohlini* from the far South Atlantic at 81–247 m. These were 2.5–12 mm long with hooks 17–90 μm high (most less than 50 μm) and pencil point or nipple-like posterior ends.

In his account of the Australian sipunculans, Edmonds (1980) lists the earlier records of *G. ohlini* but has no new records.

Golfingia pudica was discussed at length in Cutler, Cutler, and Gibbs (1983) wherein it was shown that this name had been used for two different populations, one is an *Apionsoma* species and the other, original of Selenka's, is a *Golfingia* species. Selenka said it differed from *G. vulgaris* in distribution of hooks, number of tentacles, and distribution of papillae. Not all of the type specimens have hooks but in those which do, the arrangement is not in distinct rings as Selenka alleged. Fischer (1929) merely repeated Selenka's record. Stephen's (1948) material was badly damaged and cannot now be located. Both of these collections came from the Kerguelen Islands, a common locality for *G. margaritacea ohlini.*

In summary, this taxon is defined by us as a population whose morphology grades into that of *G. margaritacea* from northern waters. The two alleged differences are the presence of hooks in some of these (see Introduction) and the difference in the shape of the posterior end of the trunk (pointed not round). After examining all the literature, the type material, and many newly collected specimens, the putative differences fade into a cloud of variation. Hooks are only present in smaller worms, and the form of the posterior end varies widely even within one dredge sample (Fig. 2). The decision to rank this at the subspecific level is based on the assumption that there is significant reduction in gene flow but that it is not completely reproductively isolated.

Known distribution.—It has been collected in Antarctic and subantarctic waters including the southern tips of South America and Africa, several southern islands and Antarctica (most between 44° and 77°S). The depths are commonly less than 300 m with a few as deep as 1425 m.

This particular population is extremely interesting from an evolutionary standpoint since the *G. margaritacea* 'superspecies' is closer to the hypothetical ancestral sipunculan than any other extant taxon (has the fewest apomorphic character states, see Cutler and Gibbs 1985). Its distribution in the southern seas places it in an excellent position (i.e., a "center of dispersal") to serve as an ancestral stock for other cold water taxa as habitats opened up during the Cenozoic (Zinsmeister and Feldmann 1984).

Golfingia anderssoni (Théel, 1911)

Phascolosoma anderssoni Théel, 1911:28–29, pl. 2, figs. 28–34, pl. 5, figs. 71–74.—Fischer, 1929:481.—Stephen, 1941:250–251; 1948:216.

Golfingia anderssoni.—Murina, 1957:992–993; 1964:222–224; 1971:42; 1972:296–298; 1974:234; 1977:222–223.—Edmonds, 1965:30.—Stephen and Edmonds, 1972:84–85.

Material examined.—Types: NHRS, three vials of specimens labeled type, no designated holotype. Also recently collected specimens from the South Atlantic.

This is a well-defined species with a solid foundation having the distinctive posterior trunk papillae and caudal appendage. In many ways it is very similar to *Nephasoma flagriferum.*

Known distribution.—Eight of the 11 published records are from the far southern latitudes at a depth range of 75–1880 m. One is from the Atlantic Ocean at 17–19°S, 4335–4613 m. There are two records, each of a single specimen, from deep water (3150 and 6135 m) in the northern Pacific Ocean (28° and 44°N). These two northern hemisphere records seem peculiar and additional records would help solidify this pattern.

Golfingia birsteini Murina 1973

Golfingia birsteini Murina, 1973:942–943, fig. 1.—Frank, 1983:10–11.

Material examined.—Type: ZIAS.

This long slender species (length up to 15 times the width) with reduced tentacles is similar to several *Nephasoma* species. The papillae are variable in shape (Murina said 'pear-shaped'). The posterior end does not bear a caudal appendage but is cone-shaped as the result of circular muscle contraction. The hooks are large and scattered, not in rings, and it has no eyespots; thus, is different than *G. elongata.*

Known distribution.—Only one record (seven worms) from the Northwest Pacific (58°N, 149°W) at 3200 m.

Golfingia capensis (Teuscher, 1874)

Phascolosoma capense Teuscher, 1874:488–489, pl. 19, figs. 4, 5, 12, 14.—Selenka et al., 1883:29–30.—Selenka, 1885:12.—Sluiter, 1898:443.—Fischer, 1895:14; 1920:414; 1922a:9–10; 1922b:16.—Leroy, 1936:425.—Stephen, 1942:251.

Golfingia capensis.—Wesenberg-Lund, 1959c:181–182; 1963:108–110.—Stephen and Cutler, 1969:114–115.—Stephen and Edmonds, 1972:87.—Cutler, 1977a:139.

Dendrostoma stephensoni Stephen, 1942: 252–253, pl. 1, fig. 5.

Dendrostomum stephensoni Wesenberg-Lund, 1963:133–134, fig. 10.

Themiste stephensoni.—Stephen and Cutler, 1969:116.—Stephen and Edmonds, 1972:212–213.—Cutler, 1977b:154.

Material examined.—ZMUH, a worm labeled "type" from Lagos but it had been identified by Fischer so probably was not Teuscher's material; also four specimens from "the Cape, Africa" but no additional station data. NHRS, one worm identified by Fischer from "Cape, Africa." UZMK, one very large worm (over 18 cm) from "Koreas Kyst, 110 m" with no indication of who identified it or when and Wesenberg-Lund's specimens of *Themiste stephensoni.* RSME, type material of *T. stephensoni.*

There is a semantic problem with the term 'villi' in this common but localized species. The contractile vessel does have bulbous swellings or vesicles along a portion of its length but these are not villi in the sense of Cutler and Cutler (1982:750). No member of this genus bears true contractile vessel villi. This expanded vessel is similar to that seen in intertidal populations from Japan (*G. margaritacea ikedai* in Cutler and Cutler 1981) and this expanded surface area is probably an adaptation to lower oxygen tension in warmer shallow waters. A few small individuals in both these populations also bear small hooks.

This species shares many characters with *G. margaritacea,* especially the shallow water Australian and Japanese populations with bulbous contractile vessels. If it is truly reproductively isolated (i.e., not an Indo-West Pacific taxon) it must differ at only a few loci. Whether one interprets the large size of some members of this population (up to 20 cm) as under genetic control or simply epigenetic plasticity is important. Given our present knowledge we cannot answer several important questions, so will, at this time, not reduce this to the status of a subspecies of *G. margaritacea.*

When we reexamined the *Themiste ste-*

phensoni material it became clear that these worms actually belonged to *G. capensis* (Gibbs and Cutler, 1987). The putative contractile vessel villi are only the bulbous vesicles characteristic of this species.

Known distribution.—South Africa to Mombasa on the east coast and Île St. Paul (40°S, 80°E). All but two records are from depths less than 100 m, the deepest is at 430 m.

Golfingia elongata (Keferstein, 1863)

Phascolosoma elongatum Keferstein, 1863: 39, pl. 3, fig. 5.
Golfingia elongata.—(see Stephen and Edmonds, 1972:90–91 for most of the lengthy synonymy prior to 1970).—Åkesson, 1961:511–530.—Stephen, 1960: 15.—Murina, 1972:299; 1975:1088; 1977:215–217.—Cutler, 1973:134–136.—Zavodnik and Murina, 1975:127; 1976:85.—Gibbs, 1977:10–11.—Cutler and Cutler, 1980b:197.—Ocharan, 1980: 117–118.—Frank, 1983:11–12.—Cutler, Cutler and Nishikawa, 1984:262–263.—Saiz-Salinas, 1984:180; 1986:18–20.
Phascolosoma charcoti Hérubel, 1906a:127–128; 1906b:651–652; 1908:2–8.—Fischer, 1929:483.
Golfingia charcoti.—Stephen and Edmonds, 1972:89.
Phascolosoma cylindratum Keferstein, 1865:428.—Selenka et al., 1883:25.—Gerould, 1913:382–383.—Leroy, 1936: 425.
Golfingia cylindrata.—Stephen and Edmonds, 1972:89.
Phascolosoma derjugini Gadd, 1911:82–83.
Golfingia derjugini.—Stephen and Edmonds, 1972:90.
Golfingia ohlini.—Wesenberg-Lund, 1959b: 61.

Material examined.—MNHU, type of *G. elongata*; RSME, type of *G. cluthensis* Stephen; additional recently collected specimens from the North Atlantic.

The type material consists of several vials of specimens in very good condition, some with extended introverts showing the 8–10 rings of hooks which characterize this well founded species.

The type materials of *Golfingia charcoti, G. cylindrata,* and *G. derjugini* cannot be located. Cutler (1973) reduced *G. cylindrata* and Cutler and Murina (1977) reduced the other two to junior synonyms and we reaffirm those actions.

Known distribution.—From the northwest Atlantic (Newfoundland to Bermuda and Cuba), the northeast Atlantic (Spitzbergen to Iberian Peninsula and the Mediterranean) from intertidal to 200 m depths. In the Pacific from the East and South China Seas at 91–590 m. There is a single worm reported from the Indian Ocean (Mauritius intertidal sand, Wesenberg-Lund 1959b).

Golfingia iniqua (Sluiter, 1912)

Phascolosoma iniquum Sluiter, 1912:14, pl. 1, fig. 4.
Golfingia iniqua.—Stephen and Edmonds, 1972:93.
Phascolosoma mutabile Southern, 1913:19–20.
Golfingia mutabilis.—Stephen and Edmonds, 1972:101.—Murina, 1977:219–221.
Phascolosoma rugosum Southern, 1913:18–19.
Not *Phascolosoma rugosum* var. *mauritaniense* Hérubel, 1925a:262.
Golfingia rugosa.—Stephen and Edmonds, 1972:107.—Murina, 1977:219.—Saiz-Salinas, 1986:24–27.

Material examined.—Types: INMD, *G. mutabile* and *G. rugosa*; MOMV, *G. iniqua*; many recently collected specimens from near the type locality.

Cutler and Murina (1977) determined this to be a junior synonym of *G. margaritacea.* However, in light of recent comparisons of all these types (and new material) we now believe that the earlier action was a mistake. The distinctions Southern made between his two species are probably only an artifact of size (e.g., number of tentacles) and/or state of contraction of his six individuals. His failure to compare this material to Sluiter's species may be due to the fact that they were published at about the same time. Sluiter's also were said to lack hooks while hooks are present in some (but not all) of Southern's worms. This species is one which has deciduous hooks and does share many characters with *G. margaritacea.* It is possible that future studies will show this to be a partially isolated subset of a polymorphic *G. margaritacea* gene pool (subspecies?). The major distinction lies in the shape of the trunk (more robust, fat and pear-shaped, length almost always less than 3 times the width) and the texture of the epidermis in the larger ones (over 10 mm) being thick with irregular lines/wrinkles/zig-zag pattern; admittedly somewhat less than absolute. The smaller individuals do not have as thick a body wall in the mid section but width/length ratio is consistently lower than other congeneric species.

Hérubel's (1925a) subspecies is a taxon we would place in *incertae sedis* since the description (based on a single worm of unknown size) is extremely brief, there are no illustrations, the type cannot be located, and the habitat (25 m depth at 8°24′W and 33°24′N) is atypical.

Known distribution.—Northeast Atlantic Ocean, 29–52°N, 10–30°W, from depths of 500–1800 m.

Golfingia mirabilis Murina, 1969

Golfingia mirabilis Murina, 1969:1732–1733, fig. 1.

Material examined.—Type: ZIAS.

This single worm was described as having shields but does not. The posterior end of the trunk is somewhat contracted, dark, papillated and rugose while at the anterior end the skin has faint zig-zag ridges and is dark. The reference to a caudal appendage in the original description is somewhat misleading as the structure is 0.7 mm long on a 36 mm trunk and is really just a nipple-like termination of trunk, not uncommon in this genus. The hooks are at least 200 μm tall and the tentacles are especially numerous, over 50 well defined units. The ventral retractor muscles originate anterior to the origins of the dorsal pair by about 10% of the trunk length, an unusual relationship within this genus. Despite the lack of an adequate data base this species seems distinct enough to be retained. There is the possibility that it is an anomalous *G. vulgaris* and if additional specimens are not collected in forthcoming years the reality of this taxon might well be questioned.

Known distribution.—Off Tanzania, 7°S, 40°E, 802 m.

Golfingia muricaudata (Southern, 1913)

Phascolosoma muricaudatum Southern, 1913:21, pl. 4, fig. 5.—Fischer, 1920:415; 1922a:10–11; 1929:483; 1931:139.

Golfingia muricaudata.—Murina, 1964: 233–237; 1971:43; 1977:209–210; 1978: 122.—Cutler, 1973:133–134; 1977a: 140.—Cutler and Cutler, 1979:949–950; 1980a:451–452; 1980b:198–199.—Frank, 1983:13.—Cutler, Cutler and Nishikawa, 1984:265–266.

Phascolosoma appendiculatum Sato, 1934: 7–10.—Murina, 1964:224–227.

Golfingia appendiculata.—Stephen and Edmonds, 1972:86.—Cutler, 1977a:139.—Murina, 1977:224–225; 1978:122.—Cutler and Cutler, 1981:60–61.—Cutler, Cutler and Nishikawa, 1984:262.

Phascolosoma hudsonianum Chamberlin, 1920:3d–4d.

Golfingia hudsoniana.—Stephen and Edmonds, 1972:91–92.

Material examined.—Types: ZMUH; numerous recently collected specimens from near the type locality; NMCO, *G. hudsoniana*; *G. appendiculata* lost. Cutler and Cutler (1981) deposited reference specimens at NSMT and USNM which had been collected from near the type locality.

This common deep-water species is well founded. It is easily distinguished by its caudal appendage (nipple-like in very small worms to up to 50% of trunk length in large ones) bearing cylindrical papillae. The nerve cord ends anterior to the tail. Deciduous hooks (up to 100 μm tall) are present in small individuals. The introvert is generally shorter than the trunk.

Our decision to reduce *G. appendiculata* to a junior synonym is based on our current understanding that this putative species, based on 16 worms in five records, is merely a few larger hookless individuals. Our analysis indicates that *G. muricaudata* starts its life with hooks but by the time an animal reaches 5–10 mm most have lost these deciduous structures.

Cutler (1973) determined *G. hudsoniana* to be a junior synonym and we reaffirm that conclusion.

Known distribution.—Common at bathyal and abyssal depths in the North Atlantic from Cape Hatteras (one Caribbean record at 17°N from 4000 m), up to 58°N, across to Europe and West Africa (at 60–70 m in upwelling areas off Ivory Coast). It occurs down to South Africa, Kerguelen and Bouvet Islands and up the east coast of Africa through the Mozambique Channel to Tanzania at bathyal depths. In the North Pacific it has been recorded from British Columbia around the Bering Sea to Japan at depths from 85–6860 m. Murina (1978) is the only record from the far south Pacific and is based on six worms from around 55°S, 159°E and 4400–5400 m deep. In this paper she used four names (*margaritacea, ohlini, muricaudata,* and *appendiculata*) with no morphological comments or indication of how she differentiated between these very similar forms.

Golfingia vulgaris vulgaris
(de Blainville, 1827)

Sipunculus vulgaris de Blainville, 1827:312–313, pl. 33, fig. 3 (see Stephen and Edmonds, 1972:110 for extensive synonymy prior to 1970).

Golfingia vulgaris.—Murina, 1971:43; 1973: 70; 1977:217–219.—Zavodnik and Murina, 1975:128; 1976:85–86.—Cutler and Murina, 1977:177–178.—Gibbs, 1977: 14–15.—Cutler and Cutler, 1979a:950.—Frank, 1983:13–14.—Cutler, Cutler and Nishikawa, 1984:266–267.—Saiz-Salinas, 1986:27–29.

Phascolosoma vulgare var. *astuta* Selenka, 1885:11.

Golfingia vulgaris astuta.—Stephen and Edmonds, 1972:111–112.

Phascolosoma vulgare var. *multipapillosum* Hérubel, 1925a:261.

Golfingia vulgaris multipapillosa.—Stephen and Edmonds, 1972:112.

Phascolosoma vulgare selenkae Lanchester, 1905:31–32.

Golfingia vulgaris selenkae.—Stephen and Edmonds, 1972:112–113.

Phascolosoma vulgare tropicum Sluiter, 1902:33–34.

Golfingia vulgaris tropica.—Stephen and Edmonds, 1972:113.

Golfingia (*Dushana*) *adriatica* Murina, 1975: 1085–1087.—Zavodnik and Murina, 1976:86.

Phascolosoma kolense Gadd, 1911:80–81, 102–103.

Golfingia kolensis.—Stephen and Edmonds, 1972:93.—Cutler and Murina, 1977:177–178.

Phascolosoma owstoni Ikeda, 1904:12–15.

Golfingia owstoni.—Stephen and Edmonds, 1972:103–104.—Murina, 1977:214–215.—Cutler and Cutler, 1981:64–65.

Phascolosoma solitarium Sluiter, 1912:15–16.

Golfingia solitaria.—Stephen and Edmonds, 1972:108.—Murina, 1977:227.

Not *Golfingia vulgarls* [sic] var. *antarctica* Murina, 1957:996–997 (=*Golfingia vulgaris murinae* nom. nov. pro Stephen and Edmonds, 1972:111) (see *G. margaritacea ohlini*).

Material examined.—Types: MOMV, *G. solitaria*; ZMUA, *G. v. tropica*; BMNH, *G. v. astuta* and *G. v. selenkae*; ZIAS, *G. adriatica.* Types of *G. vulgaris, G. kolensis, G. owstoni,* and *G. v. multipapillosum* cannot be located.

This is a common, well-founded species characterized by both ends of the trunk distinct, much darker and more heavily papillated than the mid-trunk. The introvert is shorter than the trunk and it has normal tentacles. The large hooks are scattered, dark and spine-like. Its spindle muscle is well developed and originates under the wing muscle just posterior to the anus, sometimes from two branches.

Selenka's variety *astuta* is represented by a single, dried, collapsed, hard worm which precludes any internal examination. There are no external features to distinguish it from *G. vulgaris,* therefore, we reduce this individual to the status of a junior synonym.

When Hérubel (1925a) used the name *Phascolosoma vulgare multipapillosum* he provided neither a description nor illustration. It was merely listed along with two other subspecies and consequently this has no meaning.

The two *G. v. selenkae* Lanchester described from East Africa are in good condition. However, the alleged differences are not significant (hook and papillae size, and origin of the ventral retractor muscles); these fall within the range for this species. At this time the animals do not show any indication of the dark pigment on the ends of the trunk so typical of this species. Rather, they are a uniform light brown color. Its shallow, tropical location is more noteworthy than its morphology.

Sluiter's (1902) subspecies, *G. v. tropica* was based on two worms. One of these is a *Nephasoma* species. The alleged distinctions of the remaining worm from the nominate form are within the range of variation and judged to be insignificant. Sato's (1934) use of this name was because of the hook size (60–70 μm), now known to be normal for the species.

Golfingia adriatica was based on two specimens, each lacking one dorsal retractor muscle and possessing an inner body wall with peculiar connective tissue sheets (partial dissepiments). The subgenus erected at this time was defined as having 'shields' at both ends of the trunk but this is another problem of semantics (see Introduction). The type species for the subgenus was *G. scutiger* (see below). It is clear to us that these two worms are anomalous *G. vulgaris* with ontogenetically modified retractor muscles as noted in other species (see Gibbs 1973).

Golfingia kolense (Gadd, 1911) was synonymized by Cutler and Murina (1977). *Golfingia owstoni* was discussed in Cutler and Cutler (1981:64–65) where they concluded that the alleged differences were insignificant.

The single specimen of *G. solitaria* is in good condition. It does lack hooks, the contractile vessel is bulbous, and there are prominent papillae on both ends of the trunk. No additional specimens have been recorded from the North Sea or adjacent waters and we propose that Sluiter's worm is simply one hookless representative of this population and therefore a junior synonym.

Known distribution.—In the Northeast Atlantic Ocean including Greenland, Scandinavia, the British Isles, and into the Mediterranean, Adriatic and Red Seas; south to the Azores, Canaries, and Cape Verde Islands and West Africa; in the Indian Ocean off Durban and Zanzibar; the Pacific Ocean in the Kurile-Kamchatka Trench, Japan, Malaya, Singapore and one record (Frank 1983) off British Columbia (the only one from the eastern Pacific). The total depth range is from 5–2000 m but more commonly 10–500 m, deeper records are rare. There is one very deep record from 5540 m in the Kurile-Kamchatka Trench. Its absence from the western Atlantic ocean and rarity in the eastern Pacific Ocean is noteworthy. The Indo-West Pacific warm water records may belong to a distinct population (or the following subspecies?) but there is currently insufficient data to assert this with confidence.

Golfingia vulgaris herdmani (Shipley, 1903) new status

Centrosiphon herdmani Shipley, 1903:171–174, pl. 1, figs. 4–10.—Stephen and Edmonds, 1972:268–269.
Golfingia herdmani Edmonds, 1980:19–21.
Golfingia liochros Cutler and Cutler, 1979a: 950–951, fig. 2.
Golfingia (*Golfingia*), n. sp. Cutler, 1977a: 140.
Golfingia vulgaris queenslandensis Edmonds, 1956:303–305.—Stephen and Edmonds, 1972:112.—Edmonds, 1980: 21–22.

Material examined.—The type (and only) material of *Centrosiphon herdmani* cannot be located but several recently collected Australian specimens identified by Edmonds as *G. herdmani* were examined; AMSS, Type of *G. v. queenslandensis*; MNHN, Type of *G. liochros.*

This taxon differs from the nominate form by having the anterior and posterior ends of the trunk forming a modified cap or pseudoshield consisting of dark spherical papillae arranged in irregular radiating rows especially evident on the posterior end. It also has larger hooks (120–200 μm) associated with bulbous papillae and lives in shallow warm water.

Edmonds' account of *G. herdmani* is detailed and precise. In the thirty years since *G. v. queenslandensis* was described no new material has been given this name. One of the major distinguishing features of *G. herdmani* is the peculiar nature of the anterior and posterior trunk; ". . . looking rather like aspidosiphonid caps or shields which are surrounded at their junction with trunk by a fold of body wall." However, when describing this species Edmonds (1980:19) went on to say "When the specimens are relaxed the "shields" usually become less evident and sometimes disappear." In *G. v. queenslandensis* he said: "There is a weakly developed rim between the base of the introvert and the trunk, much like that found in *G. herdmani*" (Edmonds 1980:22), therefore, in our opinion, simply two relaxed specimens of the same species. These two worms are paler but the arrangement of the posterior papillae is the same. His comment that the *G. herdmani* are internally very similar to an Australian subspecies of *G. margaritacea* is true but the same could be said for many members of this genus.

The original description of *G. liochros* compared it to two species with 'shields' now considered to be junior synonyms of *G. vulgaris.* There are external similarities to *G. v. vulgaris* but differences sufficient to retain its separate status were believed to be present. After this side-by-side comparison it is clear we were mistaken. Some worms do have bulbous contractile vessels and the size of the ventral retractors may vary from 1.5–4 times the ventral (usually 2–3). Other size-related differences we have covered in the introduction to this paper. As these worms are less than 20 mm long and the *G. v. herdmani/queenslandensis* are up to 60 mm and since all exist around the Indian Ocean we conclude that we simply have the two ends of one continuum; i.e., a shallow water Indo-West Pacific taxon.

Known distribution.—Madagascar, Mozambique Channel, Ceylon, Thailand, Great Barrier Reef and South Australia from intertidal depths (one at 300 m).

Species Transferred to Other Genera in Previous Papers

These species are listed with only brief comments. Additional details can be found in the cited references.

Golfingia recondita (Sluiter, 1900)

This was transferred to the subgenus *Mitosiphon* in Cutler and Murina (1977). In Cutler (1979) this was shifted to the subgenus *Apionsoma* which has since been elevated to generic rank (Cutler and Gibbs 1985). It is not a well founded species.

Golfingia trichocephala (Sluiter, 1902)

This followed a path similar to that of *G. recondita* except that the first shift occurred in Cutler (1973) when it was moved to the subgenus *Mitosiphon.* It is presently in the genus *Apionsoma* (Cutler 1979) and is a widespread, common species.

Species Considered *species inquirendum* or *incertae sedis*

Golfingia reticulata (Hérubel, 1925)

Phascolosoma reticulatum Hérubel, 1925a: 262; 1925b:272–277, text-figs. 1–6.
Golfingia reticulata.—Stephen and Edmonds, 1972:105–107.—Saiz-Salinas, 1986:22–24.

Material examined.—Type: MNHN.

The single type specimen is in very bad condition, partially dried out and the introvert is missing so we cannot verify any of the critical differences. The area around the type locality has been intensely sampled over the past few decades and nothing matching this description has been collected. Saiz-Salinas (1986) merely repeated the original record. Several aspects of the description are peculiar but in many ways this is similar to *G. vulgaris.* In our judgment it is best to add this name to the list of *incertae sedis.*

Golfingia scutiger (Roule, 1906)

Phascolosoma scutiger Roule, 1906:81–86, pl. 9, figs. 90, 95, 96, pl. 10, figs. 97–99.
Golfingia scutiger.—Murina, 1975:1085–1089; 1977:212.

Material examined.—Type cannot be located.

This single specimen from the coast of Morocco was omitted from Stephen and Edmonds (1972). The worm seems to have been lost to science and no one has applied this name to additional material since 1906. We strongly suspect that this is a specimen of *G. vulgaris* with the posterior end drawn in and flattened, but since we cannot verify this we hereby place it on the list of *incertae sedis.* Murina (1975) unfortunately used this enigmatic taxon as the type species for her new subgenus *Golfingia* (*Dushana*) which now ceases to have any meaning (see also *G. adriatica*).

Golfingia anguinea (Sluiter, 1902)

Phascolosoma anguineum Sluiter, 1902:36–37, pl. 3, figs. 13–16.
Golfingia anguinea.—Stephen and Edmonds, 1972:85.

Material examined.—Type: ZMUA.

The single specimen is in very poor condition. The internal organs are missing or badly distorted. The introvert was described as being four times the trunk length but it now appears torn and incomplete and is only equal to the trunk in length. The description of this introvert tip with "thread-like feeler" sounds like a ripped introvert, not the natural state. As the poor condition of this specimen precludes verification of the description and no additional specimens have been recorded, we place this name on the list of *species inquirendum* pending future clarification.

Golfingia lagensis (Fischer, 1895)

Phascolosoma lagense Fischer, 1895:13–14; 1914:76–77, pl. 2, figs. 1–3.
Golfingia lagensis.—Stephen and Edmonds, 1972:93–94.

Material examined.—Type cannot be located.

This species was based on a single 10 mm specimen which seems to have been lost to science. The presumed absence of a spindle muscle has been heavily weighted (Stephen and Edmonds 1972) but the fact that Fischer was "unable to perceive" this fine thread-like muscle in a single small worm is not surprising (see Introduction). One could place this in synonymy with *G. margaritacea* based on overall similarity as Wesenberg-Lund (1959a:209) suggested, but a more prudent option, being unable to verify anything about this specimen, is to place it on the list of *incertae sedis.*

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NATURAL HISTORY OF PLUMMERS ISLAND, MARYLAND. XXVII. THE DECLINE OF FOREST BREEDING BIRDS ON PLUMMERS ISLAND, MARYLAND, AND VICINITY

David W. Johnston and Daniel I. Winings

Abstract.—Breeding birds at five deciduous forest sites in the Washington, D.C. area have experienced alarming declines in recent decades. On Plummers Island and the adjacent mainland, 61% of the breeding species were lost over 50 years, and from 1943 to 1984 breeding populations declined 38% from 134 pairs to 83.5 pairs. For four other sites in the area, long-term breeding density losses ranged from 7% to 68%. Average losses of 0.5 species and 4.3 breeding pairs per year were calculated from the four sites. Significant among these losses were Neotropical migrants, but at most sites declines were also noted in the resident and short-distance migratory species. Similar trends have been detected in long-term studies at several other deciduous forest sites in North America. Additional patterns are reported from the Washington area sites: (1) over the years Neotropical species have been lost gradually, not abruptly, and (2) for individual species, losses have occurred in different years on different sites despite their proximity. Causes of the declines are briefly discussed, with a special focus on vehicular disturbance as a contributing factor on Plummers Island.

Accelerating tropical deforestation, the increasing widespread loss of biological diversity, and forest fragmentation in North America have attracted the attention of systematists, ecologists, conservationists, and decision-makers in recent years. Because birds are conspicuous members of forest communities, breeding bird populations are often used as indicators of forest vitality and stability both in North America and the Neotropics (Aldrich and Robbins 1970). Only by using long-term data sets, however, can bird population trends be accurately identified and critically analyzed; only in recent years have such long-term sets been available. In the greater Washington, D.C. area, near the Potomac River from the vicinity of the Capital Beltway (I-495) in Virginia and Maryland to well inside the District of Columbia (Fig. 1), breeding birds have been censused in five deciduous forest sites over periods of years ranging from 14 to 41. The present paper is an analysis of the data from these long-term censuses with an emphasis on Plummers Island, Maryland, where observations extend back to 1935 and before (Fisher 1935). Consideration is given to the dramatic loss of Neotropical migrants and the changing populations of resident birds.

Sites and methods.—On Plummers Island (PI) and the adjacent mainland (Site 2, Fig. 1) immediately east of the Cabin John Bridge, a characteristic floodplain forest is dominated by cottonwoods (*Populus deltoides*) and sycamores (*Platanus occidentalis*). This lowland forest grades into an upland forest dominated by oaks (*Quercus velutina, Q. borealis*), hickories (*Carya glabra, C. tomentosa*), tulip-tree (*Liriodendron tulipifera*), and other deciduous species. When Fisher (1935) and Aldrich and Duvall

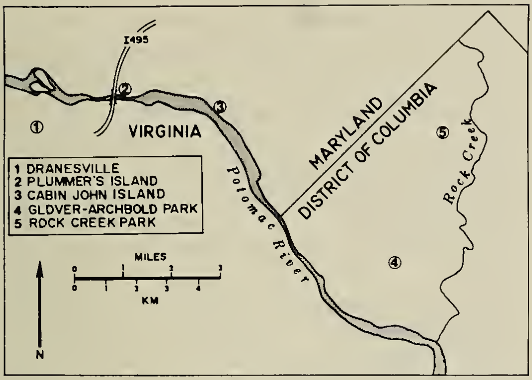

Fig. 1. The location of breeding bird census sites in the Washington, D.C. area.

(1943) reported on the birds here, the mainland portion of the site contained a 7-acre old field which subsequently experienced characteristic succession from grassland to young scrub pine (*Pinus virginiana*) (Fig. 2). By 1984, the field had long since been replaced by a forest community dominated by tulip-tree. Data used for this site in the present analysis include Fisher's descriptive report (1935) of breeding birds up to 1935, a breeding bird census by Aldrich and Duvall (1943), and our census in 1984. The total census area (island and mainland in Fig. 2) was approximately 50 acres.

Dranesville District Park (DR) (Site 1), formerly known as Burling Park, has been described as an immature oak-hickory hardwood forest (Mainland 1971), also dominated at that time by tulip-tree and several species of oaks with an understory of hickories. The census area of 27.2 acres is a virtually uniform forest surrounded by 200 acres of similar habitat. Although 14 consecutive years of censuses are available (begun in 1972), 1972 was a year of inadequate coverage, so our analysis of the Dranesville data set begins with 1973.

Cabin John Island (CJ) (Site 3) was described in detail (Anonymous 1947) as "a mature deciduous floodplain forest . . . about 100 years old," dominated then by sycamore, American elm (*Ulmus americana*), tulip-tree, black walnut (*Juglans nigra*), and other hardwoods. From the census area of 18.75 acres, 34 censuses have been published between 1947 and 1986.

The Glover-Archbold Park (GA) site (Site

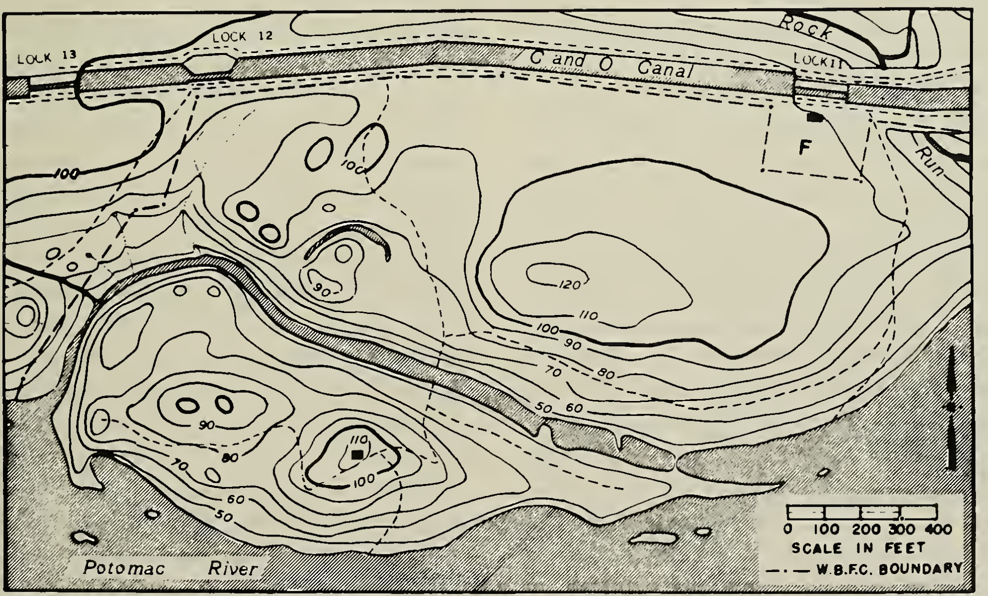

Fig. 2. The Plummers Island and adjacent mainland census site. F marks the location where the old field once existed. Map courtesy of the Washington Biologists' Field Club.

Table 1.—Breeding bird censuses on Plummers Island, 1943 and 1984. Figures are for pairs or territorial males on the 50-acre site.

	1943	1984
Red-eyed Vireo (*Vireo olivaceous*)	15	13.5
Kentucky Warbler (*Oporornis formosus*)	11	0
Northern Cardinal (*Cardinalis cardinalis*)	9	12.5
Acadian Flycatcher (*Empidonax virescens*)	9	6
Carolina Wren (*Thryothorus ludovicianus*)	7	8
Field Sparrow (*Spizella pusilla*)	6*	0
Northern Parula (*Parula americana*)	6	4
Wood Thrush (*Hylocichla mustelina*)	5	0
American Redstart (*Setophaga ruticilla*)	5	0
Prairie Warbler (*Dendroica discolor*)	4*	0
Common Yellowthroat (*Geothlypis trichas*)	4*	0
Scarlet Tanager (*Piranga olivacea*)	4	1
Yellow-throated Vireo (*Vireo flavifrons*)	3	0
Great Crested Flycatcher (*Myiarchus crinitus*)	3	2.5
Tufted Titmouse (*Parus bicolor*)	3	2
European Starling (*Sturnus vulgaris*)	3	1
Indigo Bunting (*Passerina cyanea*)	3*	2
American Goldfinch (*Carduelis tristis*)	2*	1
Song Sparrow (*Melospiza melodia*)	2	2
Yellow-breasted Chat (*Icteria virens*)	2*	0
Blue-gray Gnatcatcher (*Polioptila caerulea*)	2	0
Carolina Chickadee (*Parus carolinensis*)	2	6.5
White-breasted Nuthatch (*Sitta carolinensis*)	2	1
Red-bellied Woodpecker (*Centurus carolinus*)	2	2.5
Eastern Phoebe (*Sayornis phoebe*)	2	1
Mourning Dove (*Zenaida macroura*)	2*	0
Bobwhite (*Colinus virginianus*)	2*	0
Eastern Wood-Pewee (*Contopus virens*)	1	6
American Robin (*Turdus migratorius*)	1	0
Eastern Bluebird (*Sialia sialis*)	1	0
Common Grackle (*Quiscalus quiscula*)	1	1
American Crow (*Corvus brachyrhynchos*)	1	1
Blue Jay (*Cyanocitta cristata*)	1	1
Gray Catbird (*Dumetella carolinensis*)	1	0
Ovenbird (*Seiurus aurocapillus*)	1	0
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	1*	0
Downy Woodpecker (*Picoides pubescens*)	1	1.5
Ruby-throated Hummingbird (*Archilochus colubris*)	1	0
Yellow-billed Cuckoo (*Coccyzus americanus*)	1	0
Barred Owl (*Strix varia*)	1	1
Spotted Sandpiper (*Actitis macularia*)	1	0
Northern Oriole (*Icterus galbula*)	0	1
Hairy Woodpecker (*Picoides villosus*)	0	2.5
Prothonotary Warbler (*Protonotaria citrea*)	0	1
House Finch (*Carpodacus mexicanus*)	0	1
Total breeding pairs or territorial males	134	83.5

* Species found in old field.

4) is a 35-acre upland deciduous forest, described by Briggs (1960) as "about 100 years old" and dominated by beech (*Fagus grandifolia*), tulip-tree, and several species of oaks and maples (*Acer* spp.). From 1959 to 1986, 25 censuses have been published.

The Rock Creek Park (RC) census site (Site 5) was originally 80 acres but was reduced to 65 acres in 1963. It was described (Anonymous 1948) as a "hardwood forest with scattered pine" dominated by tulip-tree, oaks (*Q. alba, Q. prinus*), other hardwoods, and some scrub pine. From 1948 to 1986, 29 censuses have been published.

Censuses from these last four sites have been published in "The Wood Thrush," "Atlantic Naturalist," and "American Birds." None of the published, annual census analyses provide information on any substantial habitat changes within the sites since the original habitat descriptions were published.

Table 2.—Summary of breeding bird population data, Plummers Island and the adjacent mainland, 1935–1984.

Breeding birds	Up to 1935	1943	1984
Species richness	67	41	26
No. Neotropical species	28	18	9
No. resident/short-distance migrant species	39	23	17
Density (pr./100 acres)			
a. Neotropical species	—	154	74
b. Resident/s-d. migrants	—	114	93

Although some census-takers have changed at these sites over the years, techniques for censusing the breeding birds have generally followed the widely used spot-mapping/singing-male/territory-mapping technique described by Williams (1936) and discussed in detail in Ralph and Scott (1981).

Results.—For Plummers Island and the adjacent mainland, Fisher (1935) listed 67 breeding species recorded up to that time. Of these, 39 were resident and/or short-distance migrants (57%), whereas 28 were Neotropical species (43%). The census in 1943 by Aldrich and Duvall showed that 26 species had been lost from the breeding population, and, by 1984, the total species richness was further reduced from 41 to only 26, nine (35%) of which were Neotropical species (Tables 1, 2). Thus, in a span of about 50 years, 61% of the formerly breeding species were no longer found at this site. Over the 50-year period the reduction of 68% in species richness of Neotropical birds was paralled by an equally alarming decline (56%) of resident and/or short-distance migrant species. Some of the species losses can undoubtedly be attributed to habitat changes associated with old-field succession described above. For example, of the nine species breeding in or near the small field in 1943, all except the Indigo Bunting and American Goldfinch were gone by 1984, and the few remaining pairs of these two species bred only at the edge of the study site along the Potomac River.

Table 3.—Long-term breeding bird data for five deciduous forest sites in the Washington, D.C., area.

Site	Species richness	Pairs/100 ac. (mean loss per yr.*)	Percent* resident or short-distance migrant species	Percent* Neotropical migrant species
Plummers Island				
1943	41	268	35	65
1984	26	167 (2.5)	54	46
Cabin John				
1947	30	608	41	59
1986	24	344 (6.8)	69	31
Rock Creek Park				
1948	29	233	15	85
1986	25	74 (4.2)	58	42
Glover-Archbold				
1959	39	570	47	53
1986	30	529 (1.5)	69	31
Dranesville				
1973	25	327	58	42
1986	19	261 (4.7)	52	48

* Of pairs/100 ac.

Between 1943 and 1984, population density losses at the Plummers Island site were high for Neotropical species (51%) but less for the residents (18%), the latter decline being offset somewhat by small increases in the Northern Cardinal, Carolina Wren, and Carolina Chickadee. Major population and species losses for Neotropical migrants over the last 41 years included the Kentucky Warbler (11 pr. to 0), Wood Thrush (5 to 0), Yellow-throated Vireo (3 to 0), Blue-gray Gnatcatcher (2 to 0), and others (Table 1).

Analysis of the long-term data sets from the other four sites reveals some notable parallels and a few differences when compared to the PI data (Table 3). PI had a decrease in species richness of 37% in 41 years; for the other four sites, decreases in species were: 14% (RC, 39 yr), 20% (CJ, 34 yr), 23% (GA, 25 yr), and 24% (DR, 14 yr). The mean loss in species richness over the four sites was 0.5 species per year. Population density changes, on the other hand, differed widely among the sites, from 7%

(GA) and 20% (DR) to 43% (CJ) and 68% (RC), compared with 38% on PI. The mean loss over the four sites was 4.3 breeding pairs per year (on a 100-acre basis). Examination of each year's census revealed the fact that declines in total breeding pairs apparently began at different times at the different sites—about 1964 (RC), 1972 (CJ), and 1976 (GA). These analyses are in general agreement with the detailed reports for these three sites (CJ, RC, GA) discussed by Criswell (1975) and Briggs and Criswell (1986).

Focusing on the ten species with the highest initial densities at each of the sites, species showing the greatest density losses were the Red-eyed Vireo, Kentucky Warbler, Acadian Flycatcher, Northern Parula, Wood Thrush, and American Redstart, all Neotropical migrants. Interestingly, some resident species had small increases on most of the sites, e.g., Northern Cardinal, Carolina Wren, Carolina Chickadee, and Tufted Titmouse.

Discussion.—Long-term studies of breeding birds from specific sites in North American deciduous forests date back to 1923. From 1923 to 1947, breeding bird populations in one Michigan (Walkinshaw 1947) and two Ohio (Williams 1947, Preston 1960) forests showed no apparent population trends. However, the 50-year study by Kendeigh (1982) in Illinois showed a gradual increase in breeding bird density from 1927 to a peak about 1960, after which a modest decline continued through 1976. In the Illinois study, Neotropical species peaked in 1950 as 50% of the total breeding population, then decreased to only 27% by 1976. A 23-year study in Connecticut revealed a slightly increasing population from 1953 until 1964, followed by a dramatic decline beginning about 1970 (Butcher et al. 1981). Over a 16-year period from 1969 to 1984, populations in a New Hampshire forest declined steadily from 640 breeding adults to 360/100 acres with the most notable losses occurring after 1977 (Holmes et al. 1986).

Combining the analysis of these long-term trends with those from the deciduous forest sites summarized here for the Washington area, several general patterns are evident (Table 3). (1) Declines became evident at most sites after 1960 for total breeding bird densities and Neotropical species. (2) For individual species showing declines, especially the Neotropical ones, population densities gradually decreased year by year often down to a single pair. Subsequently, over the next few years, the species was often reported as an unmated or single territorial male, then as a "+" or "visitor." These latter designations usually meant that only one bird was seen once or twice on the census area but without any evidence of territoriality. Rarely did a species "return" as a breeding pair after an absence of several years, but such instances did occur with the Yellow-throated Vireo (CJ), Hooded Warbler (RC), and Prothonotary Warbler (PI). This general pattern is reported here because it strongly suggests that Neotropical species have decreased gradually and not abruptly in the breeding populations. (3) From these long-term census data, another pattern of decrease is apparent at least for the Neotropical migrants in the Washington area. Because of some differences in vegetational composition, physiography, and microclimate among these four sites, one might expect that individual species would be lost at different times. And the data support this pattern. For example, the last breeding pair of American Redstarts was found in 1973 (RC), 1974 (GA), and 1981 (CJ). For the Kentucky Warbler, a different temporal pattern of loss was evident: 1961 (RC), 1965 (CJ), 1970 (GA), and 1978 (DR). And for the Hooded Warbler, the data are: 1960 (GA), 1969 (RC), and 1978 (DR). Thus, individual Neotropical migrant species have disappeared as breeding birds in different years at the different sites despite the proximity of the sites.

Although breeding densities have declined at all five sites in recent decades, especially for the Neotropical species, some individual resident species as noted above have shown small but reasonably consistent increases. We hypothesize two explanations for these increases, the hypotheses not being mutually exclusive. Given the likelihood of reduced competition for environmental resources with the decrease of Neotropical birds, the remaining resident species could have expanded their ecological niches with a consequent increase in breeding potential. Secondly, it is also possible that during the nonbreeding season some of the resident species move into contiguous habitats where they find supplemental food resources at feeding stations. Such additional resources could conceivably reduce overwinter mortality, thus also increasing the breeding potential.

The causes of species and population declines are complex and have recently been attributed to a variety of factors, including forest fragmentation in North America (Whitcomb 1986), deforestation in the American tropics (Terborgh 1980), and the effects of Brown-headed Cowbird (*Molothrus ater*) parasitism (Brittingham and Temple 1983). Our study does not directly address these hypotheses from a cause-and-effect standpoint. However, a correlation might exist between our reported declines of breeding Neotropical migrants and accelerating deforestation in the Neotropics, a correlation also developed by several authors in Keast and Morton (1980). At least for PI, our field observations specifically suggest that human disturbance was a causal factor in population declines of some species, in addition to the successional factor discussed above. Vehicular traffic passing over the Cabin John Bridge (completed about 1962) immediately adjacent to the study area produces a deafening (to humans) noise level that could affect breeding birds at that portion of the study site despite the fact that the habitat has shown no appreciable change since then. In fact, for species still breeding on the study area in 1984, in the forest habitat immediately adjacent to the bridge 10 species showed a total reduction (1943–1984) from 11 to 6 territories.

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A NEW EXTINCT SPECIES OF GIANT PIGEON (COLUMBIDAE: *DUCULA*) FROM ARCHEOLOGICAL DEPOSITS ON WALLIS (UVEA) ISLAND, SOUTH PACIFIC

Jean Christophe Balouet and Storrs L. Olson

Abstract.—A new species of giant pigeon, *Ducula david*, is described from an archeological excavation on Uvea Island, Wallis group. The new species was contemporaneous with early Lapita culture. *Ducula david* is related to, but larger than, either *D. pacifica* or *D. galeata*. It was sympatric with *D. pacifica* and provides further evidence that more than one species of *Ducula* co-existed on small Pacific islands prior to the arrival of man, who was responsible for the extinction of larger species of *Ducula* throughout almost the entire Pacific.

The Wallis Islands, consisting of the large island of Uvea and some 22 much smaller satellites, lie in the South Pacific about 385 km northeast of Fiji and 300 km west of Samoa (13°12′ to 13°24′S; 176°6′ to 176°14′W). In the area between Fiji and Samoa, the Wallis group forms the northern point of a triangle with the Horn Islands (Futuna) to the southwest, and Niuafo'ou, a remote northern outlier of the Tonga group, to the southeast. The island of Uvea is 14 km long by 7.5 km wide, with an area of 95 km² and a maximum elevation of 142 m. The preceding is summarized from Stearns (1945) and Aubert de la Rüe (1963).

Excavations of Polynesian archeological sites on Uvea by Frimigacci, Siorat, and Vienne (see Appendix) have produced a few vertebrate remains, mainly of pig, sea turtles, and birds. Among the latter are bones belonging to an undescribed species of pigeon of the genus *Ducula*. The material described below is housed in the collections of the Département des Sciences Humaines, Office de la Recherche Scientifique et Technique Outre Mer (ORSTOM), Nouméa, New Caledonia.

Class Aves
Order Columbiformes
Family Columbidae
Genus *Ducula* Hodgson, 1836

The imperial pigeons (*Ducula*) can be distinguished from other large pigeons in the Pacific by the widely separated proximal foramina of the tarsometatarsus, the inner foramen being very large and separated from the inner side of the bone only by a thin ridge. Also, the inner cotyla is hooked anteriorly.

Ducula david, new species
Fig. 1

Holotype.—Right tarsometatarsus (MU 021 A/83 3335), lacking the hypotarsus and the distal end 1 cm below the facet for metatarsal I, internal cotyla damaged.

Type locality.—Utuleve (site WF-U-MU 21A of Frimigacci et al., see Appendix), west side of the island of Uvea, Wallis group, South Pacific.

Horizon and age.—Late Holocene archeological deposits, Bed VI^a, 0.80–0.85 m be-

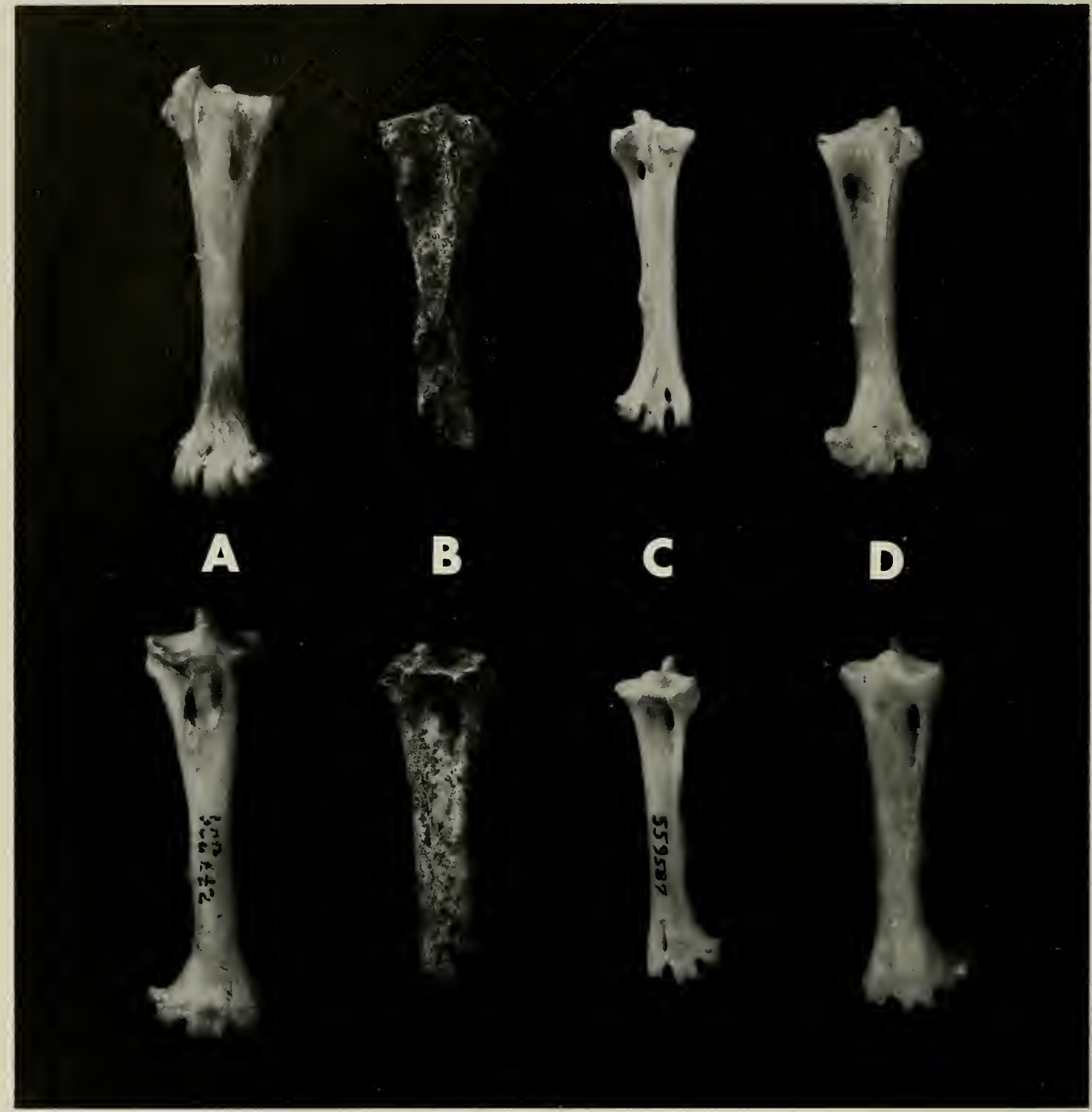

Fig. 1. Tarsometatarsi of *Ducula* in posterior (top row) and anterior (bottom row) views. A, *D. galeata*; B, *D. david*, new species, holotype; C, *D. pacifica*; D, *D. goliath*. 1.5×.

low surface, in association with Lapita ceramics of the Utuleve II type (see Appendix; Fig. 2). The radiocarbon age of the bed below that yielding the holotype is 2350–2550 YBP (Frimigacci, pers. comm.). Lapita culture appeared in Samoa and Tonga about 2500 to 3000 YBP and pottery manufacture is thought to have ceased there early in the Christian era (Green 1979, Davidson 1979). The bones of *D. david* were probably deposited between about 2000 and 2500 YBP (see Appendix).

Paratypes.—Fragment of a left coracoid (MU 021 A/83 4252) from the same locality as the holotype but from a lower level. Anterior portion of a left scapula (UMU 46 A A1 A2/83 1352) from the Malama Tagata site (see Appendix, Table 2).

Measurements of types.—See Table 1.

Etymology.—In a genus with a species

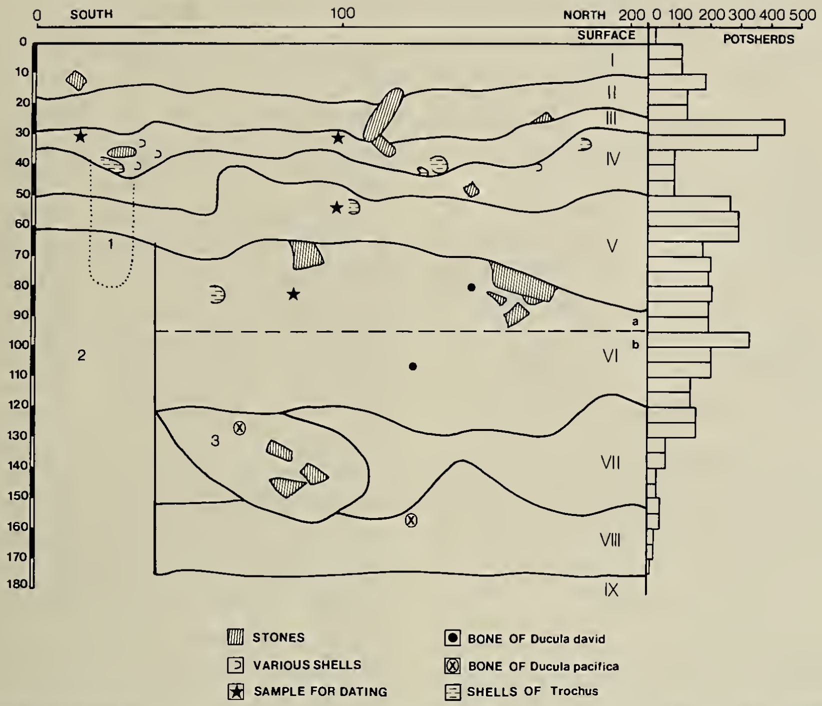

Fig. 2. Stratigraphic section of the excavation at Utuleve, Uvea, Site W-FU-MU 21A. The column on the left gives depth in cm. The column on the right shows the number of potsherds found in each 5 cm interval of the dig. Feature 1 is a post hole, feature 2 an unexcavated control column, and feature 3 a pit filling. *Trochus* is a large marine gastropod.

named *goliath,* it seems fitting to dedicate another species to David, whose name is invariably linked with the giant Philistine. In a reversal of the biblical fable, *Ducula david* was larger than *D. goliath* but perished, whereas the New Caledonian *D. goliath* is smaller and still survives.

Diagnosis.—A very large species of *Ducula,* with the tarsometatarsus larger and more robust than in either *D. goliath* or *D. galeata.* Tarsometatarsus with well developed proximal inner foramen, stout shaft, very well developed facet for metatarsal I, and proximal foramina widely separated; tubercle for tibialis anticus located on external edge of shaft.

Comparative material (skeletons) examined.—*Ducula goliath,* 1; *D. galeata,* limb bones removed from skin; *D. pacifica,* 3 + 3 partials; *D. aurorae,* 1; *D. oceanica,* 1; *D. pinon,* 2; *D. badia,* 3; *D. myristicivora,* 1 partial; *D. perspicillata,* 8; *D. radiata,* 1; *D. aenea,* 17; *D. bicolor,* 7; *D. luctuosa,* 1; *D. spilorrhoa,* 1. All specimens in National Museum of Natural History, Smithsonian Institution, except *D. goliath,* Muséum National d'Histoire Naturelle, Paris.

Comparisons.—Among the species groups of *Ducula* recognized by Goodwin (1983), that containing *D. pacifica, D. oceanica, D. aurorae,* and *D. galeata* is very uniform in tarsometatarsal morphology. *Ducula david* shares with these species the same disposition of the muscular insertions anterior and posterior to the internal cotyla, both being triangular in shape and oriented at 45° to the long axis of the bone. *Ducula pacifica* is the most similar species in osteology to *D. david.* The proximal foramina of the tarsometatarsus are more widely separated in *D. david* than in any other species, and the metatarsal facet is much better developed, occupying half the width of the shaft.

Discussion.—Throughout the Pacific, the

Table 1.—Measurements (mm) of *Ducula david*, new species, compared with other large species of *Ducula*.

	D. david	*D. galeata*	*D. goliath*
Tarsometatarsus			
Distance between proximal end of metatarsal facet and internal cotyla	20.8	20.5	18.6
Proximal width	11.9	11.5	10.3
Depth of inner cotyla	6.3	5.3	4.2
Width of inner cotyla	5.3	4.2	3.8
Distance between proximal foramina	3.2	2.0	2.4
Width of shaft at metatarsal facet	6.2	4.8	5.1
Depth of shaft at metatarsal facet	3.9	3.5	3.3

	D. david	*D. oceanica*	*D. pacifica*
Scapula			
Maximum diameter of glenoid facet	5.5	4.1	3.9
Maximum proximal width	11.9	8.9	8.6
Width of neck	4.8	3.1	3.1
Depth of neck	2.6	1.8	2.0
Coracoid			
Minimum diameter at mid-point	4.4	3.1	3.0
Maximum diameter at mid-point	4.8	3.3	3.2

very large forms of *Ducula* appear to have been especially vulnerable to extinction. The only historically known populations of pigeons of this size in Oceania are *D. goliath* in New Caledonia and *D. galeata* of Nuku Hiva, Marquesas. Recent discoveries in archeological and paleontological sites, as well as an account from Captain Cook's second voyage, have shown that *D. galeata*, or a closely similar form, occurred not only on other islands of the Marquesas (D. W. Steadman, in press), but on Henderson Island in the remote Pitcairn group (Steadman and Olson 1985), on Mangaia in the Cook group (Steadman 1985), and on Tahiti, in the Society group (Lysaght 1957). [Within *Ducula*, the specific name *Columba reinholdforsteri* Wagler, 1829, is probably a senior synonym of *Serresius galeata* Bonaparte, 1855 (Lysaght 1957; Bruce et al. 1985; Olson and Steadman, in press).] *Ducula galeata* was therefore a widespread species that might be expected in deposits on many other islands as well.

The same was probably true of *D. david*. A very large pigeon has been reported from archeological deposits in the Lakeba Islands in the Fiji archipelago (Gibbons and Clunie 1986; specimens examined by Olson and D. W. Steadman), which, from its relative proximity to the Wallis group, might be referrable to *D. david* or a closely allied form. From the island of Lifuka in the Tonga group, a species of *Ducula* even larger than *D. david* has been discovered in an archeological site (D. W. Steadman, pers. comm.).

The evidence of numerous extinct populations of large species of *Ducula* in archeological deposits shows that these birds persisted until the arrival of man, and their extinction is doubtless attributable to human influence. Whereas many man-caused extinctions of birds in the Pacific were due to habitat destruction or introduced predators (Olson and James 1984), the demise of the large species of *Ducula* was probably largely a result of direct overexploitation. For example, pigeon snaring was a very important facet of Tongan culture (McKern 1929, Gifford 1929) and the same is likely to have been true all through Polynesia.

The artificial, man-induced, pattern of distribution of pigeons in the Pacific has given rise to numerous erroneous systematic and biogeographic conclusions. Mayr (1940, 1942) has cited *D. galeata* as a classic case of allopatric speciation, as he supposed it to be only a representative of *D. pacifica* that evolved its manifestly divergent characters as a result of its great isolation in the Marquesas. Discounting the benefits of hindsight, it seems unbelievable that such a highly volant species as *D. galeata* would be confined to a single island and not be found elsewhere in the Marquesan archipelago. In any case, *D. galeata* was widely

Table 2.—Provenance of bones of *Ducula* and *Gallus* from archeological sites on Uvea, Wallis Islands.

Catalog	Bed	Depth	Pottery type	Species	Element
			Site W-FU-MU 21A Utuleve		
3335	VI[a]	0.80–0.85 m	Utuleve II	*D. david* Holotype	Tarsometatarsus
4252	VI[b]	1.00–1.10 m	Utuleve I	*D. david* Paratype	Coracoid
5275	VIII	1.50–1.60 m	Utuleve I	*D. pacifica*	Coracoid
4950	VII	1.20–1.30 m	Utuleve I	*D. pacifica*	Coracoid
941	VI[a]	0.80–0.85 m	Utuleve II	*G. gallus*	Tibiotarsus
			Site W-FU-MU 46-A Malama Tagata		
1352	8	1.40–1.43 m	Utuleve I	*D. david* Paratype	Scapula
1138	8	0.95–1.00 m	Utuleve I	*D. pacifica*	Scapula
1059	8	0.80–0.85 m	Utuleve II	*G. gallus*	Tibiotarsus

sympatric with smaller species of *Ducula* and is not merely a well-marked allospecies of *D. pacifica.* Modern concepts of biogeography and competitive exclusion have been used by Holyoak and Thibault (1978) to explain why the species of *Ducula* (and fruit-doves of the genus *Ptilinopus* as well) are allopatric throughout most of the Pacific. Paleontological and archeological evidence has now refuted these ideas by showing that two forms of *Ducula* occurred sympatrically over wide areas.

Ducula pacifica Gmelin, 1789

Material.—Two bones from the type locality of *D. david* and one other from the nearby Malama Tagata site (see Appendix, Table 2) do not differ in size or in morphology from bones of this widespread species.

Remarks.—*Ducula pacifica* occurs today in the Wallis group and has been recorded elsewhere from the Solomons east to Samoa, Tonga, and the Cook Islands.

Order Galliformes
Family Phasianidae
Genus *Gallus* Brisson, 1760
Gallus gallus Linnaeus, 1758

Material.—Two distal ends of tibiotarsi.

Remarks.—These bones of domestic fowl, a species imported to the island by Polynesians, show significant variation in size (UMU 46 A, A1–A2/83 1059—distal width 12.1 mm, distal depth 13.5; UMU 24 A 83 941—distal width 10.3, distal depth 10.8).

Acknowledgments

We are deeply indebted to Dr. D. Frimigacci who permitted our study of the specimens from Wallis Island and supplied the archeological documentation. Our collaboration at the National Museum of Natural History was made possible by a short-term visitor's grant to Balouet from the Office of Fellowships and Grants of the Smithsonian Institution. We are grateful to David W. Steadman for sharing information and commenting on the manuscript.

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Appendix

Preliminary Report on Archeological Sites on Wallis (Uvea) Island Yielding Bones of Pigeons (*Ducula*)

D. Frimigacci, C. Sand, J. P. Siorat, and B. Vienne
(translated and edited by Storrs L. Olson)

The site yielding bones of *Ducula david* (designated WF-U-MU 21A) is located at Utuleve, at about the midpoint of the western side of the island of Uvea. The entire archeological sequence of the island was exposed in this excavation. In the eight beds that were recognized (Fig. 2) are ceramics that correspond to three distinct levels: Utuleve I, the oldest, and Utuleve II and III, all three belonging to the same cultural unit, the Lapita. The superficial soil at the site was covered with wild yams and with numerous potsherds strewn about. The description of the different beds follows, with color designations from the Munsell soil color chart in parentheses.

Bed I.—Black humic soil (7.5 YR 3/2) heavily disturbed by agricultural activity.

Bed II.—Black sandy clay (7.5 YR 3/2) invariably culturally altered. Pottery and food remains more abundant than in Bed I.

Bed III.—Dark sandy soil (10 YR 3/1) spared by farmers. This is an archeological filling composed of large shells, most often burnt, hearth stones, and a great number of potsherds. A post hole is contemporaneous with this level (Feature 1 in Fig. 2).

Bed IV.—Light sandy soil (10 YR 3/3) with some burnt shells representing the base of Bed III.

Bed V.—Gray sandy soil (10 YR 3/2) in which the pottery is different from the overlying beds. Numerous shells present. This bed is an archeological filling with a very great density of remains at the surface. A control column was left in place below this bed (Feature 2 in Fig. 2).

Bed VI^a.—Deep ochraceous sandy soil with food remains and hearth stones. First appearance of potsherds with stamped impressions.

Bed VI^b.—Light ochraceous sandy soil (10 YR 3/3), the difference in color from VI^a being most noticeable on the west face. Elsewhere the color of Bed VI is uniformly light ochre. The greatest concentration of pottery is found at the surface of Bed VI^b and the first dotted and geometric Lapita decorations appear here.

Bed VII.—Brown sandy soil (10 YR 6/4) in which was found a pit filling of black sediment rich in pottery and food remains (Feature 3 in Fig. 2).

Bed VIII.—Very light sandy dune soil (10 YR 7/4), without anthropic coloration, in which some potsherds still occur.

Bed IX.—Consolidated beach sand consisting of coarse shell fragments, archeologically sterile.

One bone of *Ducula david* and one of *D. pacifica* were recovered from a site (WF-U-MU-O46-A) at the stone monument of Malama Tagata, also in the Utuleve region. The same three cultural levels (Utuleve I, II and III) as in the preceding site were present here. The bones come from a low level (ca. 1.5 m below surface; Table 2) in a dark sandy clay layer (Bed 8) resting immediately above a basalt monument.

The pigeon bones from the preceding two sites came from levels containing ancient Lapita pottery. At site WF-U-MU 21A, Utuleve III pottery occurred in beds I to IV. This most recent ceramic type is undecorated and is found throughout Uvea. Utuleve II pottery appears in beds V and VI^a. This is much finer than the preceding, with rare decorations confined to the borders. The same pottery, which goes back to the first centuries BC, is found at Futuna (Kirch 1976; Frimigacci, Siorat, and Vienne, in prep.), and is comparable to that from the Singatoka site on Fiji dating to the same epoch. Utuleve I pottery, which is even more ancient, with dentate stamped (*pointillé*) decorations, appears in beds VI^b to VIII. The same ceramic sequence (Utuleve I, II, III) is revealed at Futuna (Frimigacci, Siorat, and Vienne, in prep.).

The stratigraphic position of the bones shows that these pigeons coexisted with the first human occupants of Uvea. The extinction of *Ducula david* may have taken place in the first centuries AD. The Polynesians attached considerable significance to pigeons. Tongan nobles used to construct "pigeon mounds," called *sia heulupe,* from which they evidently snared pigeons (McKern 1929).

(DF) Centre National de la Recherche Scientifique, UA 275, Paris, France; (JPS) Musée Neo-Calédonian, Nouméa, New Caledonia; (BV) Institut Français de Recherche Scientifique pour le Developpement en Cooperation, Nouméa, New Caledonia.

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SPRINGSNAILS (GASTROPODA: HYDROBIIDAE) OF ASH MEADOWS, AMARGOSA BASIN, CALIFORNIA–NEVADA

Robert Hershler and Donald W. Sada

Abstract.—Aquatic snails of the family Hydrobiidae were sampled from numerous springs in Ash Meadows, California–Nevada, during 1985–1986. The fauna of this lush oasis is represented by at least three lineages and composed of 11 species in two genera, *Pyrgulopsis* Call and Pilsbry, 1886 and *Tryonia* Stimpson, 1865. Nine species are described herein as new. Nine species are locally endemic (three are restricted to single springs), while the remaining two are restricted to Amargosa River drainage. *Pyrgulopsis* species are well-differentiated in shell and anatomical features (mostly penial morphology), whereas *Tryonia* species show marked variation only in the former.

Stepwise discriminant analyses were done using shell morphometric data from three separate species groups in Ash Meadows. Separate analyses were done using standard measurements and Raupian parameters as a local test of their effectiveness in discriminating between closely related forms. Classification was uniformly high (86–93%) when the former data set was used, supporting taxonomy presented herein. Raupian parameters produced less successful classifications (48–71%), probably due to absence of shape diversity among similar-shelled members of species groups considered.

Ash Meadows springsnails parallel local fishes in having affinities with taxa from the Death Valley System and Colorado River drainages. Distributional evidence suggests that local differentiation of snails has primarily occurred within narrow ranges of altitude, in contrast to patterns documented for local fishes.

Gill-breathing springsnails (Gastropoda: Hydrobiidae) inhabiting the series of intermontane valleys that constitute the Death Valley System (Miller 1943) of southeastern California and southwestern Nevada are poorly known, as they are throughout the arid Southwest. While only two species have been described from this region, based on material collected by the United States Department of Agriculture 1891 Death Valley Expedition, unpublished data (see Taylor 1966, Landye 1973, Hershler 1985, Taylor in Williams et al. 1985) suggest that many additional species are present in the region, with diversity and localization of endemic taxa likely surpassing that documented for the region's well studied ichthyofauna (see Miller 1948, Soltz and Naiman 1978, Minckley et al. 1986).

An ongoing survey of the region's Hydrobiidae was initiated during 1985 by the senior author to obtain material for systematic study of the fauna. Fieldwork during 1985–1986 included survey of all known springs in Ash Meadows, a lush oasis renowned for its highly endemic biota (Beatley 1977, Soltz and Naiman 1978, Reveal 1979). We present herein a description of this faunule as the first of a series of papers on systematics of springsnails of the Death Valley System.

Eleven springsnail species are recognized,

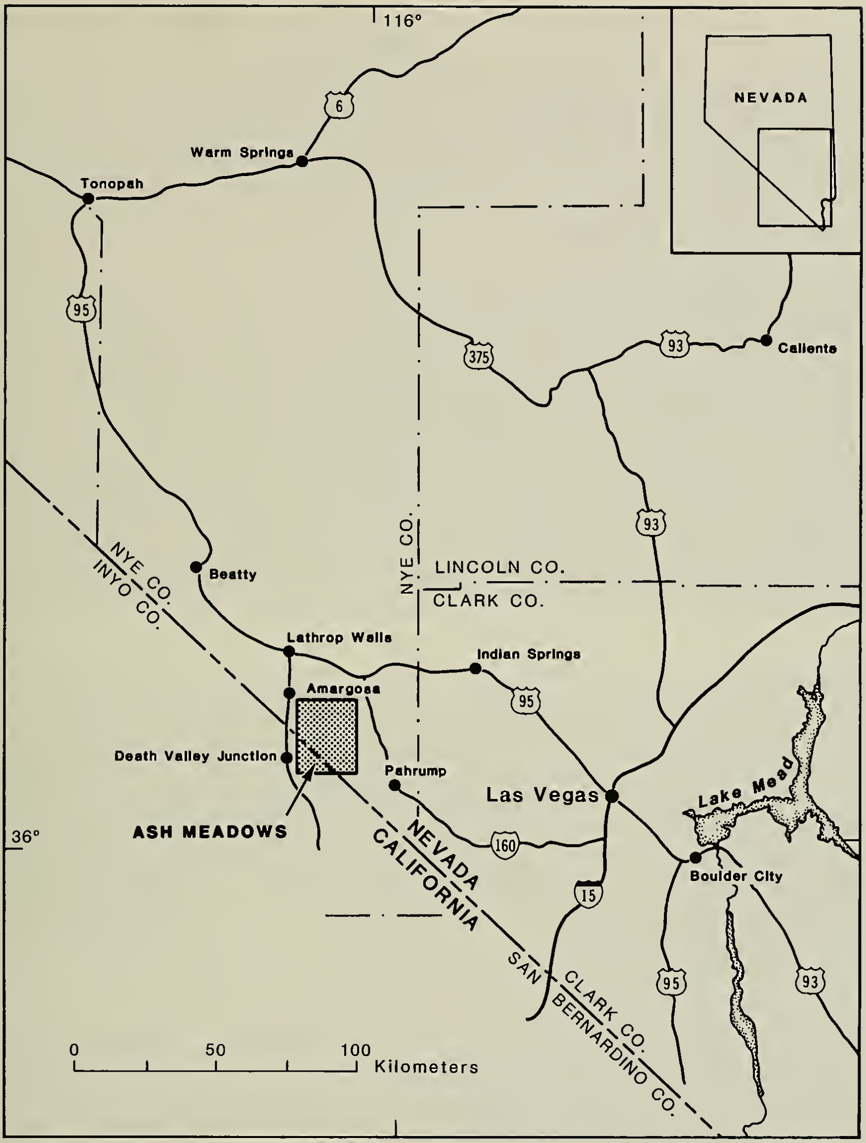

Fig. 1. Map showing location of Ash Meadows, Nevada–California.

representing two genera, *Pyrgulopsis* Call and Pilsbry, 1886, and *Tryonia* Stimpson, 1865. Nine species are new, and nine are endemic to Ash Meadows, three of which are restricted to single springs. Non-endemic forms are restricted to Amargosa River drainage in the eastern part of the Death Valley System. Both total and endemic diversity are striking, clearly exceeding values for local fishes, and seldom matched by springsnail fauna of similarly sized regions (Taylor 1966). Three lineages are recognized in the fauna, which has affinities with springsnails from Death Valley System and Colorado River drainages. Shell morphometric data were gathered from selected populations and subjected to stepwise discriminant function analyses, with standard measurements and Raupian parameters (Raup 1966) used in separate analyses as a local test of relative effectiveness in discriminating between closely related taxa.

The taxonomic work presented herein is that of Hershler. Other parts of the paper were co-written.

Environmental Setting

Ash Meadows occupies ca. 25,000 ha in Amargosa Desert along the California–Nevada border 60 km W of Death Valley (Fig. 1). Local terrain slopes from neighboring hills of 1300 m elevation southwest to elevation of 560 m in Amargosa Valley. Mean annual temperature is 18.5°C (Dudley and Larson 1976), with summer highs often exceeding 40°C. Local rainfall is scant, averaging ca. 7.0 cm annually (Dudley and Larson 1976).

Shadscale (*Atriplex confertifolia*) and *Haplopapus acaradenius* dominate on xeric soils in Ash Meadows, and salt grass (*Distichlis spicata*) and rushes (*Juncus balticus* and *J. nodosus*) are spread over mesic areas where moisture is maintained by spring discharge or seasonal precipitation. Ash trees (*Fraxinus velutina* var. *coriacea*), mesquite (*Prosopis julifera* and *P. pubescens*), wild grape (*Vitus arizonica*), and salt grass are predominant riparian flora (Beatley 1971). The name "Ash Meadows" refers to local abundance of ash trees (Carlson 1974).

Approximately 50 springs are scattered throughout Ash Meadows, many emerging from old lake beds along a fault-controlled spring line in northern and eastern parts of the area. Springs (Figs. 2–4) vary in size from the large limnocrene, Crystal Pool, ca. 20 m in diameter and discharging 189 liters/sec, to seeps less than 1.0 m across and discharging only a few cc/sec (Dudley and Larson 1976, Garside and Schilling 1979). Total annual spring discharge is estimated as 671 liters/sec (Winograd and Thordarson 1975). Individual spring outflows extend 0.1–10 km before disappearing into soil. Springs are either isolated by expanses of arid terrain, or continuously or seasonally connected by confluence of outflows. Large springs are thermal (28–32°C). Typically lower temperatures of smaller springs may be due to rapid heat loss associated with small discharge. Springs along the eastern part of Ash Meadows are generally warmer than those to the west. All spring water is potable. Total dissolved solids range between 410 and 870 mg/liter (Dudley and Larson 1976), and specific conductivity ranges from 550–800 micromhos/cm (Winograd and Thordarson 1975). Sodium is the dominant cation, with concentrations ranging from 0.18–0.23 meq/liter; followed by magnesium and calcium. Bicarbonate ion is the most abundant anion, with typical concentration of 4.9 meq/liter (Dudley and Larson 1976, Garside and Schilling 1979). Local spring discharge is old water (ca. 10,000 years; Winograd and Thordarson 1975) transported to the area by deep carbonate aquifers draining about 7200 km^2 of southern Nevada (Winograd and Thordarson 1975). While currently endorheic, the area has had past connections with nearby Amargosa River, located a few km to the west (albeit intermittent at this point), which continues to the south before turning back north to terminate in Death Valley.

Ash Meadows is among the most significant endangered aquatic ecosystems in western North America (Williams et al. 1985). Including springsnails described herein, a total of 22 species-group aquatic or riparian taxa are considered local endemics, a total unmatched by any similar-sized area in the United States. Approximately 4000 ha. of the area (16% of total), including most springs, has been perturbed by mining, agriculture, and a municipal development. Establishment of a number of exotic species has further altered the ecosystem, with invading biota including bullfrogs (*Rana catesbeiana*), mosquito fish (*Gambusia affinis*), sailfin mollies (*Poecilia latipinna*), redrim melania snail (*Melanoides tuberculata*),

Fig. 2. Photographs of Ash Meadows springs: a, Big Spring (11/8/85); b, Crystal Pool (11/8/85).

crayfish (*Procambarus clarki*), and salt cedar (*Tamarisk* sp.). Perturbation has caused population decline of virtually all endemic taxa, 12 of which are federally listed as threatened or endangered (USDI 1986). All other endemic species, including most springsnails recognized herein, are candidates for future listing (USDI 1985a, b). There is, however, cause for optimism as The Nature Conservancy purchased the area in 1984 and sold it to U.S. Fish and Wildlife Service, which established the Ash Meadows National Wildlife Refuge (Sada and Mozejko 1984).

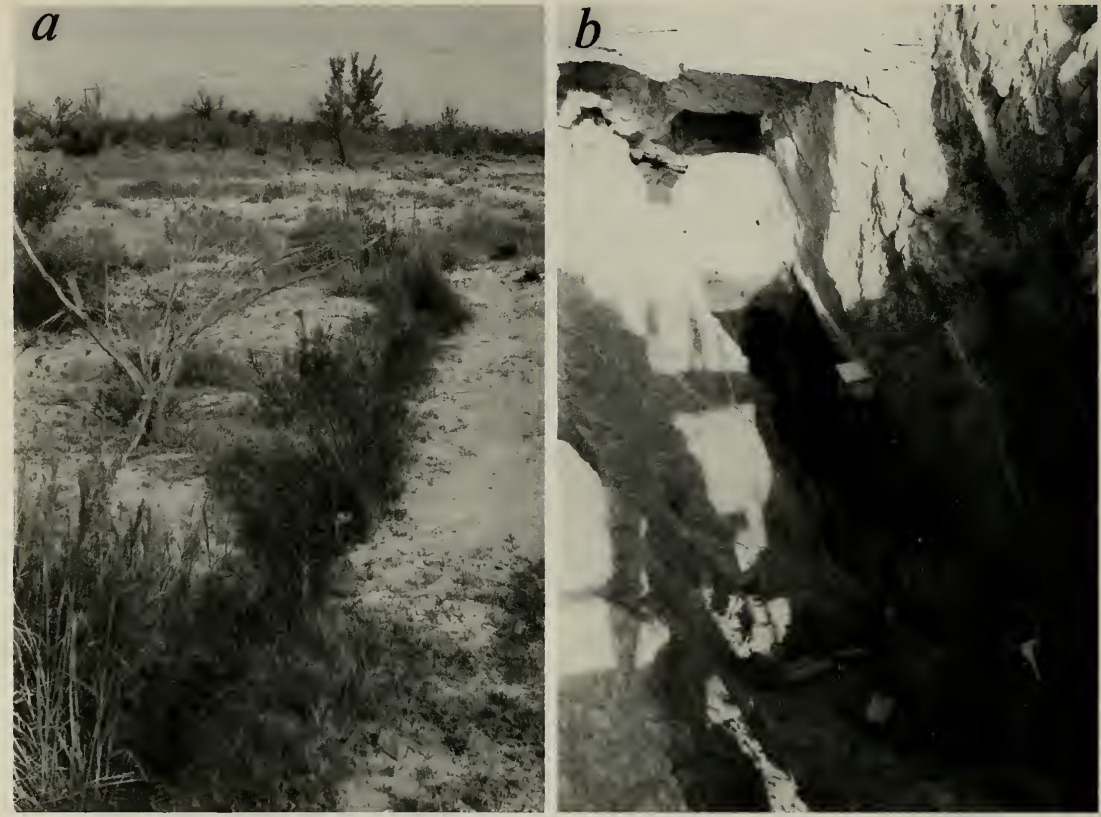

Fig. 3. Photographs of Ash Meadows springs: a, Outflow of North Indian Spring (11/10/85); b, Devils Hole (11/10/85).

List of Recognized Taxa

Pyrgulopsis micrococcus (Pilsbry).
P. erythropoma (Pilsbry, in Stearns 1893).
P. fairbanksensis Hershler and Sada, new species.
P. crystalis Hershler and Sada, new species.
P. isolatus Hershler and Sada, new species.
P. nanus Hershler and Sada, new species.
P. pisteri Hershler and Sada, new species.
Tryonia angulata Hershler and Sada, new species.
T. variegata Hershler and Sada, new species.
T. ericae Hershler and Sada, new species.
T. elata Hershler and Sada, new species.

Materials and Methods

Material examined.—Most localities visited, including all sites having snails, are shown in Figs. 5 and 6. Snails were collected by either washing rocks or sifting soft sediments with a fine-mesh hand sieve. Water temperature and conductivity were measured with a YSI Model 33, S-C-T meter. Dissolved oxygen concentrations were determined using a YSI 97 oxygen meter. Detailed descriptions of all localities visited in Ash Meadows are in Appendix 1. A few additional snailless sites were visited, including seeps by Crystal Pool. Collections often included shells of locally extinct springsnails that will be discussed further in a future publication. Distributions of species in Ash Meadows are shown in Figs. 16, 25, and 44.

Snails were relaxed with menthol crystals, fixed in 4% buffered formalin and preserved in 70% ethanol. This material is housed in the National Museum of Natural History, Smithsonian Institution (USNM) collec-

Fig. 4. Photographs of Ash Meadows springs: a, Outflow of Purgatory Spring (source at upper right corner) (11/6/85); b, Outflow of small spring at Point of Rocks (11/8/85).

tion, with paratypes of new species also deposited in the Florida State Museum (UF). Unless otherwise stated, catalog numbers in text refer to USNM material.

Morphologic study.—Shells, opercula, and radulae were photographed using a HITACHI S-570 scanning electron microscope (SEM). Generalized radular formulae were based on examination of SEM photos and are given in following order of tooth types: centrals, laterals, inner marginals, outer marginals. Intact bodies for dissection were obtained by decalcifying shells in concentrated Bouin's Solution and removing re-

Table 1.—Shell parameters for *Pyrgulopsis* species. Shell height (SH) and width (SW) are given in mm. NW = number of whorls, T = translation rate, D = distance of generating curve from coiling axis, AS = apertural shape, W = whorl expansion rate.

Species and locality		Parameter						
		NW	SH	SW	T	D	AS	W
P. micrococcus								
Purgatory Spring	$\bar{x}$	4.35	2.51	1.69	4.77	−0.041	1.26	1.86
(n = 12)	s	0.23	0.18	0.09	0.55	0.05	0.06	0.32
Spring (N) S of Rogers Spring	$\bar{x}$	4.33	2.57	1.66	4.71	−0.001	1.24	1.60
(n = 15)	s	0.20	0.16	0.12	0.68	0.05	0.04	0.48
Spring (S) S of Rogers Spring	$\bar{x}$	4.36	2.59	1.68	4.42	−0.028	1.26	1.52
(n = 9)	s	0.18	0.14	0.08	0.37	0.04	0.05	0.25
Spring S of Five Springs	$\bar{x}$	4.30	2.32	1.53	4.67	−0.023	1.26	1.45
(n = 14)	s	0.18	0.15	0.10	0.94	0.06	0.07	0.33
Shaft Spring	$\bar{x}$	4.48	2.59	1.67	5.71	−0.043	1.24	1.79
(n = 11)	s	0.31	0.19	0.06	0.65	0.07	0.04	0.39
Springs (E) near Crystal Reservoir	$\bar{x}$	4.38	2.47	1.60	5.10	−0.099	1.33	2.42
(n = 15)	s	0.25	0.20	0.13	0.92	0.087	0.08	0.79
Spring at Clay Pits	$\bar{x}$	4.23	1.98	1.34	4.67	−0.049	1.19	1.45
(n = 10)	s	0.34	0.11	0.10	0.47	0.05	0.05	0.33
Springs S of Clay Pits	$\bar{x}$	4.36	2.08	1.33	5.78	−0.107	1.17	1.68
(n = 11)	s	0.23	0.15	0.08	0.66	0.05	0.06	0.39
Frenchy Springs (E)	$\bar{x}$	4.41	2.06	1.34	4.62	−0.017	1.20	1.23
(n = 11)	s	0.20	0.10	0.07	0.48	0.06	0.05	0.20
Frenchy Springs (W)	$\bar{x}$	4.03	1.70	1.21	4.08	−0.054	1.22	1.53
(n = 15)	s	0.19	0.09	0.07	0.71	0.04	0.03	0.31
Last Chance Spring	$\bar{x}$	4.23	2.36	1.53	4.84	−0.033	1.20	1.32
(n = 15)	s	0.18	0.14	0.11	0.44	0.05	0.10	0.23
P. fairbanksensis								
Fairbanks Spring	$\bar{x}$	3.29	2.84	2.56	3.13	−0.045	1.13	1.71
(n = 14)	s	0.34	0.24	0.17	0.59	0.07	0.07	0.36
P. crystalis								
Crystal Spring	$\bar{x}$	3.17	2.04	2.16	2.34	0.14	1.20	2.08
(n = 3)	s	0.29	0.20	0.22	0.06	0.05	0.12	0.95
P. erythropoma								
King's Pool	$\bar{x}$	3.41	2.28	2.13	3.60	−0.077	1.20	1.77
(n = 14)	s	0.23	0.20	0.14	0.78	0.06	0.05	0.66
Point of Rocks Springs (1)	$\bar{x}$	3.38	1.82	1.77	3.04	−0.066	1.21	2.79
(n = 12)	s	0.29	0.09	0.09	0.24	0.04	0.09	0.97
Point of Rocks Springs (2)	$\bar{x}$	3.60	2.38	2.13	3.58	−0.08	1.22	2.19
(n = 10)	s	0.13	0.12	0.15	0.42	0.04	0.06	0.38
Point of Rocks Springs (3)	$\bar{x}$	3.64	2.36	2.22	3.79	−0.08	1.17	2.44
(n = 16)	s	0.32	0.16	0.11	0.49	0.27	0.05	0.87
Point of Rocks Springs (4)	$\bar{x}$	3.30	1.66	1.61	3.06	−0.053	1.24	2.54
(n = 16)	s	0.14	0.12	0.14	0.28	0.04	0.05	1.14
P. pisteri								
Scruggs Spring	$\bar{x}$	4.03	2.50	2.23	3.46	−0.031	1.13	2.09
(n = 19)	s	0.20	0.17	0.12	0.56	0.05	0.05	0.53
Marsh Spring	$\bar{x}$	3.77	2.28	2.06	3.61	−0.081	1.11	2.19
(n = 12)	s	0.29	0.18	0.12	0.65	0.05	0.03	0.80

Table 1.—Continued.

Species and locality		NW	SH	SW	T	D	As	W
P. nanus								
Five Springs	$\bar{x}$	3.50	1.72	1.64	3.22	0.002	1.16	2.51
(n = 14)	s	0.20	0.09	0.10	0.33	0.04	0.04	0.85
Mary Scott Spring	$\bar{x}$	3.66	2.04	1.78	3.60	−0.057	1.07	1.96
(n = 17)	s	0.28	0.20	0.15	0.53	0.06	0.11	0.64
Collins Ranch Spring	$\bar{x}$	3.50	1.62	1.49	3.18	−0.021	1.18	2.19
(n = 12)	s	0.21	0.12	0.12	0.29	0.03	0.07	0.45
P. isolatus								
Spring at Clay Pits	$\bar{x}$	4.00	2.94	2.39	3.53	−0.066	1.17	1.91
(n = 13)	s	0.14	0.14	0.11	0.31	0.05	0.04	0.47

(Parameter spans columns NW–W.)

maining pellicle. Selected animals were dried using a DENTON DCP-1 Critical Point Drier and then photographed using SEM.

Both standard measurements and Raupian parameters were obtained from selected series of adult specimens. While sexual dimorphism is common in hydrobiids, our intent was to characterize roughly typical adult form and therefore our measurements were based on randomly selected series of unsexed shells with complete and/or thickened inner lips (denoting adulthood). Shells were cleaned with CLOROX to remove surface deposits, and oriented in standard apertural aspect (Fig. 7) after counting of whorls (NW). Points and aspects of shell outline necessary for obtaining measurements, including position of coiling axis (Co, approximated as bisector of spire angle), were drawn on paper using camera lucida (12, 25 or 50×). Distances between points were then determined with a millimeter ruler. The following standard shell measurements were made (Fig. 7):

1) Shell Height (SH).
2) Shell Width (SW).
3) Length of Body Whorl (LBW).
4) Width of Body Whorl (WBW).
5) Aperture Length (AL) = length of line segment ab.
6) Aperture Width (AW) = length of line segment cd, perpendicular bisector of ab.

The following additional measurements were made in order to generate Raupian parameters:

1) Y = distance along coiling axis from apical tip to intersection (e) of line perpendicular to axis and passing through center of generating curve, approximated as intersection (f) of line segments ab and cd.
2) R = length of line segment ef, perpendicular distance from coiling axis to generating curve.
3) D1 = length of line segment ge, perpendicular distance from coiling axis to inner edge of aperture.
4) D2 = length of line segment eh, perpendicular distance from coiling axis to outer edge of aperture.
5) S1 = length of line segment ij, perpendicular distance from coiling axis to suture half a whorl back from aperture.
6) S2 = length of line segment kl, perpendicular distance from coiling axis to suture at posterior end of body whorl.

Raupian parameters (slightly modified from Raup 1966) were generated as follows:

1) Translation Rate (T) = Y/R.
2) Whorl Expansion Rate (W) = $(S1/S2)^2$. Note that W is approximated by measurements separated by a half whorl increment, hence the need to square the ratio. This is a crude approximation of W as only a single ratio was used, rather than the mean of (or preferably a function based on) a series of such measurements representing ontoge-

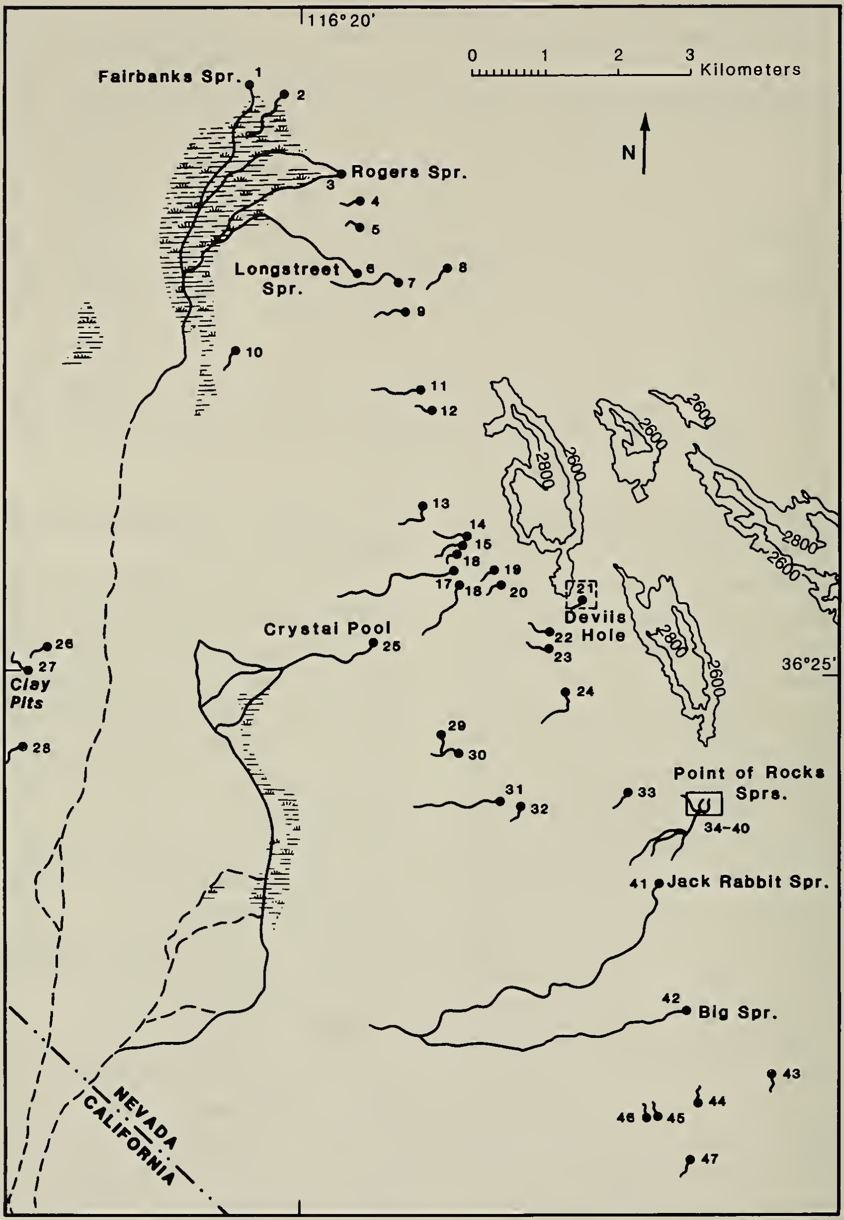

Fig. 5. Map of Ash Meadows, showing collecting localities. Adapted from Ash Meadows Quadrangle, Nevada–California (1952), USGS 15 minute series (topographic). Enclosed area at Point of Rocks enlarged in Fig. 6.

netic variation. The suture at posterior junction of aperture and body whorl was not used in this computation as hydrobiid shells typically have loosened coiling during the last quarter whorl of growth.

3) Distance from coiling axis to generating curve (D) = D1/D2.

4) Aperture Shape (AS) = AS/AW.

Data analysis.—Descriptive statistics were generated using SYSTAT (Wilkinson 1986) and are summarized in Tables 1 and 2.

Stepwise discriminant function (canonical variates) analyses were performed using SPSS-X (Klecka 1975). Since the goal of

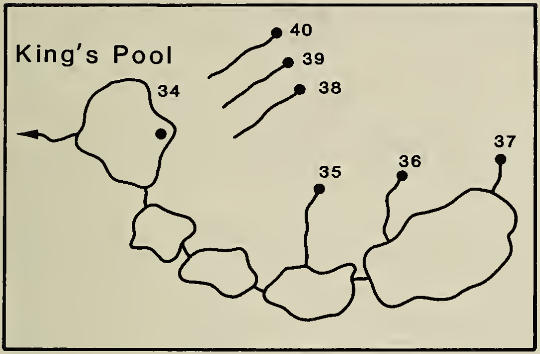

Fig. 6. Map of Point of Rocks area (enclosed by rectangle in Fig. 5), showing location of springs. Filled circle in King's Pool indicates location of spring orifice.

these analyses was to gauge distinctiveness of similar allopatric species, and as discriminant function analysis is most effective when the number of groups is small, separate analyses were done on each of three sets of three or four congeners considered closely related (Table 3). Note that the highly distinctive *P. micrococcus* was excluded. Discriminant analyses were constructed using all specimens measured for each species (considered as separate groups). Separate analyses using Raupian and standard shell parameters (excluding NW) were done to compare effectiveness of these data sets in discriminating species, yielding a total of six runs. Variables were selected in discriminant analyses on basis of providing the largest Mahalanobis distance between closest pairs of groups. In six of eight initial runs, continued selection of variables eventually resulted in decreased separation of closest groups. These were therefore rerun, using only variables providing continually increasing separation with each step. Pooled within-groups covariance matrix was used to compute probabilities of group membership.

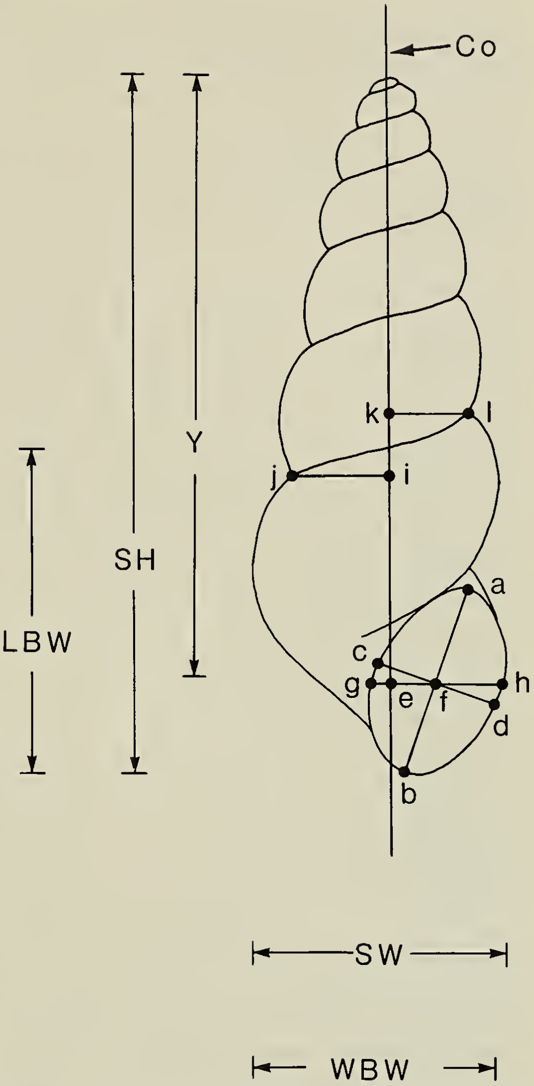

Fig. 7. Points and measurements used in morphometric analysis. Co, Coiling axis; LBW, Length of body whorl; SH, Shell height; SW, Shell width; WBW, Width of body whorl; Y, Translation along coiling axis. See text for explanation of points a–l.

Key to Ash Meadows Hydrobiidae

1. Penis simple or bilobed distally, with glandular ridge on surface (*Pyrgulopsis*) 2
– Penis with small, papillae-like lobes, glandular ridge absent (*Tryonia*) 8
2. Penis bilobed 3
– Penis simple, without lobes 6
3. Penial lobe much shorter than filament .... *Pyrgulopsis fairbanksensis*, new species
– Lobe about same length or longer than filament 4
4. Penial lobe about same length as

Table 2.—Shell parameters for *Tryonia* species. Shell height (SH) and width (SW) are given in mm. NW = number of whorls, T = translation rate, D = distance of generating curve from coiling axis, AS = apertural shape, W = whorl expansion rate.

Species and locality		Parameter						
		NW	SH	SW	T	D	AS	W
T. angulata								
Fairbanks Spring	$\bar{x}$	5.98	3.56	1.72	6.40	−0.074	1.51	1.53
(n = 12)	s	0.27	0.24	0.07	0.53	0.02	0.08	0.30
Crystal Spring	$\bar{x}$	5.48	3.28	1.70	6.52	−0.009	1.45	1.23
(n = 12)	s	0.27	0.21	0.11	0.74	0.02	0.09	0.11
Big Spring	$\bar{x}$	5.65	3.08	1.52	5.98	−0.076	1.46	1.45
(n = 15)	s	0.72	0.30	0.11	0.59	0.04	0.06	0.34
T. variegata								
Five Springs	$\bar{x}$	6.20	3.73	1.71	7.74	−0.052	1.46	1.52
(n = 16)	s	0.75	0.82	0.12	1.86	0.06	0.13	0.33
Chalk Spring	$\bar{x}$	7.46	5.22	1.73	13.41	−0.056	1.58	1.38
(n = 14)	s	0.40	0.57	0.11	3.23	0.09	0.10	0.28
Mary Scott Spring	$\bar{x}$	6.75	5.15	1.81	12.17	−0.083	1.56	1.52
(n = 7)	s	0.43	0.29	0.12	0.46	0.03	0.10	0.29
Scruggs Spring (N)	$\bar{x}$	7.11	4.33	1.85	8.69	−0.047	1.57	1.44
(n = 11)	s	0.17	0.30	0.11	1.21	0.05	0.09	0.19
Scruggs Spring (S)	$\bar{x}$	7.08	4.42	1.75	8.28	−0.071	1.55	1.51
(n = 15)	s	0.31	0.18	0.07	0.69	0.03	0.08	0.26
Marsh Spring	$\bar{x}$	7.16	4.51	1.81	10.42	−0.080	1.62	1.62
(n = 16)	s	0.27	0.22	0.07	1.28	0.06	0.08	0.31
Indian Spring (N)	$\bar{x}$	7.17	4.82	1.86	10.48	−0.078	1.51	1.50
(n = 15)	s	0.50	0.32	0.11	0.90	0.04	0.06	0.25
School Spring	$\bar{x}$	6.44	4.24	1.76	9.46	−0.063	1.53	1.66
(n = 9)	s	0.21	0.23	0.18	0.88	0.04	0.06	0.28
Devils Hole	$\bar{x}$	6.67	3.44	1.69	6.38	0.067	1.33	1.31
(n = 13)	s	0.66	0.20	0.08	0.84	0.05	0.06	0.21
Collins Ranch Spring	$\bar{x}$	5.96	2.90	1.29	6.86	−0.112	1.48	1.61
(n = 11)	s	0.19	0.10	0.08	0.30	0.05	0.17	0.22
Springs (W) near Crystal Reservoir	$\bar{x}$	7.59	5.61	2.06	9.63	−0.082	1.57	1.36
(n = 14)	s	0.52	0.38	0.15	1.32	0.04	0.08	0.18
Springs (E) near Crystal Reservoir	$\bar{x}$	8.66	6.41	2.04	14.05	−0.137	1.51	1.48
(n = 17)	s	0.66	0.58	0.14	3.06	0.07	0.21	0.37
Point of Rocks Springs (4)	$\bar{x}$	7.03	4.08	1.73	9.51	−0.069	1.63	1.41
(n = 10)	s	0.46	0.27	0.08	1.50	0.08	0.07	0.21
Point of Rocks Springs (5)	$\bar{x}$	6.19	3.74	1.69	7.83	−0.073	1.61	1.43
(n = 12)	s	0.39	0.41	0.13	0.99	0.06	0.06	0.16
T. ericae								
Scruggs Spring	$\bar{x}$	5.19	1.57	0.87	6.41	−0.026	1.28	1.49
(n = 9)	s	0.58	0.19	0.05	1.23	0.06	0.08	0.27
Springs (N) N of Collins Ranch	$\bar{x}$	4.28	1.37	0.76	5.15	−0.093	1.33	1.57
(n = 10)	s	0.34	0.16	0.04	0.59	0.05	0.07	0.24
T. elata								
Point of Rocks Springs (1)	$\bar{x}$	6.37	1.88	0.83	9.00	−0.068	1.38	1.43
(n = 15)	s	0.27	0.11	0.06	1.23	0.07	0.06	0.29
Point of Rocks Springs (4)	$\bar{x}$	5.62	2.31	0.94	8.89	−0.056	1.39	1.42
(n = 15)	s	0.45	0.25	0.06	1.89	0.07	0.10	0.27

filament, glandular ridge elongated along long axis of lobe ....
.... *Pyrgulopsis micrococcus* (Pilsbry)

– Lobe longer than filament, glandular ridge elongated along distal edge of lobe 5

5\. Shell <2.4 mm high; penis extending only slightly anterior to mantle collar ....
...... *Pyrgulopsis nanus,* new species

– Shell >2.6 mm high; penis extending well anterior to mantle collar .. *Pyrgulopsis isolatus,* new species

6\. Distal penis much wider than filament ....
...... *Pyrgulopsis pisteri,* new species

– Distal penis only slightly wider than filament 7

7\. Aperture ovate, adnate to or slightly separated from body whorl; glandular ridge small, circular ...
... *Pyrgulopsis erythropoma* (Pilsbry)

– Aperture greatly enlarged, very broadly ovate, well separated from body whorl; glandular ridge enlarged, elongate ....
.... *Pyrgulopsis crystalis,* new species

8\. Whorls angled well below sutures; outer apertural lip strongly sinuate
...... *Tryonia angulata,* new species

– Subsutural angulations absent; outer apertural lip straight to moderately sinuate 9

9\. Shell typically <2.0 mm tall, elongate-conic ....
.... *Tryonia ericae,* new species

– Shell typically >2.0 mm tall, turriform to aciculate 10

10\. Shell 1.8–2.9 mm tall, with moderately rounded and slightly shouldered whorls ....
.... *Tryonia elata,* new species

– Shell 2.8–7.5 mm tall; whorls well-rounded and typically unshouldered *Tryonia variegata,* new species

Systematics

Family Hydrobiidae Troschel, 1857
Genus *Pyrgulopsis* Call and Pilsbry, 1886

Fluminicola Stimpson, 1865:52 [in part].
Pyrgulopsis Call and Pilsbry, 1886:9.—Hershler and Thompson, 1987:28 [with references].

Diagnosis.—Shell globose to conical, 1.2–8.0 mm tall. Aperture simple, often loosened from body whorl, inner lip often thickened. Umbilicus absent to open. Protoconch usually covered with wrinkled pits. Teleoconch smooth or unicarinate on periphery, growth lines often prominent. Taenioglossate radula with basal cusps on central teeth. Head/foot, mantle, and penis often with distinctive pigmented (melanin) regions. Penis with small distal lobe (reduced or absent in a few species) and narrow filament of varying length. Penial surface typically having one to fifteen glandular ridges, sometimes borne on fleshy crests. Females oviparous. Capsule gland with 2 tissue sections and near-terminal opening. Bursa copulatrix often partly posterior to albumen gland. Seminal receptacle relatively small (absent in one species).

Comparisons.—*Fluminicola erythropoma* Pilsbry and similar Ash Meadows taxa described below have globose-neritiform shells characteristic of the genus. However, they are much smaller than typical *Fluminicola* and have smooth protoconchs and penial glandular ridges, features seen in neither *F. nuttalliana* (Lea), the generic type species, nor in any other lithoglyphine examined by Thompson (1984). Possession of penial glandular ridges in these taxa indicates that they are nymphophilines (see Thompson 1979 for subfamilial diagnosis) convergent upon *Fluminicola.* Unusual character states (i.e., *Fluminicola*-like shell, unlobed penis, dark body pigmentation) occur among these species, suggesting that they comprise a distinctive species group. However, variation indicates gradation toward states typical of *Pyrgulopsis,* to which they are therefore assigned. *Fluminicola avernalis* Pilsbry and *F. merriami* Pilsbry and Beecher from southern Nevada, which also have penial glandular ridges (Hershler, pers. obs.), are also transferred to *Pyrgulopsis.*

Remarks.—Congeners differ primarily in shell features, penial form and pattern of glandular ridge positioning. An expanded description is given below for *P. erythropoma* as representative of the *Fluminicola*-like group.

Pyrgulopsis micrococcus (Pilsbry)
Oasis Valley springsnail
Figs. 8a, 9–16

Amnicola micrococcus Pilsbry in Stearns, 1893:277.

Fontelicella micrococcus.—Gregg and Taylor, 1965:109.—Landye, 1973:18.—Taylor, 1975:123.—USDI, 1984b:21673.

Pyrgulopsis micrococcus.—Hershler and Thompson, 1987:30.

Material examined.—NEVADA, NYE COUNTY: small spring in Oasis Valley ANSP 67279 (holotype, 123622 (paratypes from type lot).—Spring in Oasis Valley (Thirsty Canyon), Nye County, Nevada, T10S, R47E, SE ¼ sec. 32, 850297, 18 Nov 1985.—Spring 0.2 km S of Rogers Spring, 850334, 859180, 7 Nov 1985.—Spring 0.3 km S of Rogers Spring, 850336, 859181, 7 Nov 1985; 850335, 7 Jul 1986.—Purgatory Spring, 850333, 859179, 6 Nov 1985.—Spring 1.0 km S of Five Springs, 850338, 859182, 8 Nov 1985; 850337, 7 Jul 1985.—Shaft Spring, 850331, 859183, 10 Nov 1985.—Chalk Spring, 850340, 10 Nov 1985.—Spring (southern) N of Collins Ranch Spring, 850342, 859195, 9 Nov 1985; 850341, 8 Jul 1986.—Spring N of Clay Pits, 850343, 859184, 11 Nov 1985; 850344, 8 Jul 1986.—Spring at Clay Pits, 850345, 859185, 11 Nov 1985; 850346, 8 Jul 1986.—Spring S of Clay Pits, 850347, 859186, 11 Nov 1985; 850348, 8 Jul 1986.—Spring (western) near Crystal Reservoir, 850349, 10 Nov 1985.—Spring (eastern) near Crystal Reservoir, 850350, 859187, 10 Nov 1985.—Frenchy Springs (western), 850352, 859189, 10 Nov 1985.—Frenchy Springs (eastern), 850351, 859188, 10 Nov 1985.—Last Chance Spring, 850353, 859190, 10 Nov 1985. CALIFORNIA, INYO COUNTY: Shoshone Spring (Shoshone), T22N, R7E, NW corner sec. 30, 12 Mar 1985.—Tecopa Hot Springs (Tecopa), T21N, R7E, NE corner sec. 33, 12 Mar 1985.—Spring by Grimshaw Lake (Tecopa), T21N, R7E, NE corner sec. 9, 13 Mar 1985.—Springs in Amargosa Gorge (Tecopa), T21N, R7E, SE corner sec. 9, 13 Mar 1985.

Diagnosis.—A small-sized species, with moderate-spired, globose to ovate-conic shell. Penis with single glandular ridge on ventral surface of moderate-sized lobe.

Description.—Shell (Figs. 8a, 9, 10) 1.6–2.8 mm high, up to one and a half times taller than wide. Whorls, 3.75–5.0, well-rounded, with impressed sutures and slight sutural shelving. Spire convex, often irregularly so due to bulging of whorls. Body whorl 63–80% of shell height. Shell colorless, transparent; periostracum light brown. Aperture ovate-pyriform, usually separated from body whorl in adult specimens. Inner lip moderately thickened and slightly reflected; outer lip thin. Umbilicus chink-like to open. Growth lines moderately pronounced.

Visceral coil usually darkly pigmented, especially on stomach. Melanic pigmentation of head/foot variable; ranging from absent to sparse covering of light brown pigment to near uniform (except for central portion on sides) black. Dense, dark, subepithelial pigment granules sometimes present in sides of head/foot. Penial filament usually with dark subepithelial pigment along much of length (Figs. 12–14).

Radular (Fig. 11) formula: 5-1-5/1-1, 3-1-4, 20–26, 31; width of central tooth, 0.023 mm. Cusps on central teeth dagger-like. Stomach slightly longer than style sac. Posterior stomach edge with small caecum.

Fig. 8. SEM micrographs of shells of *Pyrgulopsis* spp.: a, *P. micrococcus,* paratype, USNM 123622, spring in Oasis Valley; b, e, h, *P. erythropoma,* King's Pool (b, paratype, ANSP 73667; e, h, USNM 859207); c, f, i, *P. crystalis,* Crystal Pool (c, holotype, USNM 859205; f, i, paratypes, USNM 859206); d, g, *P. fairbanksensis,* Fairbanks Spring (d, holotype, USNM 859203; g, paratype, USNM 859204).

Kidney relatively elongate. Ctenidium with up to 20 triangular filaments. Anterior fifth (ca.) of prostate gland pallial. Penis (Figs. 12–14) small, barely extending anterior to mantle collar, near-straight, thickened, 2 or more times longer than wide. Vas deferens located along outer edge of penis (not figured). Filament thickened and short. Penial lobe simple, rarely extending distal to tip of filament. Glandular ridge usually occupying most of penial lobe, but sometimes reduced or absent. Pallial oviduct complex (Fig. 15) typical of genus. Capsule gland opening slit-like. Posterior section of capsule gland somewhat longer than anterior section. Albumen gland slightly longer than capsule

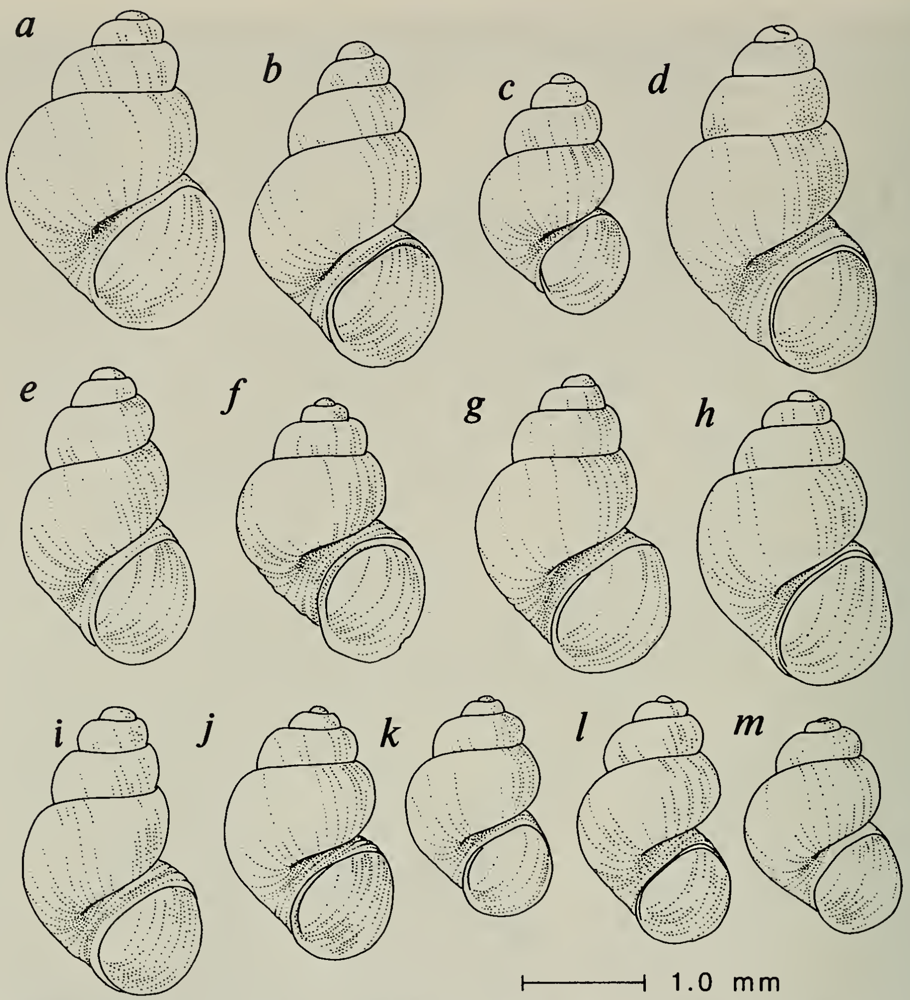

Fig. 9. Shells of *P. micrococcus*: a, b, USNM 850297, spring in Oasis Valley; c, d, USNM 859180, spring 0.2 km S of Rogers Spring; e, f, USNM 859181, spring 0.3 km S of Rogers Spring; g, h, USNM 859179, Purgatory Spring; i, j, USNM 859182, spring 1.0 km S of Five Springs; k, USNM 859195, spring (southern) N of Collins Ranch Spring; l, USNM 859184, spring N of Clay Pits; m, USNM 859185, spring at Clay Pits.

gland. Oviduct looping twice before receiving duct of seminal receptacle. Bursa copulatrix club-shaped, variable in size, but always larger than seminal receptacle. Bursa partly posterior to albumen gland.

Type locality.—Small spring in Oasis Valley, Nye County, Nevada (precise location unknown).

Distribution and habitat.—Restricted to Amargosa River drainage: Oasis Valley (several springs) and Ash Meadows (15 sites, Fig. 16) in Nye County, Nevada; and Shoshone Spring and numerous springs in vicinity of Tecopa in Inyo County, California. Typically common in soft sediments in upper segments of small springbrooks.

Syntopic with *P. nanus,* n. sp. (described below) in spring north of Collins Ranch Spring, and with *P. isolatus,* n. sp. (described below) in spring S of Clay Pits.

Comparisons.—Distinguished from several Arizona species possessing single glan-

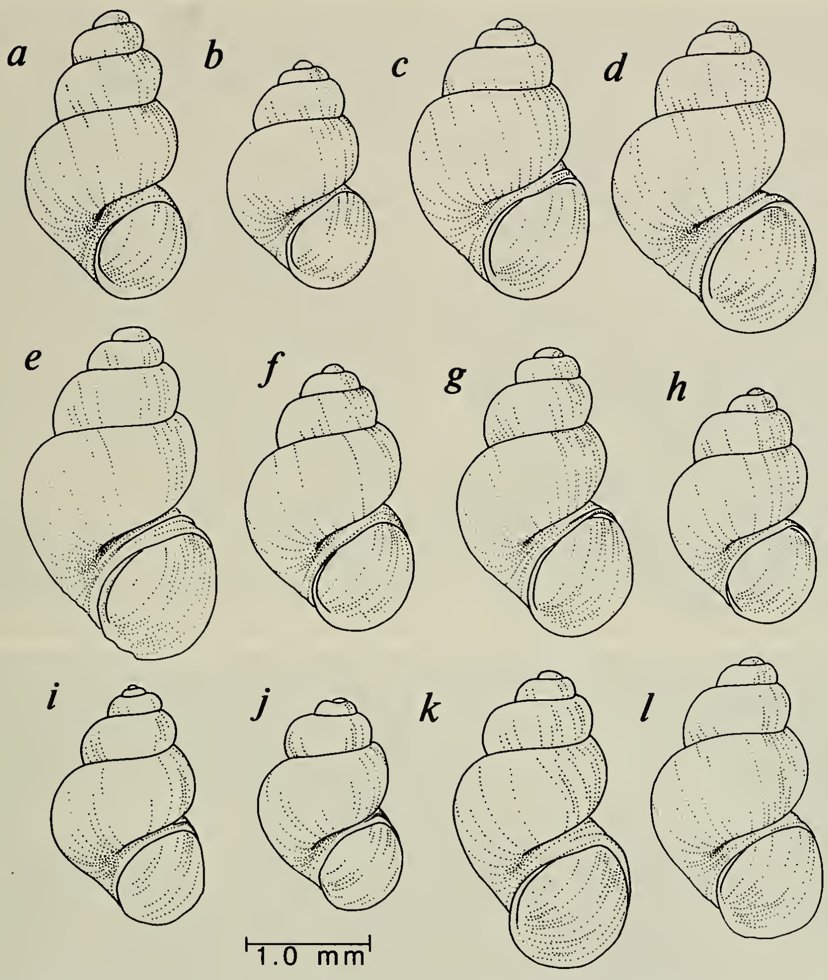

Fig. 10. Shells of *P. micrococcus*: a, b, USNM 859186, spring S of Clay Pits; c, d, USNM 859187, spring (eastern) near Crystal Reservoir; e, f, USNM 859183, Shaft Spring; g, h, USNM 859188, Frenchy Springs (eastern); i, j, USNM 859189, Frenchy Springs (western); k, l, USNM 859190, Last Chance Spring.

dular ridge on penial lobe (Hershler and Landye 1988) by narrower shell and invariant location of glandular ridge on ventral surface of penial lobe. Additional study is needed to determine status of similar forms occurring in springs in Death Valley and adjacent basins to the west. Specimens collected by Nelson and Bailey in 1891 from Saratoga Spring in Death Valley (USNM 123904) and referred to *P. micrococcus* by Pilsbry (in Stearns 1893) represent an undescribed congener belonging to the *Fluminicola*-like group.

Additional descriptive information for this species is provided by Gregg and Taylor (1965), and Hershler and Thompson (1987).

Pyrgulopsis erythropoma (Pilsbry)
Ash Meadows pebblesnail
Figs. 8b, e, h, 17, 18d–i, 19b, c,
20–22, 23a–c, 24a, c, 25

Fluminicola fusca Haldeman var. *minor.*—Pilsbry in Stearns, 1893:282.
Fluminicola erythropoma Pilsbry, 1899:125.

Fig. 11. SEM micrographs of radula of *P. micrococcus,* USNM 850297, spring in Oasis Valley, showing the four tooth types: a, Centrals (bar = 12 μm); b, Laterals (bar = 10 μm); c, Inner marginals (bar = 8.6 μm); d, Outer marginals (bar = 6.0 μm).

"*Fluminicola*" *erythropoma.*—Landye, 1973:15.—Taylor, 1975:79.

Fluminicola erythropoma.—Sada and Mozejko, 1984:A-1 (Appndx.).—USDI, 1984b:21673.

Point-of-Rocks Springs snail.—Taylor in Williams et al., 1985:43.

Material examined.—NEVADA, NYE COUNTY: Point of Rocks Springs, King's

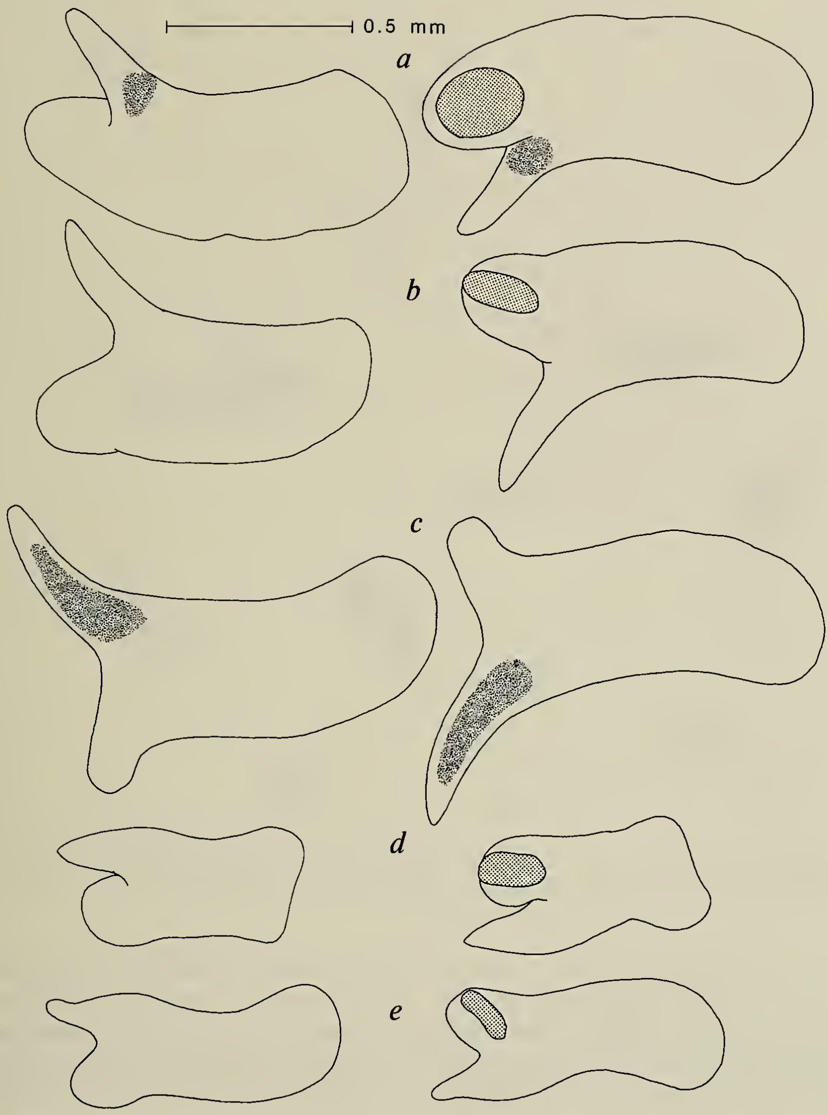

Fig. 12. Penes of *P. micrococcus*: a, b, USNM 850297, spring in Oasis Valley; c, USNM 850334, spring 0.2 km S of Rogers Spring; d, USNM 850333, Purgatory Spring; e, USNM 850338, spring 1.0 km S of Five Springs. Dorsal aspects to left, ventral aspects to right; light screened areas indicate glandular ridges, darker screened areas indicate melanic pigment.

Pool, ANSP 73607 (holotype), ANSP 73667 (paratypes from type lot); 850371, 859207, 8 Nov 1985; 857861, 8 Jul 1986.—Point of Rocks Springs (Locality 35), 850372, 859208, 8 Nov 1985.—Point of Rocks Springs (Locality 36), 857862, 859209, 8 Nov 1985; 857863, 8 Jul 1986.—Point of Rocks Springs (Locality 37), 857864, 859210, 8 Nov 1985.—Point of Rocks Springs (Locality 38), 857865, 8 Nov 1985.—Point of Rocks Springs (Locality 39), 857866, 9 Nov 1985.—Point of Rocks Springs (Locality 40), 856867, 859211, 9 Nov 1985.

Diagnosis.—A small-sized species with very short-spired, globose-turbinate shell. Penis simple, with small glandular ridge near base on dorsal surface.

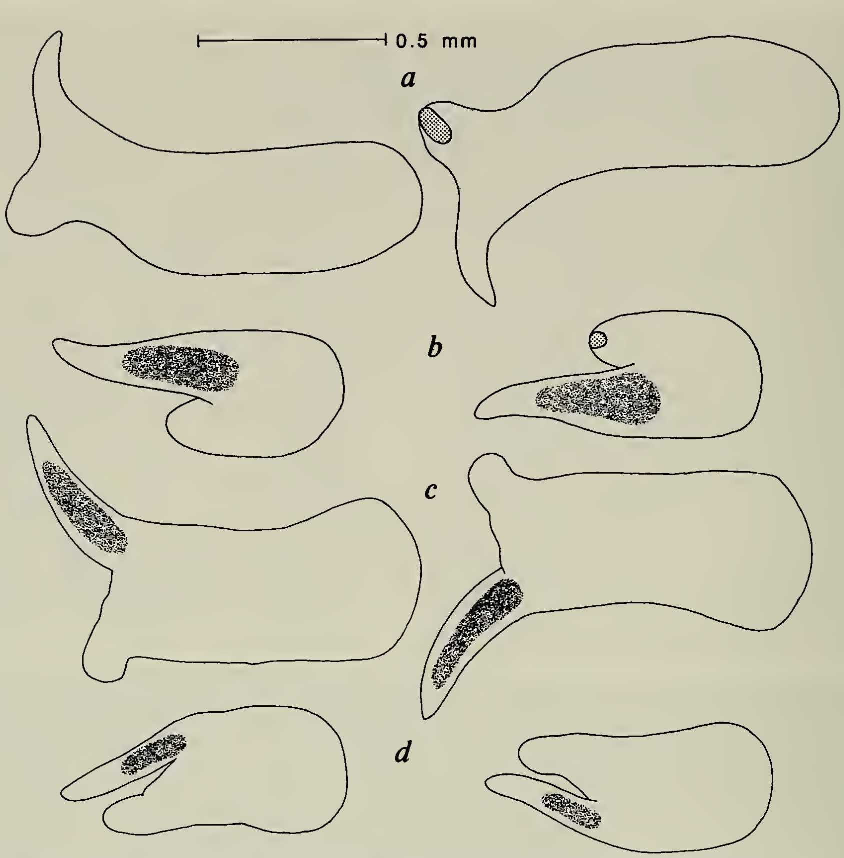

Fig 13. Penes of *P. micrococcus*: a, USNM 850331, Shaft Spring; b, USNM 850344, spring N of Clay Pits; c, USNM 850346, spring at Clay Pits; d, USNM 850348, spring S of Clay Pits.

Description.—Shell (Figs. 8b, e, h, 17, 18d–i) 1.6–2.4 mm high, slightly taller than wide. Whorls, 3.0–4.0, well-rounded, with impressed sutures. Spire convex, with apex often highly eroded. Body whorl ca. 90% of shell height. Shell transparent when fresh; periostracum thin, amber-colored, sometimes absent. Aperture broadly ovate, angulate above. Inner lip moderately thickened, slightly reflected, narrowly adnate above (rarely free). Outer lip fairly thin. Umbilicus broadly open. Protoconch (Fig. 17) surface slightly wrinkled; teleoconch with pronounced growth lines and faint spiral striations.

Visceral coil uniformly dark brown. Head/foot, including snout and distal parts of tentacles, usually covered with very dark brown epithelial pigment, with central areas on sides of head/foot somewhat lighter. Sole of foot unpigmented. Dark internal pigment filling much of penial filament, sometimes extending into proximal penis (Fig. 23a–c).

Radular (Fig. 20) formula: 7-1-7/1-1, 4-1-5, 26–28, 27–28; width of central tooth, 0.029 mm. Cusps on central teeth narrow, dagger-like. Head/foot morphology as for genus although foot relatively broad and thickened. Ciliation on cephalic tentacles sparse, irregular (Fig. 19b). Ctenidium with about 15 filaments. Testis a single, lobate mass filling most of digestive gland and partly overlapping posterior stomach (Fig. 21). Prostate gland longer than wide, with small pallial portion. Vas deferens extending along outer edge of penis without coiling; exiting slightly distal to penis base (Fig. 22). Penis (Figs. 19c, 22, 23a–c) small, blade-like, much longer than wide, tapering distally so that base of filament indistinct.

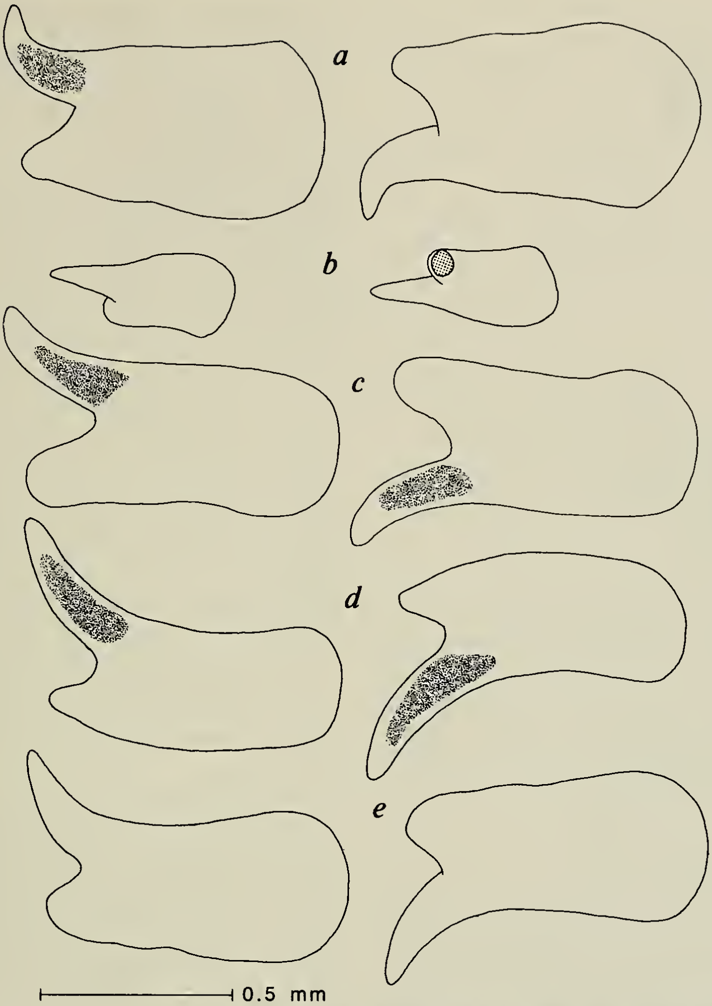

Fig. 14. Penes of *P. micrococcus*: a, USNM 850349, spring (western) near of Crystal Reservoir; b, USNM 850350, spring (eastern) near Crystal Reservoir; c, USNM 850351, Frenchy Springs (eastern); d, USNM 850352, Frenchy Springs (western); e, USNM 850353, Last Chance Spring.

Glandular ridge circular to somewhat elongate, positioned at one-third to one-half of length of penis from base. Pallial oviduct complex (Fig. 24a, c) as for genus. Capsule gland opening slit-like. Anterior capsule gland section much longer than posterior section. Capsule gland slightly longer than albumen gland. Oviduct looping once lateral to albumen gland. Seminal receptacle very small relative to bursa copulatrix. Club-shaped bursa copulatrix partly posterior to albumen gland; width of bursa duct variable.

Type locality.—King's Pool at Point of Rocks, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Endemic to six springs at Point of Rocks near eastern end of spring line in Ash Meadows (Fig. 25). Springs all within 0.5 km of one another at 702–707 m elevation. In King's Pool, species restricted to opening of large orifice, where large numbers of snails were clinging to travertine and were abundant. Also found in five small springbrooks in area (common in three), on stones and travertine in swift current.

Comparisons.—Similar to other Ash

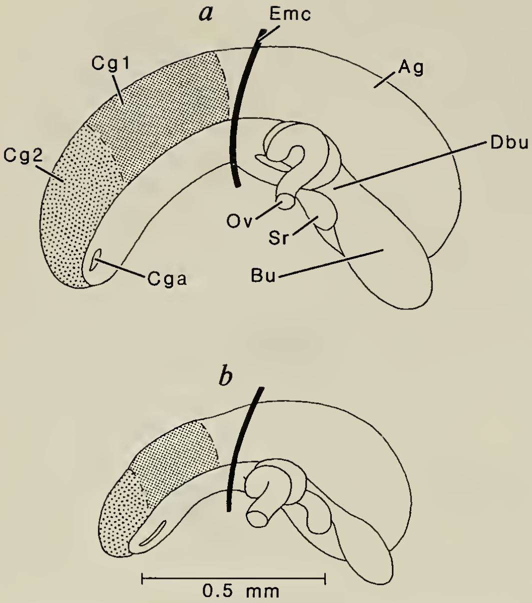

Fig. 15. Pallial oviducts of *P. micrococcus,* viewed from left side: a, USNM 850297, spring in Oasis Valley; b, USNM 850350, spring (eastern) near Crystal Reservoir. Ag = albumen gland; Bu = bursa copulatrix; Cga = capsule gland opening; Cg1 = posterior capsule gland section; Cg2 = anterior capsule gland section; Dbu = duct of bursa copulatrix; Emc = posterior end of pallial cavity; Ov = oviduct; Sr = seminal receptacle.

Meadows congeners found in large spring pools as all have globose-neritiform shell with very reduced spire. These differ from *P. avernalis* and *P. merriami* by lacking penial crests. Distinguished from *P. fairbanksensis,* n. sp. (described below) by smaller size, thinner inner shell lip and unlobed penis. Separated from *P. crystalis,* n. sp. (described below), a probable sister species, by globose (versus neritiform) shell and thicker penial filament. Distinguished from both of above by narrower, more numerous cusps on radular teeth.

Pyrgulopsis fairbanksensis, new species
Fairbanks springsnail
Figs. 8d, g, 18a, b, 19a, 24d, 25–27

Material examined.—NEVADA, NYE COUNTY: Fairbanks Spring, 859203 (holotype), 859204 (paratypes), UF 93955 (paratypes), 850369, 7 Nov 1985; 850367, 7 Jul 1986.

Diagnosis.—A moderate-sized species with very short-spired, globose-turbinate shell having especially thickened inner lip. Penis with small lobe bearing single glandular ridge ventrally.

Description.—Shell (Figs. 8d, g, 18a, b) 2.5–3.4 mm high, slightly taller than wide. Whorls, 3.0–4.0, well-rounded. Sutures impressed. Spire convex, apex usually eroded. Body whorl ca. 90% of shell height. Shell transparent when fresh; amber periostracum very thin or absent. Aperture broadly ovate, angulate above. Inner lip well thickened and reflected above, adnate to or slightly separated from body whorl above. Outer lip thin. Umbilicus chink-like, umbilical area often eroded. Growth lines pronounced on teleoconch; spiral striations faint. Paucispiral operculum, typical of genus, shown in Fig. 19a.

Visceral coil dark brown. Head/foot variably covered with grey-brown pigment. Small pigment patch on base of penial filament.

Radular (Fig. 26) formula: 3(4)-1-4/1-1, 3-1-4(5), 16–18, 20–25; width of central tooth, 0.053 mm. Central cusps on central and lateral teeth broad. Dimorphism of cusp size on lateral teeth pronounced (Fig. 26c). Heavy wear evident on ribbons. Ctenidial filaments, ca. 20. Penis (Fig. 27) small, elongate, with relatively small, blunt distal lobe. Filament elongate, tapering. Glandular ridge small, circular, located along or just proximal to tip of lobe. Albumen gland longer than capsule gland, with significant pallial portion (Fig. 24d). Seminal receptacle minute. Bursa copulatrix partly posterior to albumen gland.

Type locality.—Fairbanks Spring, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Endemic to type locality, a large spring at relatively low elevation (695 m) in northern part of Ash Meadows (Fig. 25). Common on travertine at spring orifice.

Etymology.—Named for Fairbanks Spring.

Comparisons.—Separated from similar

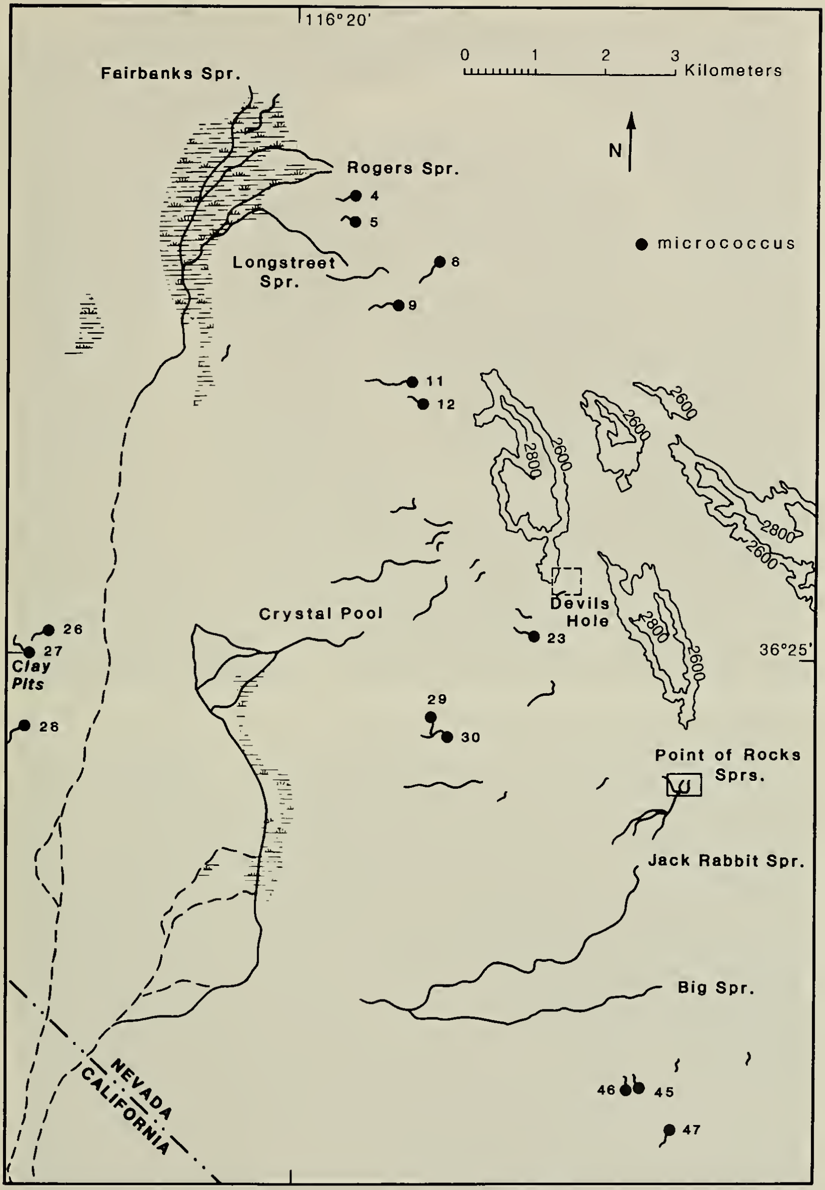

Fig. 16. Map showing distribution of *P. micrococcus* in Ash Meadows.

Ash Meadows *Pyrgulopsis* by highly thickened inner shell lip and unique penis, elongate with small lobe and long filament.

Pyrgulopsis crystalis, new species
Crystal springsnail
Figs. 8c, f, i, 18c, 23d, 24b, 25, 28

Material examined.—NEVADA, NYE COUNTY: Crystal Spring, 859205 (holotype), 859206 (paratypes), UF 93956 (paratypes), 850368, 8 Nov 1985; 850370, 7 Jul 1986.

Diagnosis.—A small-sized species, with globose-neritiform shell. Spire very short; aperture broad and enlarged. Penis simple, with narrow filament and large glandular ridge.

Description.—Shell (Figs. 8c, f, i, 18c) 1.8–2.6 mm high; width typically slightly ex-

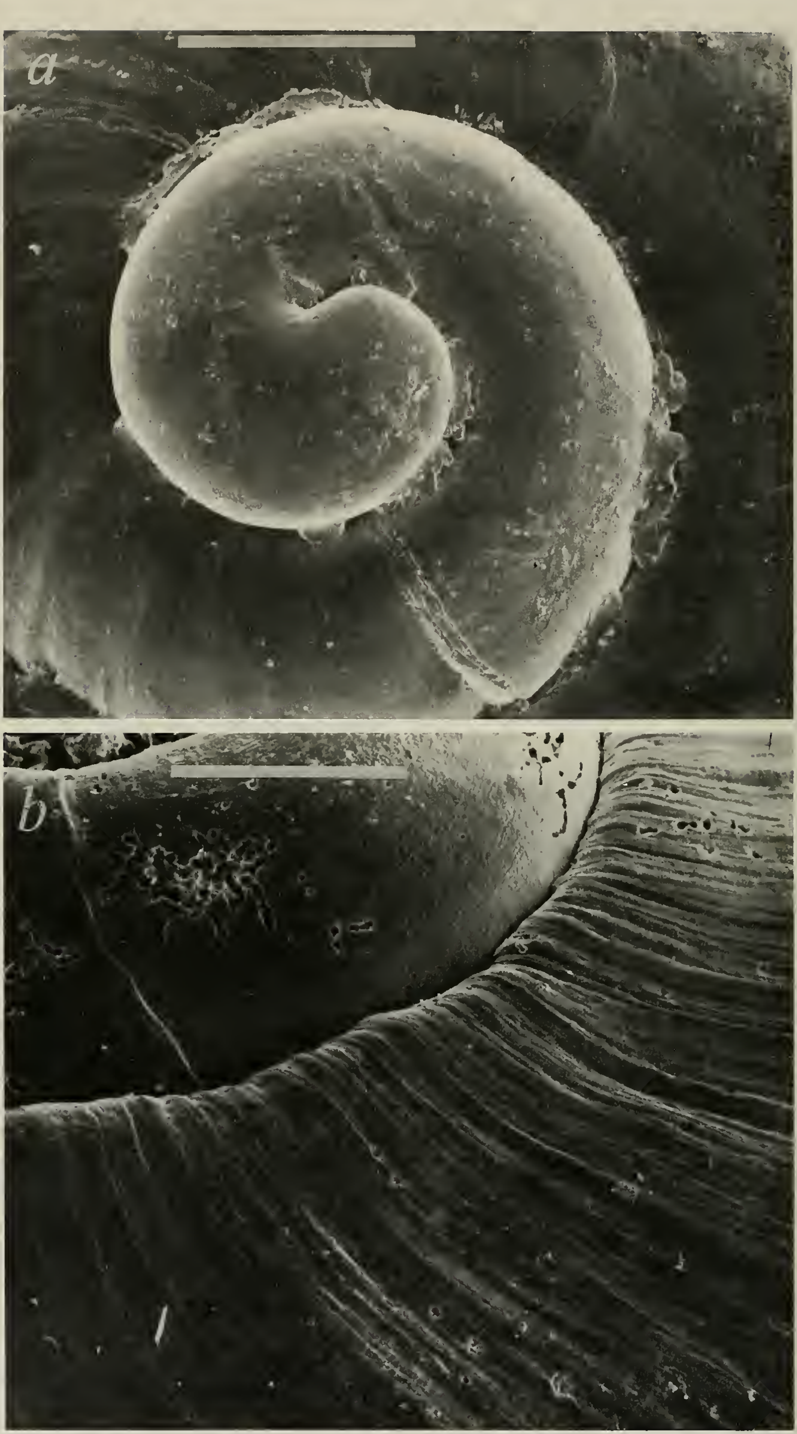

Fig. 17. SEM micrographs of shells of *P. erythropoma*: a, Protoconch (bar = 120 μm), USNM 857863, Point of Rocks Springs (Locality 36); b, Close-up showing strong growth lines on teleoconch (bar = 86 μm), USNM 857864, Point of Rocks Springs (Locality 37).

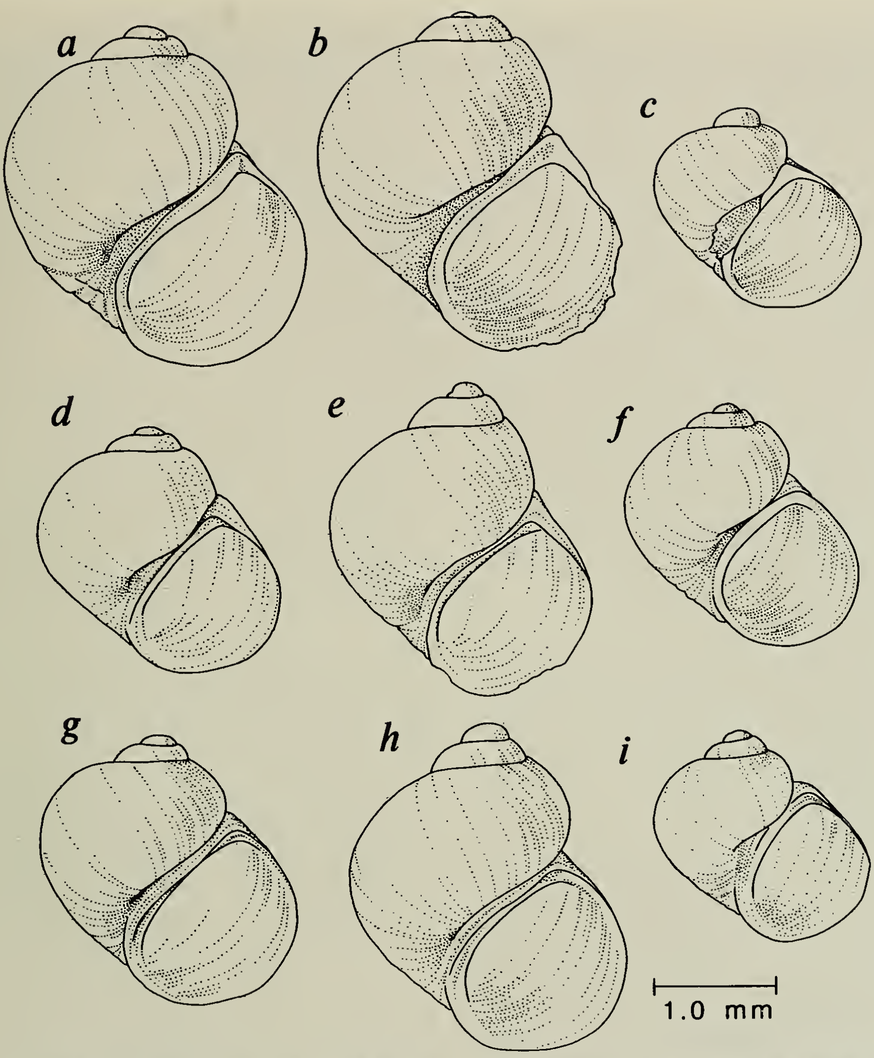

Fig. 18. Shells of *Pyrgulopsis* spp.: a, b, Paratypes, *P. fairbanksensis,* USNM 859204, Fairbanks Spring; c, Paratype, *P. crystalis,* USNM 859206, Crystal Spring; d–i, *P. erythropoma* (d, e, USNM 859207, King's Pool; f, USNM 859208, Point of Rocks Springs [Locality 35]; g, h, USNM 859210, Point of Rocks Springs [Locality 37]; i, USNM 859211, Point of Rocks Springs [Locality 40]).

ceeding length. Whorls, 3.0–3.5, highly convex, with deeply impressed sutures. Spire outline concave due to greatly expanded body whorl, which gives shell neritiform appearance. Apex often uneroded; protoconch somewhat tilted relative to subsequent whorls (Fig. 8c). Body whorl ca. 90% of shell height. Shell colorless, transparent, quite thin; periostracum very light brown. Aperture very broadly ovate (near-circular), only slightly angled above, well separated from body whorl in largest specimens. Inner lip moderately thickened and slightly reflected above; outer lip thin. Umbilicus broadly open. Growth lines prominent; spiral lines very weak–absent.

Visceral coil dark brown. Head/foot variably dusted with grey-brown melanin. Penial filament with small pigment patch proximally (Fig. 23d).

Radular (Fig. 28) formula: 3(4)-1-3(4)/1-1, 2(3)-1-3, 14, 16–18; width of central tooth,

Fig. 19. SEM micrographs of operculum, cephalic tentacles, and penes of *Pyrgulopsis* spp.: a, Operculum of *P. fairbanksensis* (bar = 0.43 mm), USNM 850368, Fairbanks Spring; b, c, *P. erythropoma,* USNM 857863 (b, left cephalic tentacle showing irregular patches of cilia [bar = 150 μm]; c, penis [indicated by arrow] [bar = 0.3 mm]); d, penis of *P. isolatus* (bar = 0.3 mm), USNM 850366, spring S of Clay Pits.

0.047 mm. Cusps on central and lateral teeth fairly broad. Heavy wear apparent on ribbons. Ctenidium with 15–20 filaments. Prostate gland small, ca. 25% of length pallial. Small penis (Fig. 23d) longer than wide, tapering distally. Filament narrow, elongate. Glandular ridge elongate and large, filling much of ventral surface of penis. Cap-

Fig. 20. Radula of *P. erythropoma,* USNM 857864, Point of Rocks Springs (Locality 37): a, Centrals (bar = 12 μm); b, Laterals (bar = 8.6 μm); c, Inner marginals (bar = 8.6 μm); d, Outer marginals (bar = 8.6 μm).

sule gland opening broad. Albumen and capsule glands near-equal in length (Fig. 24b). Seminal receptacle minute. Distal edge of bursa copulatrix even with posterior end of albumen gland.

Type locality.—Crystal Pool, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Endemic to and rare in type locality, a large, low elevation (668 m) spring in Ash Meadows (Fig.

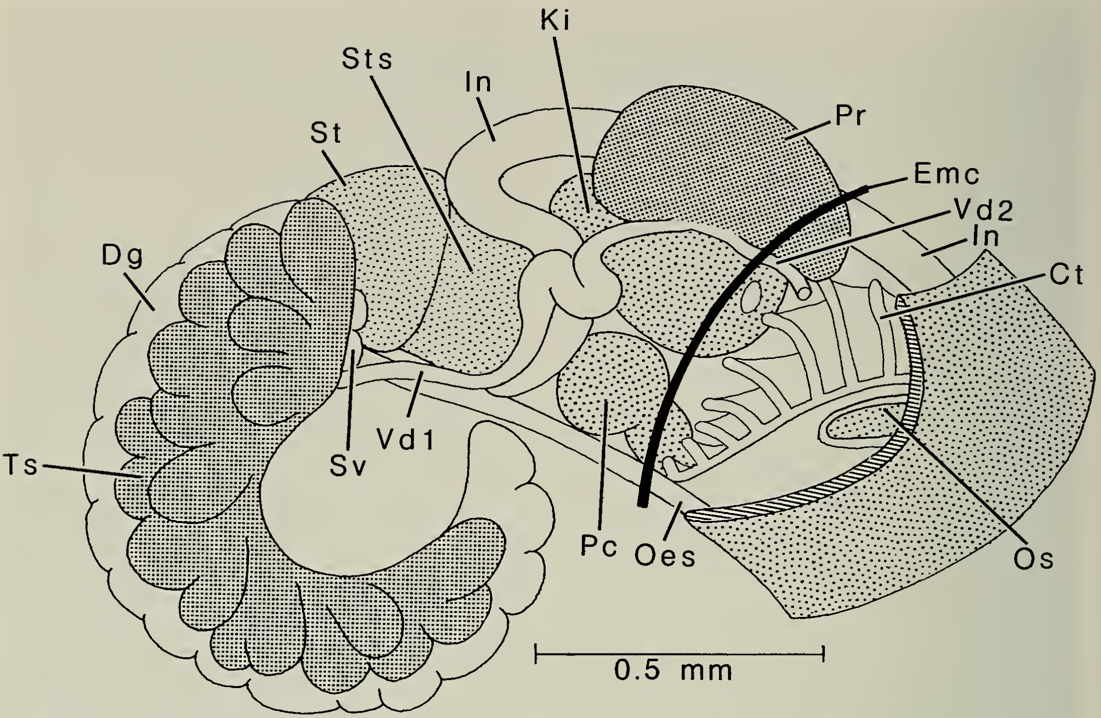

Fig. 21. Male anatomy (minus head) of *P. erythropoma,* USNM 857861, King's Pool. Pallial roof cut away to expose contents of posterior portion of cavity; prostate gland (Pr) lifted (dorsally) slightly to expose kidney. Ct = ctenidium; Dg = digestive gland; Emc = posterior end of pallial cavity; In = intestine; Ki = kidney; Oes = oesophagus; Os = osphradium; Pc = pericardium; Pr = prostate gland; St = stomach; Sts = style sac; Sv = seminal vesicle; Ts = testis; Vd1 = posterior vas deferens; Vd2 = anterior vas deferens.

25). Snails only found clinging to travertine walls of chasm-like orifices in deepest (>four meters) part of spring.

Etymology.—Named after Crystal Pool.

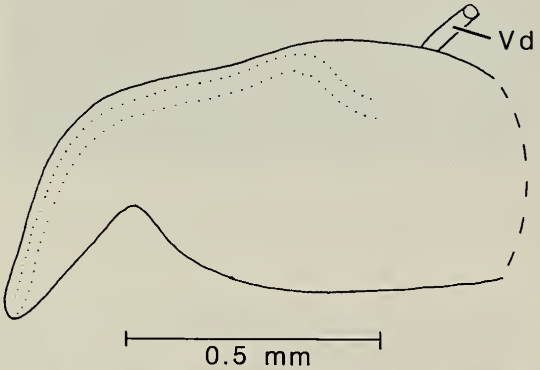

Fig. 22. Penis of *P. erythropoma,* USNM 857851, King's Pool, showing location of vas deferens (dotted line in penis). Vd = vas deferens.

Comparisons.—Neritiform shell and simple penis with slender filament and large glandular ridge distinguish this from other *Fluminicola*-like *Pyrgulopsis.*

Pyrgulopsis nanus, new species
Distal-gland springsnail
Figs. 25, 29a, d, 30–32, 33a, b

Large gland Nevada springs snail.—Sada and Mozejko, 1984: fig. 5.
"*Fluminicola*" sp.—USDI, 1984b:21673.
Large gland Nevada spring snail.—Taylor in Williams et al., 1985:43.

Material examined.—NEVADA, NYE COUNTY: Five Springs, 859191 (holotype), 859192 (paratypes), UF 93957 (paratypes), 850354, 7 Nov 1985.—Mary Scott Spring, 850355, 859113, 9 Nov 1985; 850356, 8 Jul 1986.—Collins Ranch Spring,

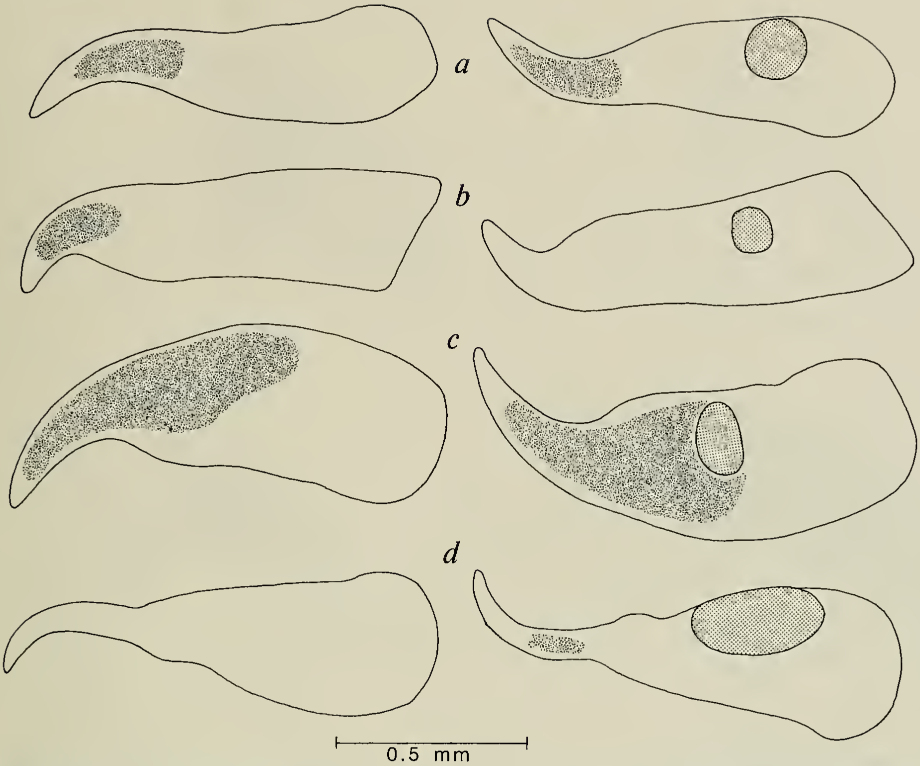

Fig. 23. Penes of *P. erythropoma* and *P. crystalis*: a–c, *P. erythropoma* (Pilsbry) (a, USNM 857861, King's Pool; b, USNM 857863, Point of Rocks Springs [Locality 36]; c, USNM 857864, Point of Rocks Springs [Locality 37]); d, *P. crystalis* new species, USNM 850370, Crystal Pool.

850357, 859194, 9 Nov 1985; 850360, 8 Jul 1986.—Spring (northern) N of Collins Ranch Spring, 850359, 859196, 9 Nov 1985; 850360, 8 Jul 1986.

Diagnosis.—A small-sized species with globose, short-spired shell. Penis with short filament and large lobe bearing glandular ridge along distal edge.

Description.—Shell (Figs. 29a, d, 30) 1.5–2.4 mm high, slightly taller than broad. Whorls, 3.0–4.0, convex and inflated, with impressed sutures. Spire straight or slightly convex. Body whorl ca. 83% of shell height. Shell colorless, transparent; amber periostracum thin. Aperture broadly ovate, pyriform above. Inner lip slightly thickened and reflected, narrowly adnate to or slightly separated from body whorl. Outer lip thin. Umbilicus chink-like to broadly open. Growth lines pronounced; spiral striae weakly developed.

Visceral coil typically uniformly dark brown. Head/foot variably dusted with brown melanin; grey pigment often concentrated along sides of operculigerous lobe. Proximal half of penial filament usually darkly pigmented externally (Fig. 32).

Radular (Fig. 31) formula: 4(5)-1-4(5)/1-1, 2-1-3, 20–22, 21; width of central tooth, 0.035 mm. Central tooth broadly trapezoidal, cusps fairly narrow. Penis (Fig. 32) longer than wide. Elongate lobe characteristic; width of lobe variable but typically subequal to width of penis near base. Filament short, rarely exceeding lobe in length, narrow compared to lobe. Glandular ridge typically located at or just proximal to tip of lobe; ridge size and shape variable, ranging from small and circular to thickened and elongate. Albumen gland somewhat longer than capsule gland; posterior section of latter sometimes greatly reduced (Fig. 33a, b).

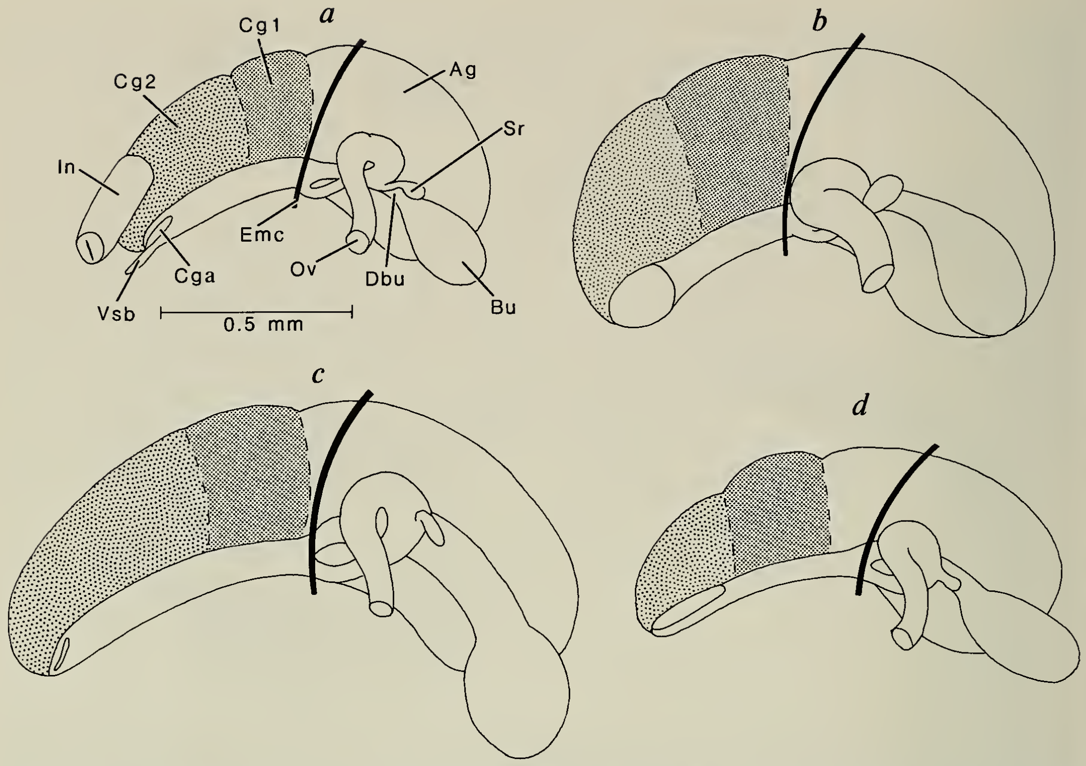

Fig. 24. Pallial oviducts of *Pyrgulopsis* spp., viewed from left side: a, c, *P. erythropoma* (a, USNM 857867, King's Pool; c, USNM 857863, Point of Rocks Springs [Locality 36]); b, *P. crystalis,* USNM 850370, Crystal Pool; d, *P. fairbanksensis,* USNM 850368, Fairbanks Spring. Capsule gland vestibule (Vsb) and position of intestine (In) shown only in a. Ag = albumen gland; Bu = bursa copulatrix; Cga = capsule gland opening; Cg1 = posterior capsule gland section; Cg2 = anterior capsule gland section; Dbu = duct of bursa copulatrix; Emc = posterior end of pallial cavity; In = intestine; Ov = oviduct; Sr = seminal receptacle; Vsb = capsule gland vestibule.

Seminal receptacle minute. Bursa copulatrix small, club-shaped to near-spherical, partly posterior to albumen gland.

Type locality.—Five Springs, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Restricted to four small Ash Meadows springbrooks within 10 km of one another at or above 700 m elevation (Fig. 25). Common in upper segments of streams on soft sediment and loose travertine.

Etymology.—From Latin *nanus,* a dwarf, referring to small size of species.

Comparisons.—Unusual penial morphology shared by *P. isolatus,* n. sp. (described below). Separable from this probable sister species by smaller size, smaller penis (relative to body size), more globose shell, and narrower cusps on central radular teeth.

Pyrgulopsis pisteri, new species
Median-gland springsnail

Figs. 29b, e, 33c, 34a–e, 35, 36

Median-gland Nevada spring snail.—Sada and Mozejko, 1984: fig. 5.

"*Fluminicola*" sp.—USDI, 1984:21673.

Median-gland Nevada spring snail.—Taylor in Williams et al., 1985:43.

Material examined.—NEVADA, NYE COUNTY: Marsh Spring, 859197 (holotype), 859198 (paratypes), UF 94958 (paratypes), 850364, 10 Nov 1985.—North

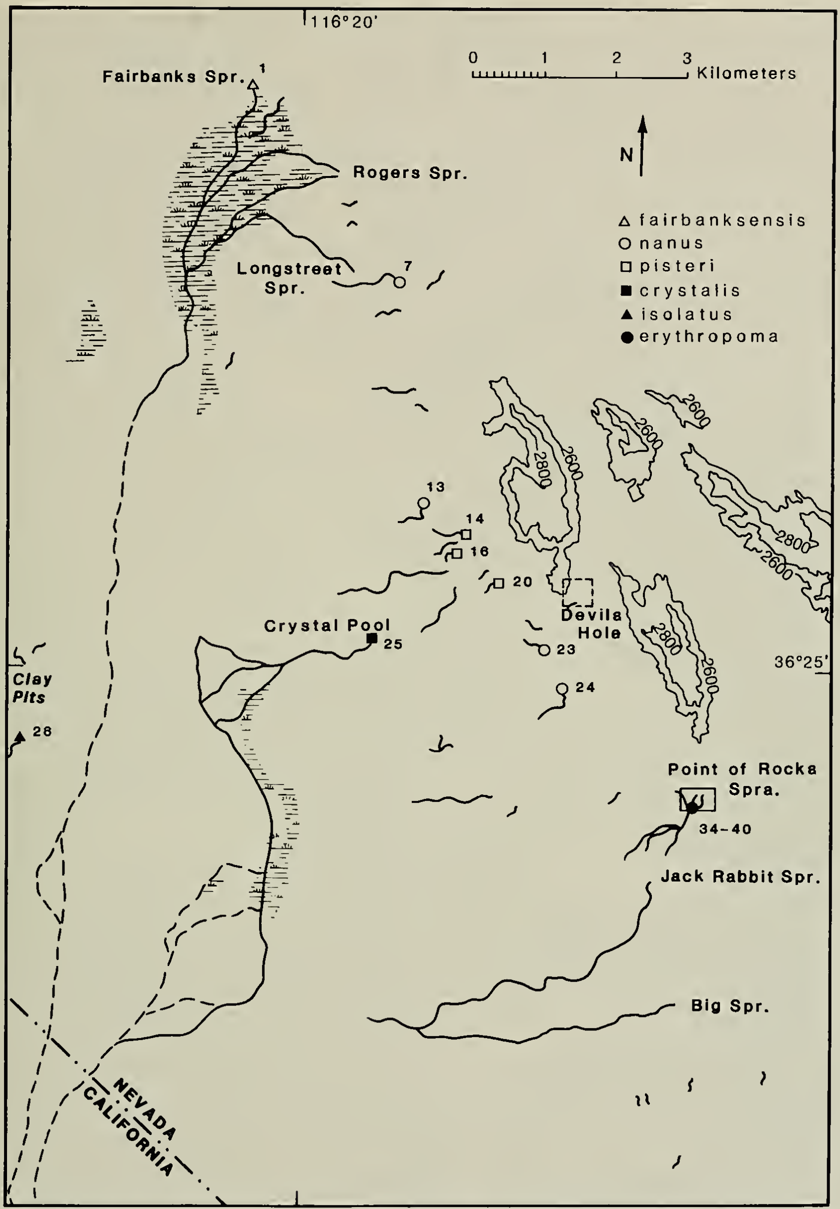

Fig. 25. Map showing distribution of *Pyrgulopsis* spp. in Ash Meadows.

Scruggs Spring, 850362, 859199, 10 Nov 1985; 850361, 8 Jul 1986.—Observation pond below School Spring, 850365, 859200, 10 Nov 1985.

Diagnosis.—A small-sized species with globose shell with short spire. Penis simple, nontapering, with glandular ridge positioned ventrally near mid-point.

Description.—Shell (Figs. 29b, e, 34a–e) 1.8–2.7 mm high, slightly taller than broad. Whorls, 3.25–4.50, convex and inflated. Sutures impressed. Spire slightly convex. Body whorl ca. 83% of shell height. Shell colorless, transparent, with very thin, light brown periostracum (sometimes absent). Aperture broadly ovate, somewhat angled above. Inner lip slightly thickened and reflected; narrowly adnate to or slightly separated from

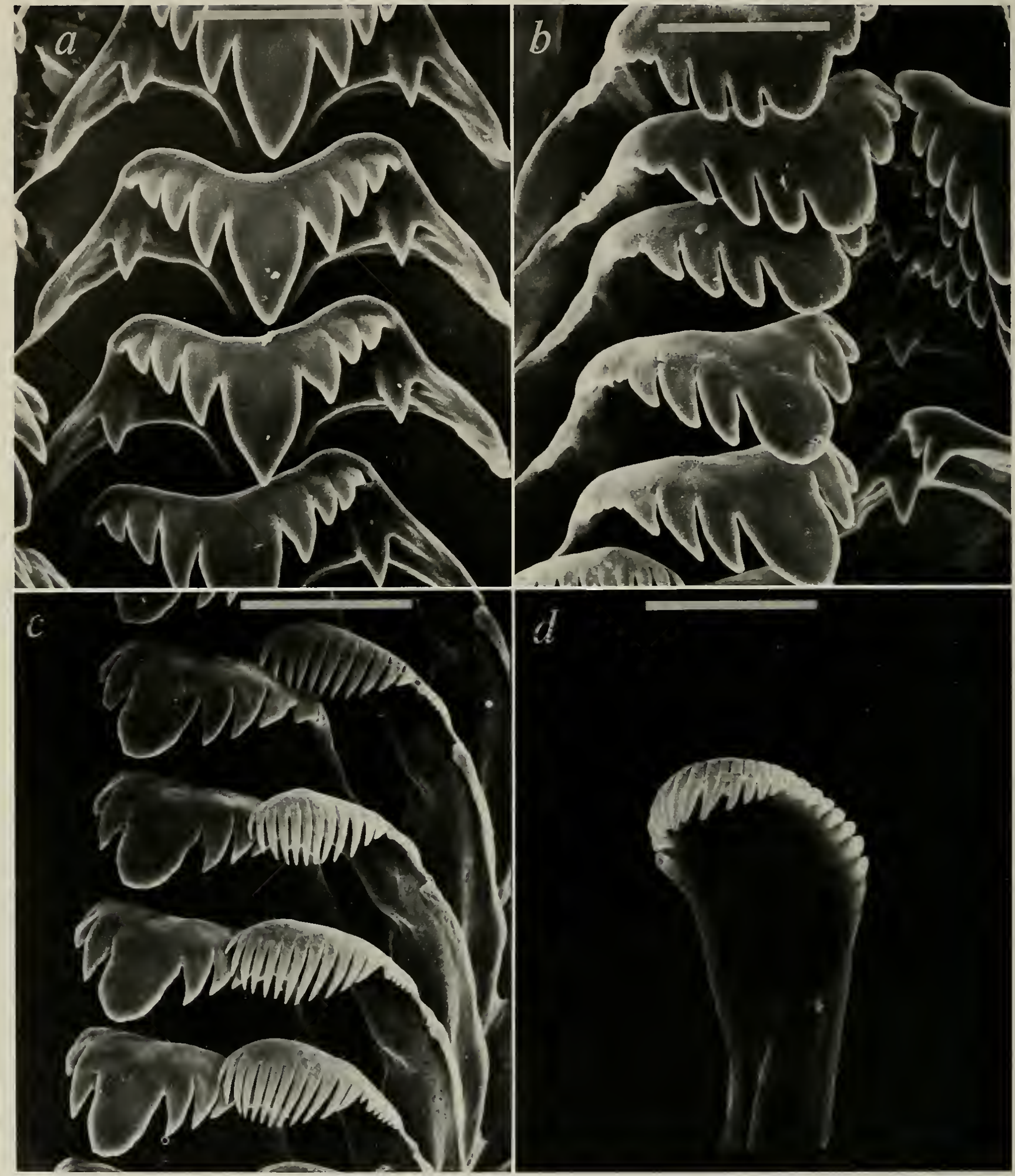

Fig. 26. Radula of *P. fairbanksensis,* USNM 850368, Fairbanks Spring. a, Centrals (bar = 20 μm); b, Laterals (bar = 23.1 μm); c, Laterals and inner marginals (bar = 27 μm); d, Outer marginal (bar = 10 μm).

body whorl. Outer lip thin. Umbilicus chinklike to broadly open. Growth lines pronounced, often somewhat elevated near end of body whorl. Spiral striae moderately pronounced.

Visceral coil typically uniform dark brown or black. Head/foot variably dusted with brown melanin; grey pigment often concentrated along sides of operculigerous lobe. Proximal half of penial filament darkly pigmented, with pigment often extending into distalmost penis (Fig. 36).

Radular (Fig. 35) formula: 3(4)-1-3(4)/1-1, 3-1-3(4), 16–17, 14; width of central tooth, 0.045 mm. Cusps on central teeth moderately wide. Ctenidial filaments, ca. 20. Pros-

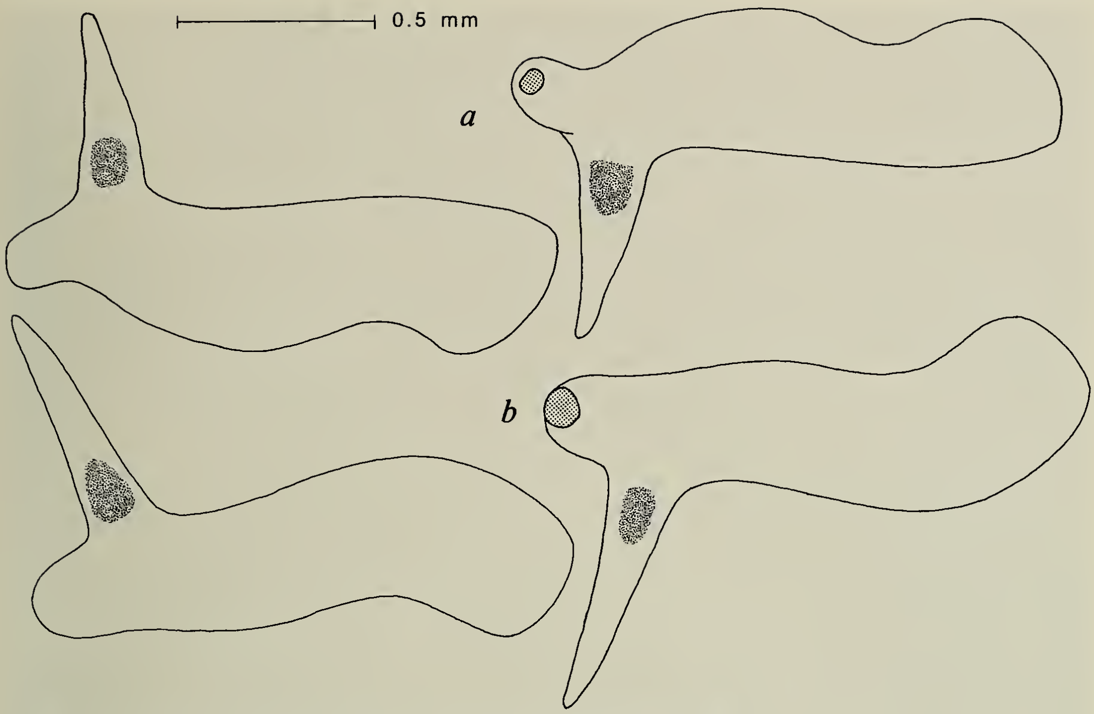

Fig. 27. Penes of *P. fairbanksensis,* USNM 850368, Fairbanks Spring.

tate gland small, largely pallial. Penis (Fig. 36) near-rectangular, with narrow filament arising from broad distal end. Filament less than half of penis length. Glandular ridge typically large and circular, positioned at or near inner edge of penis. Albumen gland slightly longer than capsule gland (Fig. 33c). Seminal receptacle minute. Bursa copulatrix quite small, near-spherical, partly posterior to albumen gland; duct of bursa narrow.

Type locality.—Marsh Spring, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Restricted to small-sized Marsh and North Scurggs Springs, and an observation pond below School Spring, all within two km of one another above 702 m elevation in Ash Meadows. Common in springpools and outflows of former two springs, on aquatic macrophytes, and travertine. Rare in observation pond, on soft, detritus-covered substrate.

Etymology.—Named after E. P. Pister, in recognition of his tremendous effort over the past 20 years to preserve native aquatic fauna of the Death Valley System.

Comparisons.—Shell similar to that of *P. nanus* and *P. isolatus,* n. sp. (described below), but species separable from above by absence of penial lobe and position of glandular ridge. Simple penis having glandular ridge near mid-point of ventral surface similar to those of *P. erythropoma* and *P. crystalis,* but species distinguished from above by high-spired shell, untapered shape of penis, and habitat of small springs (compared to large spring pools).

Pyrgulopsis isolatus, new species
Elongate-gland springsnail
Figs. 19d, 25, 29c, f, 33d, 34f, g, 37, 38

Material examined.—NEVADA, NYE COUNTY: Spring S of Clay Pits, 859201 (holotype), 859202 (paratypes), UF 93959 (paratypes), 850366, 8 Jul 1986.

Diagnosis.—A large-sized species, with

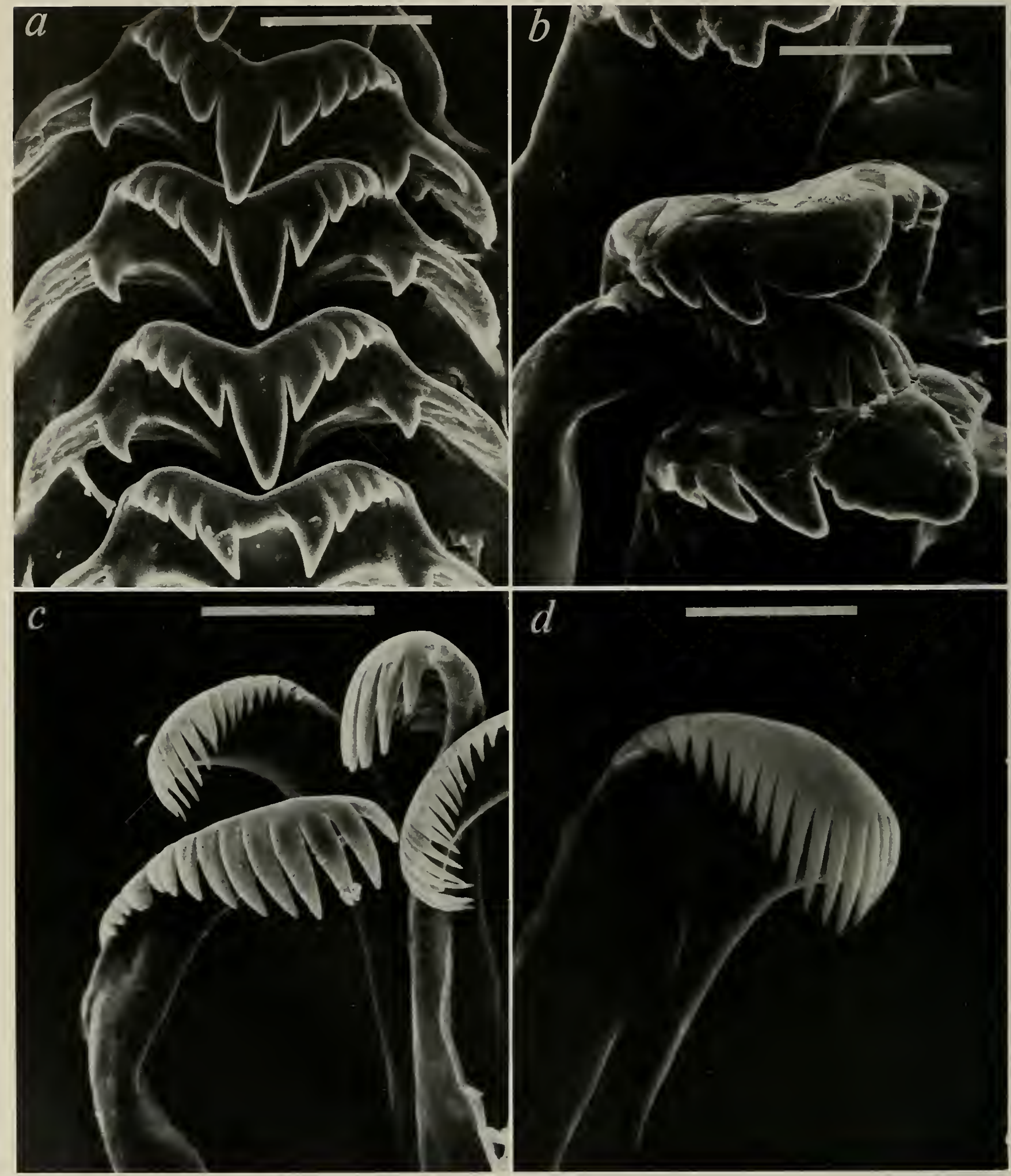

Fig. 28. Radula of *P. crystalis,* USNM 850370, Crystal Pool. a, Centrals (bar = 17.6 μm); b, Laterals and inner marginal (bar = 17.6 μm); c, Inner marginals (bar = 15.0 μm); d, Outer marginal (bar = 8.6 μm).

broadly conical shell having moderate spire. Penis enlarged, rectangular, with enlarged lobe bearing elongate glandular ridge distally.

Description.—Shell (Figs. 29c, f, 34f, g) 2.6–3.1 mm high, ca. one-fifth taller than wide. Whorls 3.75–4.25, convex and inflated, with impressed sutures. Spire straight or

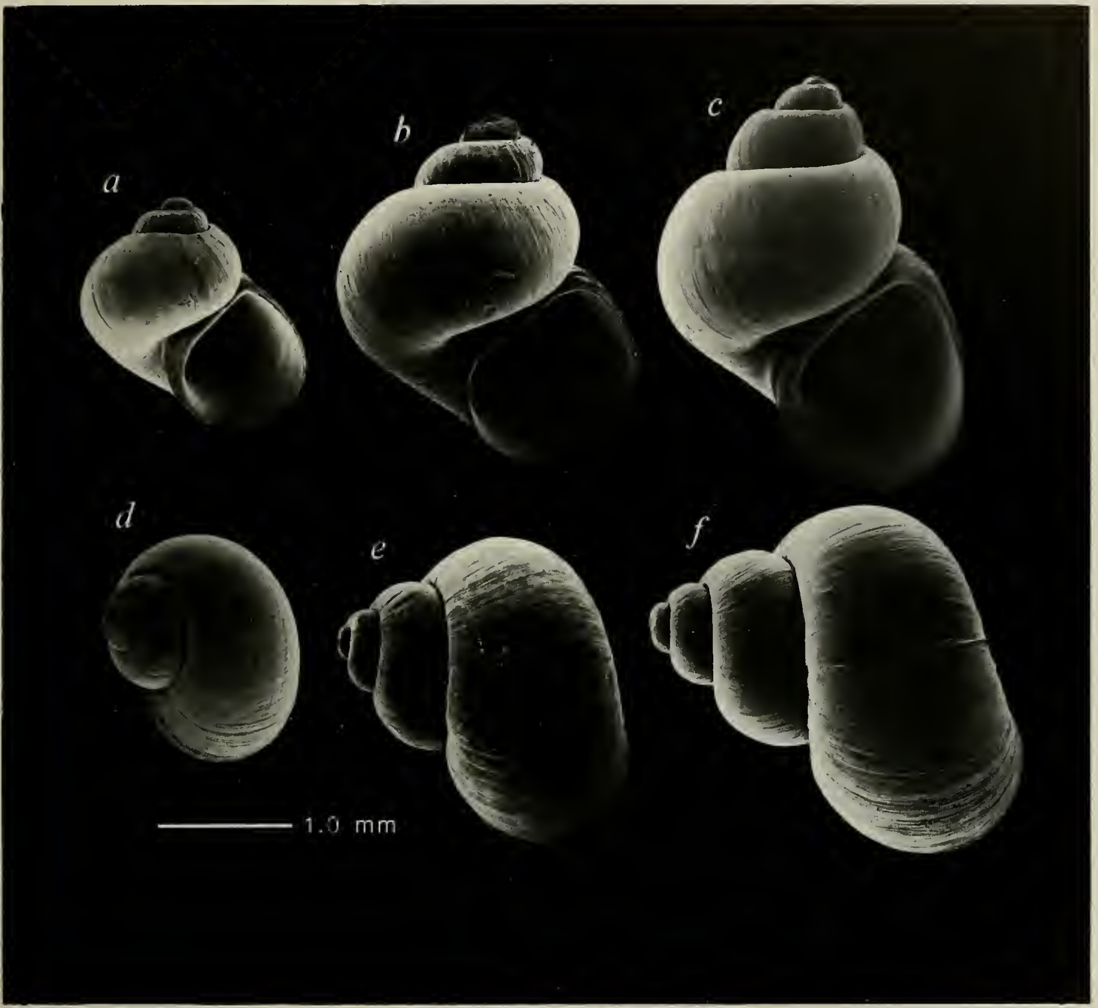

Fig. 29. SEM micrographs of shells of *Pyrgulopsis* spp.: a, d, *P. nanus,* Five Springs (a, holotype, USNM 859191; d, Paratype, USNM 859192); b, e, *P. pisteri,* Marsh Spring (b, holotype, USNM 859197; e, paratype, USNM 859198); c, f, *P. isolatus,* spring S of Clay Pits (c, holotype, USNM 859201; f, paratype, USNM 859202).

slightly convex. Body whorl ca. 80% of shell height. Shell colorless, transparent; periostracum light brown. Aperture ovate, slightly angular above. Inner lip slightly thickened and reflected; often slightly separated from body whorl. Outer lip thin. Umbilicus chink-like to broadly open. Growth lines pronounced; spiral striae weakly developed.

Visceral coil typically uniformly dark brown. Head/foot variably dusted with brown melanin; grey pigment often concentrated along sides of operculigerous lobe. Virtual entirety of penial filament usually darkly pigmented (Fig. 38).

Radular (Fig. 37) formula: 4-1-4/1-1, 3-1-3(4), 22–24, 24–27; width of central tooth, 0.044 mm. Central cusps of central and lateral teeth broad. Ctenidial filaments, ca. 20. Prostate gland large, with very small pallial portion. Penis (Figs. 19d, 38) extending well anterior to mantle collar, nontapering, with deep folds along much of length. Lobe often as long as distal penis, nontapering or even expanding distally. Fil-

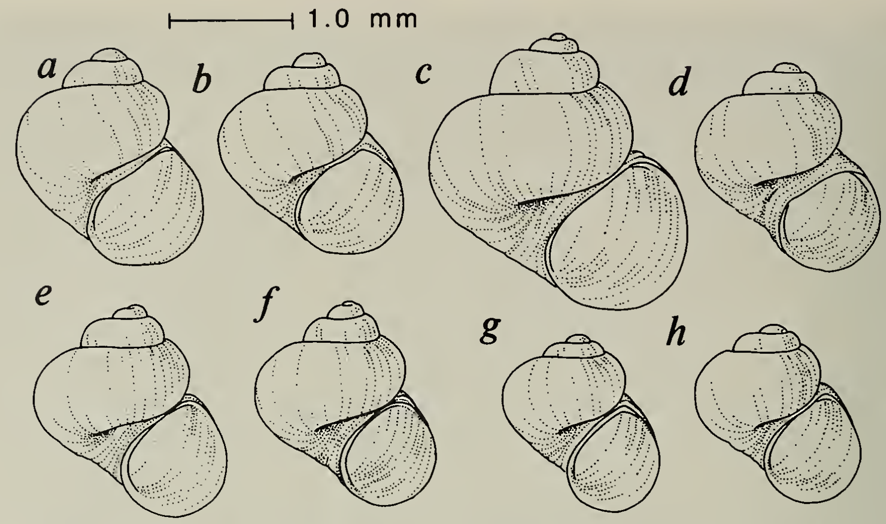

Fig. 30. Shells of *P. nanus*: a, b, Paratypes, USNM 859192, Five Springs; c, d, USNM 859193, Mary Scott Spring; e, f, USNM 859194, Collins Ranch Spring; g, h, USNM 859196, spring 1.0 km N of Collins Ranch Spring.

ament very short relative to penis length. Glandular ridge narrowly elongate, typically extending along entire distal edge of lobe. Albumen gland longer than capsule gland (Fig. 33d). Seminal receptacle minute. Bursa copulatrix enlarged, more than half of length posterior to albumen gland.

Type locality.—Spring at Clay Pits, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Endemic to type locality W of Carson Slough, Ash Meadows (Fig. 25). Most common in small stream outflow from marsh.

Etymology.—From New Latin *isolatus,* detached or separate, referring to endemism in area disjunct from most other Ash Meadows waters.

Comparisons.—Most similar to *P. nanus* (see above).

Genus *Tryonia* Stimpson, 1865

Tryonia Stimpson, Hershler and Thompson, 1987:26 [with references].

Diagnosis.—Shell elongate-conic to turreted, 1.2–7.0 mm tall. Aperture simple, unthickened. Umbilicus narrow or absent. Sexual dimorphism often pronounced (males smaller). Protoconch smooth or with slight wrinkling. Teleoconch smooth or with spiral lines and/or axial striations or varices; growth lines often prominent. Operculum paucispiral. Central radular teeth dagger-like; basal cusps present. Penis flattened, elongate, with varying numbers of papillae at base and along inner curvature. Females ovoviviparous. Capsule gland reflected posteriorly; albumen gland greatly reduced. Spermathecal duct opens posterior to capsule gland opening.

Remarks.—Congeners differ mostly in subtle shell features, with number and location of penial papillae sometimes varying. Additional study will be necessary to confirm our impression that detailed anatomy of Ash Meadows *Tryonia* varies little from that described below for *T. angulata,* n. sp.

Tryonia angulata, new species
Sportinggoods Tryonia
Figs. 39a, 40, 41, 42a, d, 43, 44

Sportinggoods Tryonia.—Sada and Mozejko, 1984: fig. 5.

Tryonia sp.—USDI, 1984:21673.

Fig. 31. Radula of *P. nanus,* USNM 850354, Five Springs. a, Centrals (bar = 15 μm); b, Laterals and inner marginals (bar = 13.6 μm); c, Inner marginals (bar = 7.5 μm); d, Outer marginal (bar = 6 μm).

Sportinggoods tryonia.—Taylor in Williams et al., 1985:43.

Material examined.—NEVADA, NYE COUNTY: Fairbanks Spring, 859151 (holotype), 859152 (paratypes), UF 93960 (paratypes), 850298, 7 Nov 1985; 850299, 7 Jul 1986.—Crystal Pool, 850300, 859153, 8 Nov 1985.—Big Spring, 850302, 859212, 8 Nov 1985; 850301, 8 Jul 1986.

Diagnosis.—A fairly large-sized species, with elongate-conic shell. Whorls with sub-

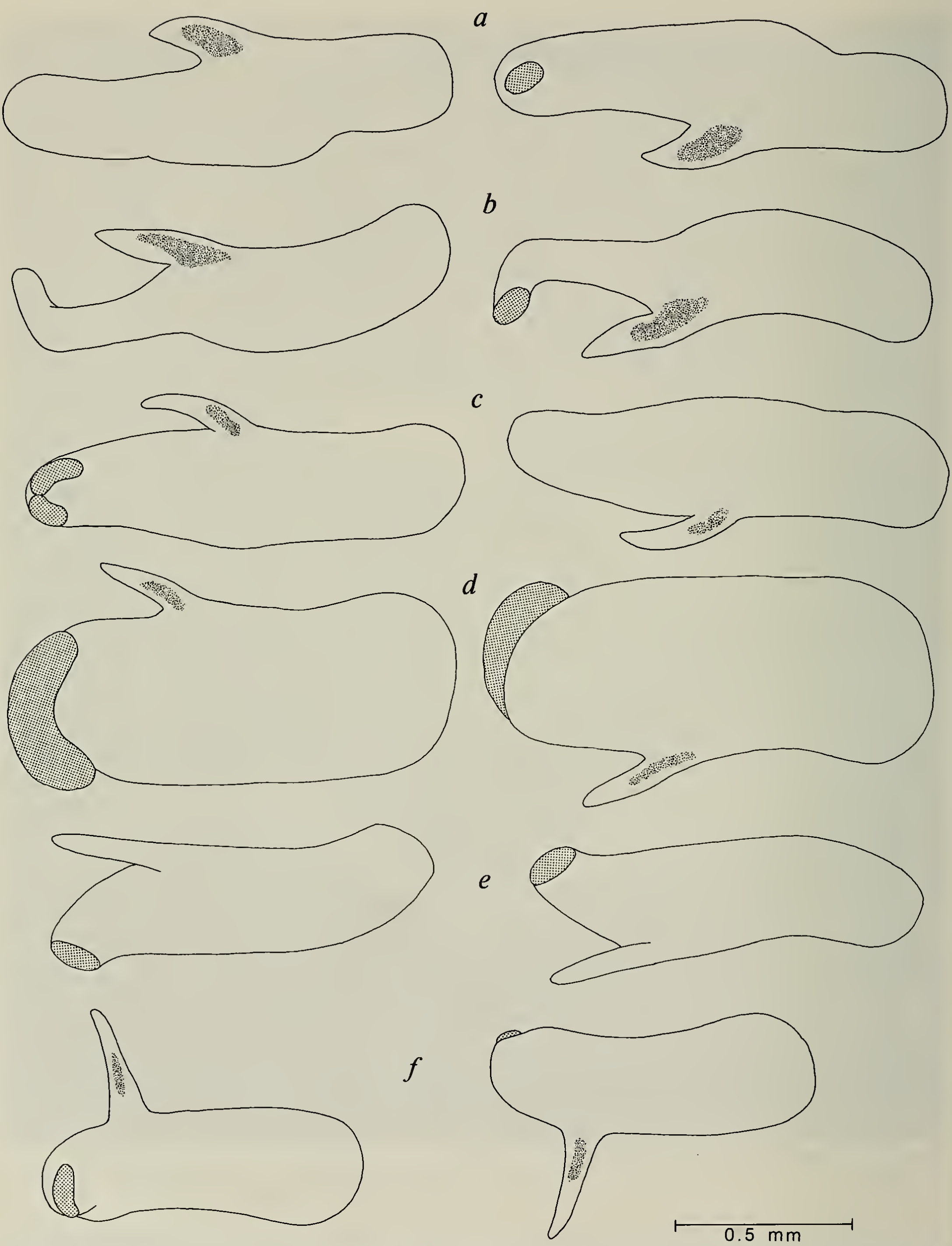

Fig. 32. Penes of *P. nanus*: a, b, USNM 850354, Five Springs; c, d, USNM 850356, Mary Scott Spring; e, USNM 850360, spring (southern) N of Collins Ranch Spring; f, USNM 850358, Collins Ranch Spring.

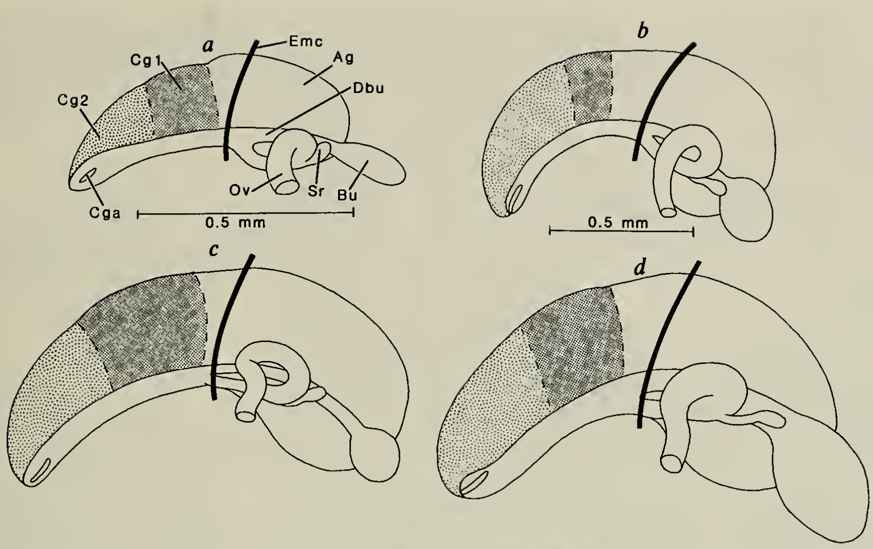

Fig. 33. Pallial oviducts of *Pyrgulopsis* spp., viewed from left side: a, b, *P. nanus* (a, USNM 850354, Five Springs; b, USNM 850356, Mary Scott Spring); c, *P. pisteri,* USNM 850364, Marsh Spring; d, *P. isolatus,* USNM 850366, spring S of Clay Pits. "c" and d drawn to same scales as a and b, respectively. Ag = albumen gland; Bu = bursa copulatrix; Cga = capsule gland opening; Cg1 = posterior capsule gland section; Cg2 = anterior capsule gland section; Dbu = duct of bursa copulatrix; Emc = posterior end of pallial cavity; Ov = oviduct; Sr = seminal receptacle.

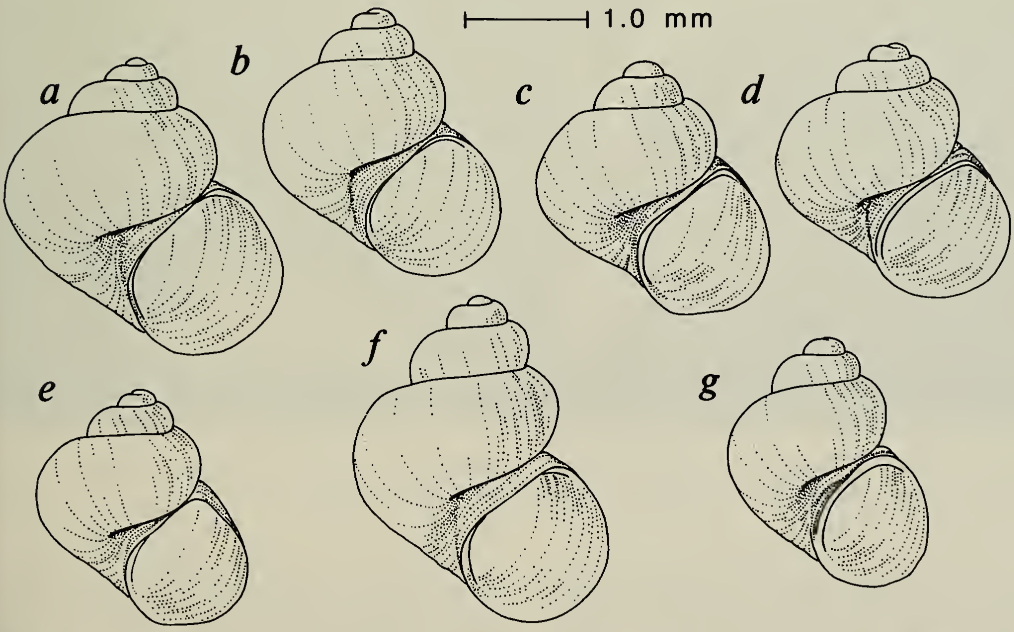

Fig. 34. Shells of *P. pisteri* and *P. isolatus*: a–e, *P. pisteri* (a, b, USNM 859199, North Scruggs Spring; c, d, paratypes, USNM 859198, Marsh Spring; e, USNM 859200, observation pond below School Spring); f, g, *P. isolatus,* paratypes, USNM 859202, spring S of Clay Pits.

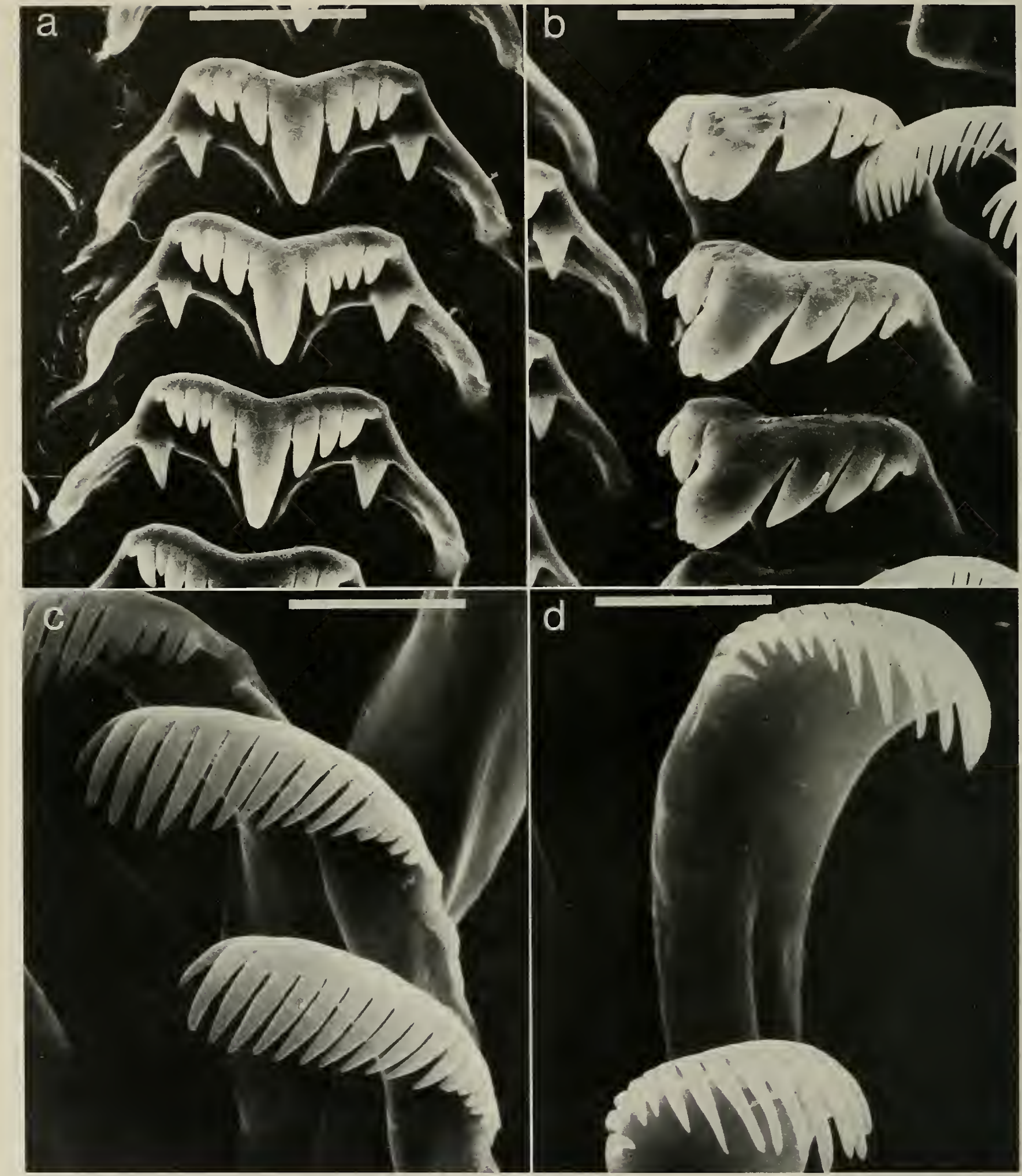

Fig. 35. Radula of *P. pisteri,* USNM 850364, Marsh Spring. a, Centrals (bar = 20 μm); b, Laterals (bar = 20 μm); c, Inner marginals (bar = 12 μm); d, Outer marginals (bar = 6.7 μm).

sutural angulations; outer apertural lip strongly sinuate. Central radular teeth with 2 pairs of basal cusps. Penis with 3 papillae on inner curvature (2 distal); outer curvature often with papilla at base.

Description.—Shell (Figs. 39a, 40) 2.7–4.0 mm high, about twice as tall as wide. Whorls, 5.0–7.0, well-rounded, fairly rapidly expanding, with impressed sutures. Translation rate (T) moderate, 5.2–7.9. Spire

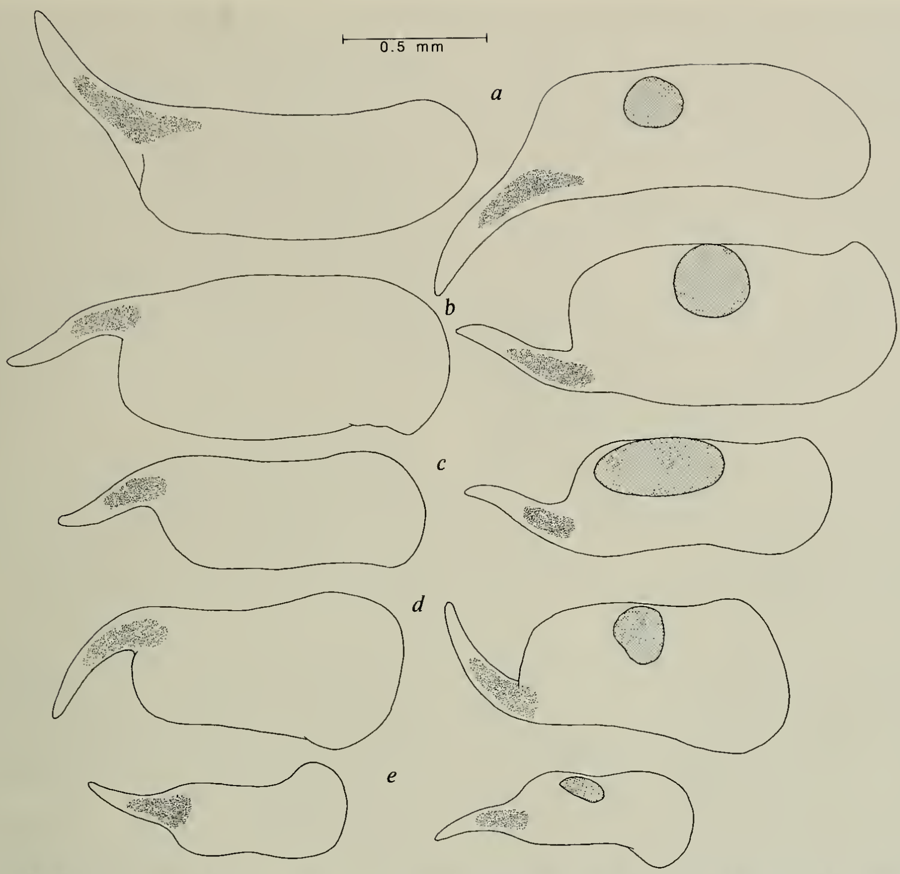

Fig. 36. Penes of *P. pisteri*: a, b, USNM 850362, North Scruggs Spring; c, d, USNM 850364, Marsh Spring; e, USNM 850365, observation pond below School Spring.

slightly convex; apex often eroded. Body whorl ca. 60% of shell height. Shell colorless, transparent (although eroded apex whitened); periostracum light brown. Aperture narrowly ovate, slightly angled above, usually fairly broadly adnate to body whorl above. Inner lip slightly thickened, reflected below; outer lip thin. Umbilicus chink-like. Growth lines moderately pronounced.

Visceral coil darkly pigmented with melanin, especially on digestive gland and stomach. Snout and sides of head/foot variably dusted with grey or brown pigment. Operculigerous lobe darkly pigmented internally. Penis frequently with small, distal pigment patch. Proximal papillae often darkly pigmented and bases of distal papillae sometimes streaked with melanin.

Radular (Fig. 41) formula: 5-1-5/2-2, 3-1-4, 22, 34; width of central tooth, 0.025 mm. Cusps on outer marginals (Fig. 41d) relatively numerous. Ctenidium with up to 25 small filaments. Prostate gland (Fig. 42a) bean-shaped, with more than one-third of length pallial. Posterior vas deferens (Vd1) enters left side of prostate gland, near posterior edge; anterior vas deferens (Vd2) exits from anterior tip of gland as thickened tube. Vas deferens only slightly looping in penis. Penis elongate, projecting well anterior to mantle collar, coiling counter-clockwise. Distal edge of penis blunt, with slight bulge on inner side. Penis with 2 distal, flask-shaped papillae on inner curvature; usually closely spaced near distal tip; and single papilla at base on inner curvature. Single, enlarged papilla often present at base on outer curvature. General organization of pallial

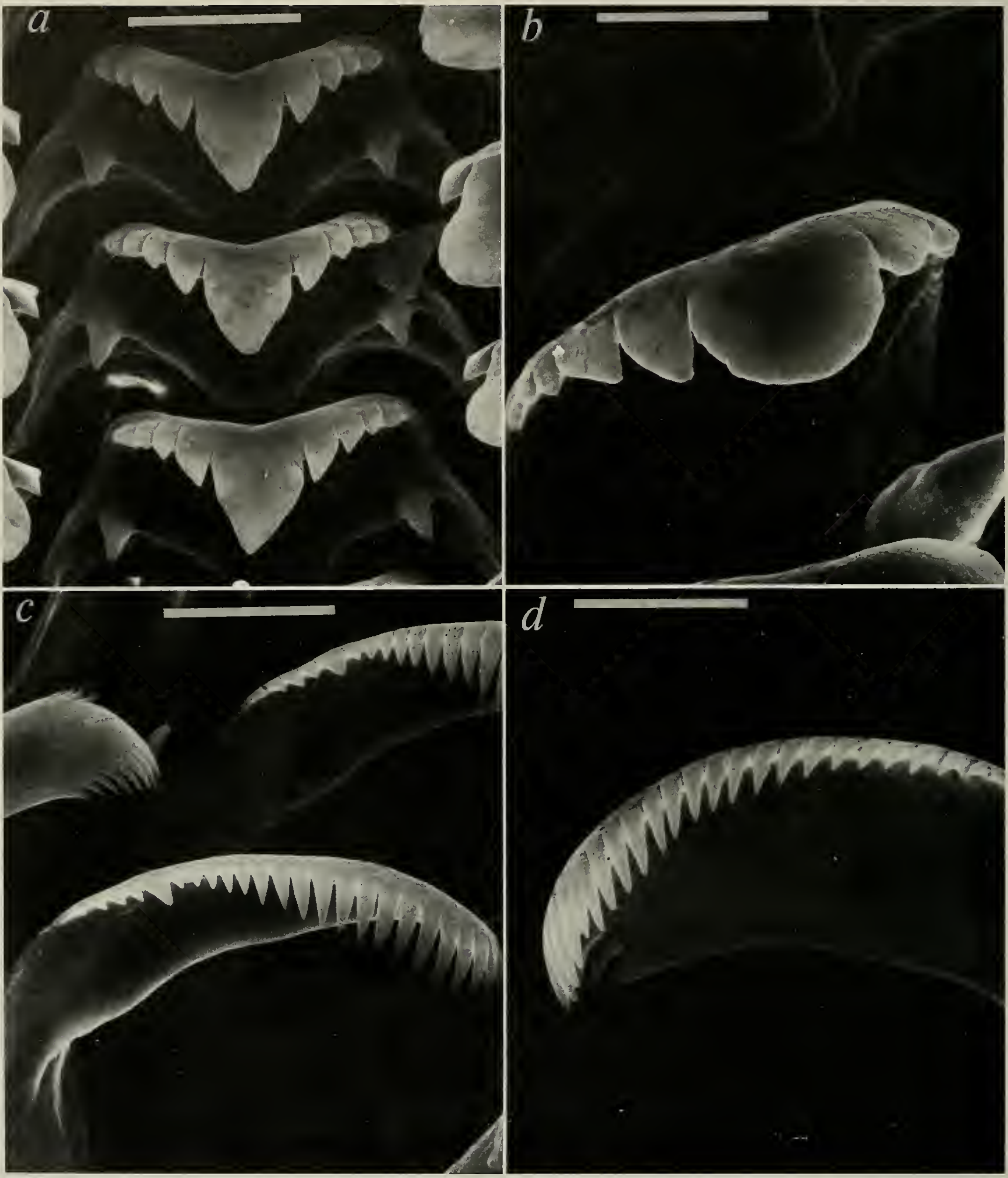

Fig. 37. Radula of *P. isolatus,* USNM 850366, spring S of Clay Pits. a, Centrals (bar = 15 μm); b, Lateral (bar = 10 μm); c, Inner marginals (bar = 10.7 μm); d, Outer marginal (bar = 5 μm).

oviduct complex (Fig. 43) as for genus. Capsule gland with small anterior sphincter (Cg2, Fig. 43a) and small (4–8) number of shelled embryos. Bursa copulatrix (Bu) ovate, partly covered by pallial oviduct; seminal receptacle (Sr) minute, positioned ventral to anterior portion of bursa. Oviduct (Ov) with small distal loop; oviduct and albumen gland (Ag) joining ventral to bursa, posterior to rear wall of pallial cavity (Emc). Just anterior to this point, oviduct joins duct of seminal receptacle (Fig. 43b), which then loops several times before joining narrow duct of bursa at or just posterior to end of pallial

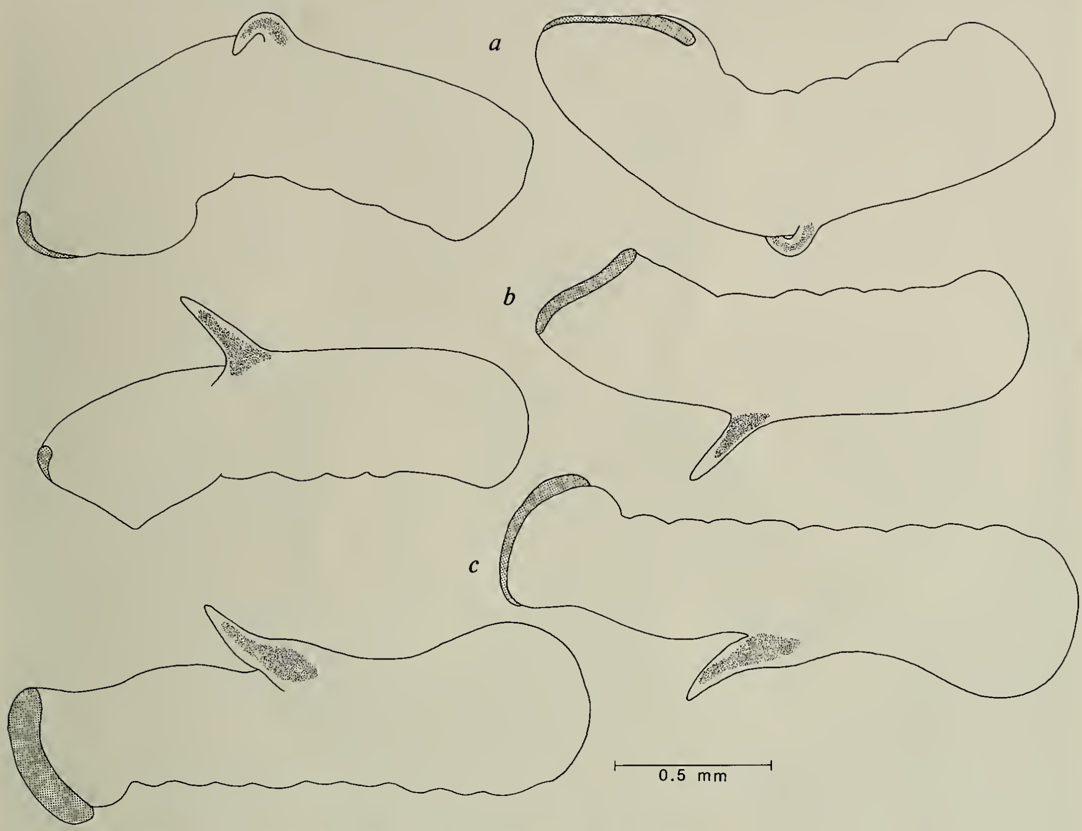

Fig. 38. Penes of *P. isolatus,* USNM 850366, spring S of Clay Pits.

cavity. Spermathecal duct (Sd) pressed against capsule gland, opening at about one-third of pallial cavity length from posterior wall.

Type locality.—Fairbanks Spring, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Endemic to three large limnocrenes in Ash Meadows at ca. 671 m elevation (Fig. 44). Common at all three sites.

Etymology.—From Latin *angulus,* corner or bend, referring to characteristic angulate shell whorls.

Comparisons.—Shell form of *T. angulata* reminiscent of that of *T. clathrata* Stimpson from southeastern Nevada but separated from latter by smaller size, absence of teleoconch sculpture, and pattern of penial lobation. United with other Ash Meadows *Tryonia* by possession of three papillae on inner curvature (two distal); pattern differing from those seen in *T. clathrata* (>four papillae on inner curvature; Hershler and Thompson 1987) and taxa from Arizona (two papillae; Hershler and Landye 1988) and New Mexico (single papilla; Taylor 1983).

Distinguished from other Ash Meadows *Tryonia* by combination of large size and elongate-conic shell shape; angulate whorl profile; and strongly sinuate outer apertural lip. Most closely resembles *T. variegata,* n. sp. (described below), as both are relatively large-sized and occasionally have a papilla on outer penial curvature.

Tryonia variegata, new species
Amargosa Tryonia

Figs. 39e–g, 42b, e, g, h, 44–52

Tryonia.—Minckley and Deacon, 1975:108.
Small solid Tryonia.—Sada and Mozejko, 1984: fig. 5.

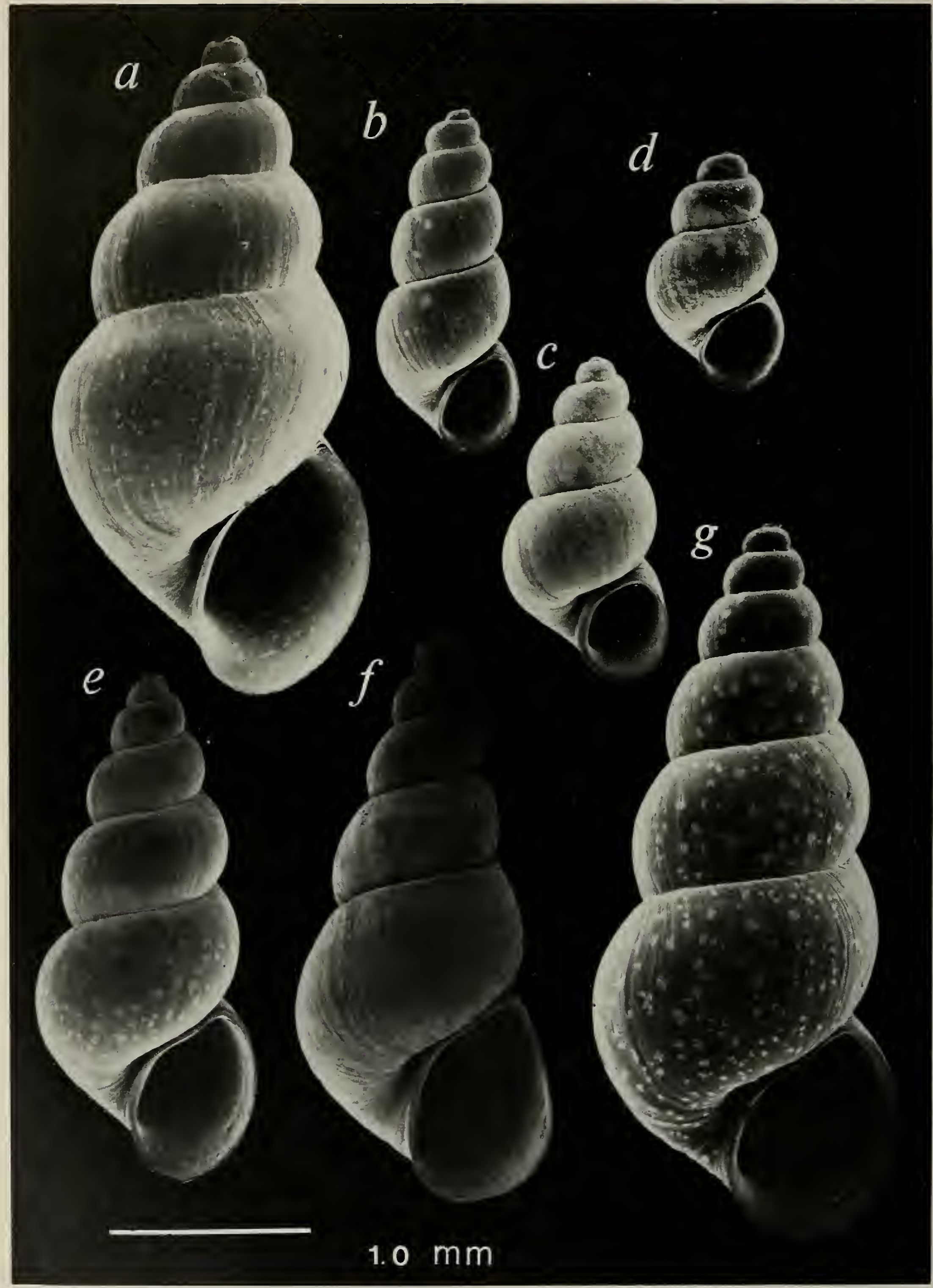

Fig. 39. SEM micrographs of shells of *Tryonia* spp.: a, *T. angulata,* holotype, USNM 859151, Fairbanks Spring; b, *T. elata,* holotype, USNM 859159, Point of Rocks Springs (Locality 35); c, d, *T. ericae* (c, holotype, USNM 859162, North Scruggs Spring; d, USNM 859165, spring (northern) N of Collins Ranch Spring); e–g, *T. variegata* (e, USNM 859157, Collins Ranch Spring; f, USNM 859155, Devils Hole; g, holotype, USNM 859166, Five Springs). Spots on shells are artifacts of SEM preparation.

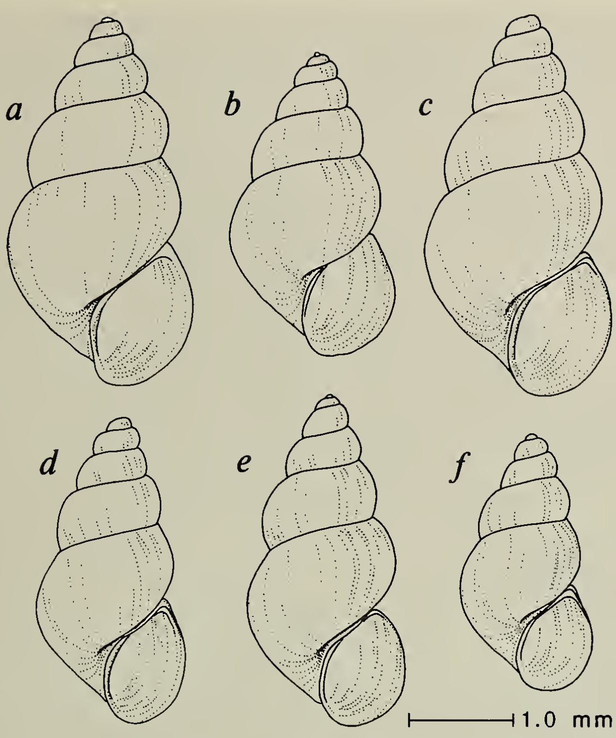

Fig. 40. Shells of *T. angulata*: a, b, Paratypes, USNM 859152, Fairbanks Spring; c, d, USNM 859153, Crystal Pool; e, f, USNM 859212, Big Spring.

Point of Rocks Tryonia.—Sada and Mozejko, 1984: fig. 5.

Devils Hole Amargosa Tryonia.—Sada and Mozejko, 1984: fig. 5.

Amargosa Tryonia snail.—USDI, 1984: 21673.

Point of Rocks Tryonia snail.—USDI, 1984:21673.

Amargosa tryonia.—Taylor in Williams et al., 1985:43.

Point-of-Rocks tryonia.—Taylor in Williams et al., 1985:43.

Material examined.—NEVADA, NYE COUNTY: Five Springs, 859166 (holotype), 859167 (paratypes), UF 93961 (paratypes), 850314, 7 Nov 1985.—Chalk Spring, 850315, 859168, 10 Nov 1985.—Mary Scott Spring, 850316, 859169, 9 Nov 1985; 850317, 8 Jul 1986.—North Scruggs Spring, 850327, 859175, 9 Nov 1985; 850326, 8 Jul 1986.—South Scruggs Spring, 850318, 859170, 9 Nov 1985.—Marsh Spring, 850319, 859171, 10 Nov 1985; 850320, 8 Jul 1986.—North Indian Spring, 850321, 859172, 10 Nov 1985.—South Indian Spring, 850322, 10 Nov 1985.—School Spring, 850323, 859173, 10 Nov 1985; Observation pond below School Spring, 850324, 10 Nov 1985.—Devils Hole, 859155, 850304, 8 Nov 1985; 850303, 8 Jul 1986.—Spring (southern) N of Collins Ranch Spring, 850307, 859158, 9 Nov 1985; 850308, 8 Jul 1986.—Collins Ranch Spring, 859156, 859157, 850305, 9 Nov 1985; 850306, 8 Jul 1986.—Spring S of Clay Pits, 850331, 10 Jul 1986.—Spring (western) near Crystal Reservoir, 850325, 859174, 10 Nov 1985.—Spring (eastern) near Crystal Reservoir, 850328, 859176, 9 Nov 1985.—Point of Rocks Springs (Locality 38), 850329, 859177, 8 Nov 1985.—Point of Rocks Springs (Locality 39), 850330, 859178, 9 Nov 1985. CALIFORNIA, INYO

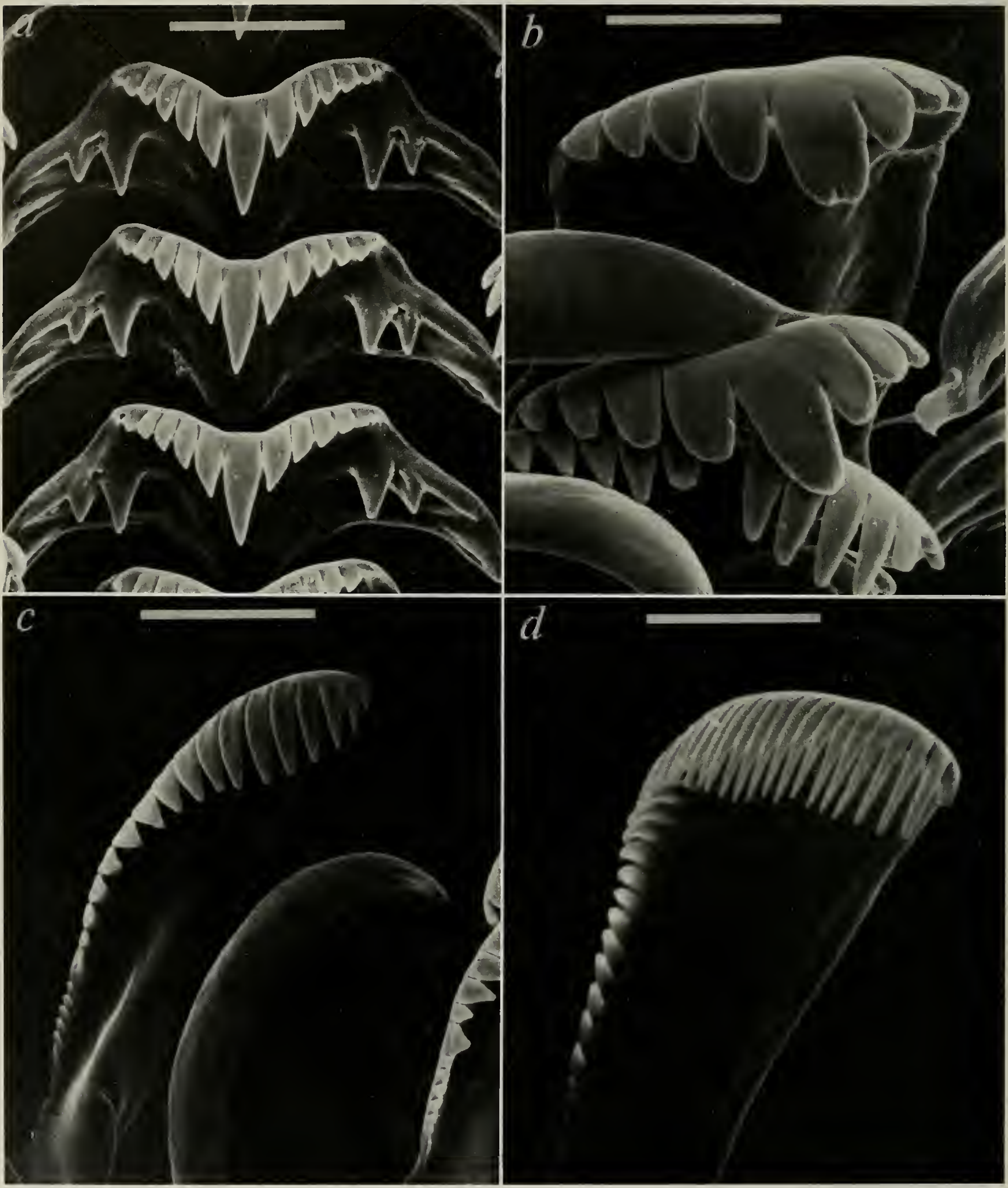

Fig. 41. Radula of *T. angulata,* USNM 850299, Fairbanks Spring. a, Centrals (bar = 8.6 μm); b, Laterals (bar = 6 μm); c, Inner marginals (bar = 7.5 μm); d, Outer marginal (bar = 3.8 μm).

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Fig. 43. Female reproductive anatomy of *T. angulata,* USNM 850299, Fairbanks Spring: a, Pallial oviduct and associated structures, viewed from right side; b, Bursa copulatrix complex, viewed from right side. Position of bursa and anterior portion of duct in b indicated by dashed lines. Ag = albumen gland; Bu = bursa copulatrix; Cga = capsule gland opening; Cg1 = posterior section of capsule gland; Cg2 = anterior section of capsule gland; Dsr = duct of seminal receptacle; Emc = posterior end of pallial cavity; Oov = opening of oviduct into albumen gland; Osd = opening of spermathecal duct; Ov = oviduct; Sd = spermathecal duct; Sr = seminal receptacle.

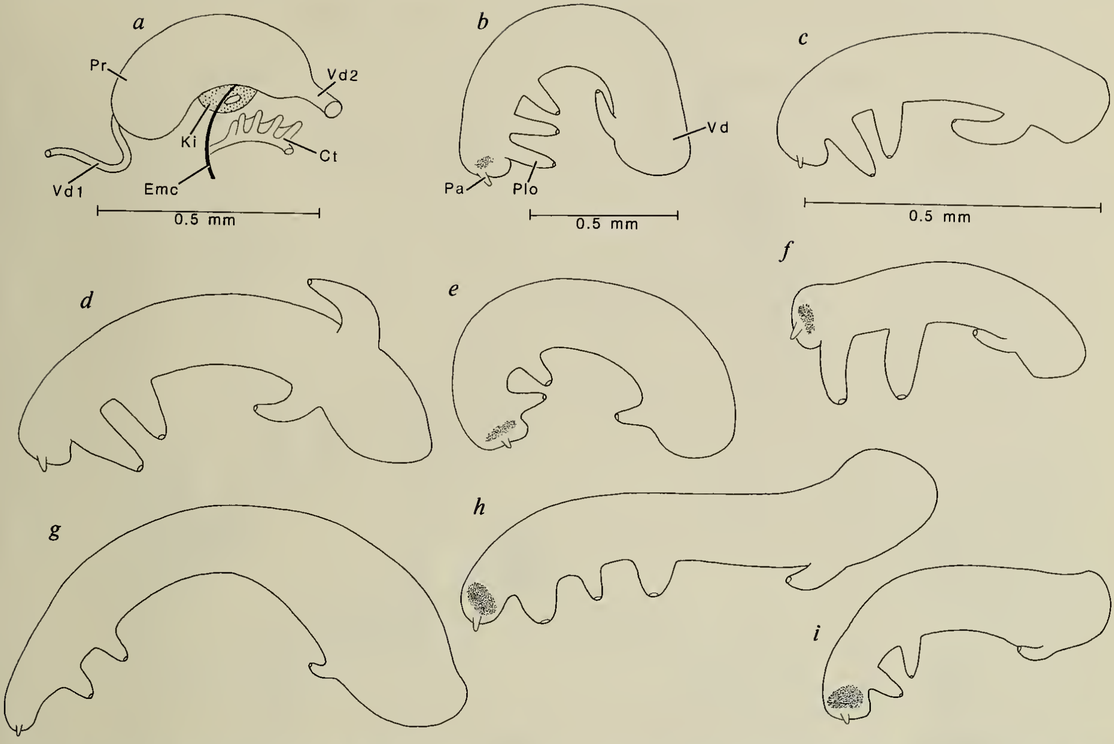
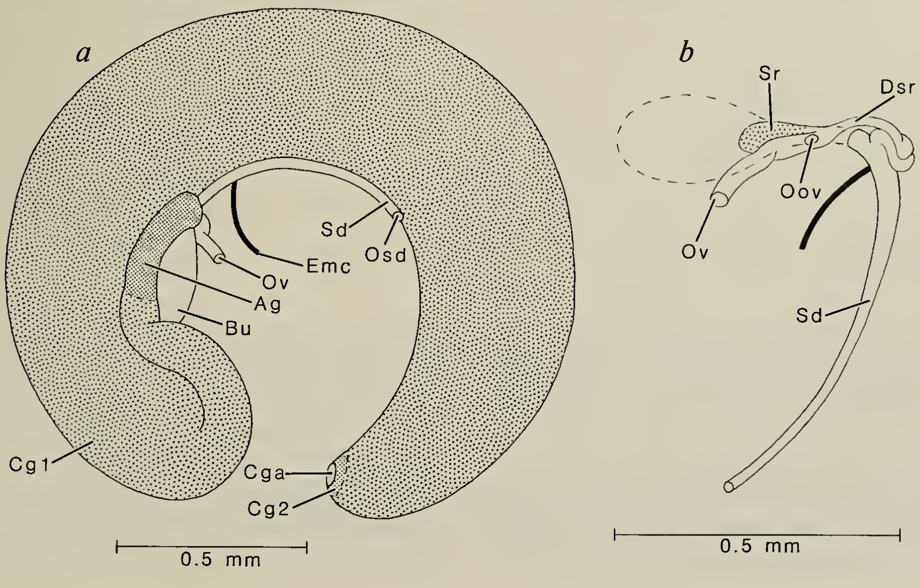


Fig. 42. Male reproductive anatomy of *Tryonia* spp.: a, d, *T. angulata,* USNM 850299, Fairbanks Spring (a, prostate gland and associated structures and organs, viewed from right side; d, penis); b, e, g, h, Penes of *T. variegata* (b, USNM 850329, Point of Rocks Springs [Locality 38]; e, USNM 850314, Five Springs; g, USNM 850303, Devils Hole; h, USNM 850305, Collins Ranch Spring); c, Penis of *T. elata,* USNM 850309, Point of Rocks Springs [Locality 35]; f, i, Penes of *T. ericae* (f, USNM 850312, North Scruggs Spring; i, USNM 850313, spring (northern) N of Collins Ranch Spring). "a," d, b, e, g, h; and c, f, i drawn to same scales, respectively. Ct = ctenidium; Emc = posterior end of pallial cavity; Ki = kidney; Pa = terminal papilla; Plo = penial lobe; Pr = prostate gland; Vd1 = posterior vas deferens; Vd2 = anterior vas deferens.



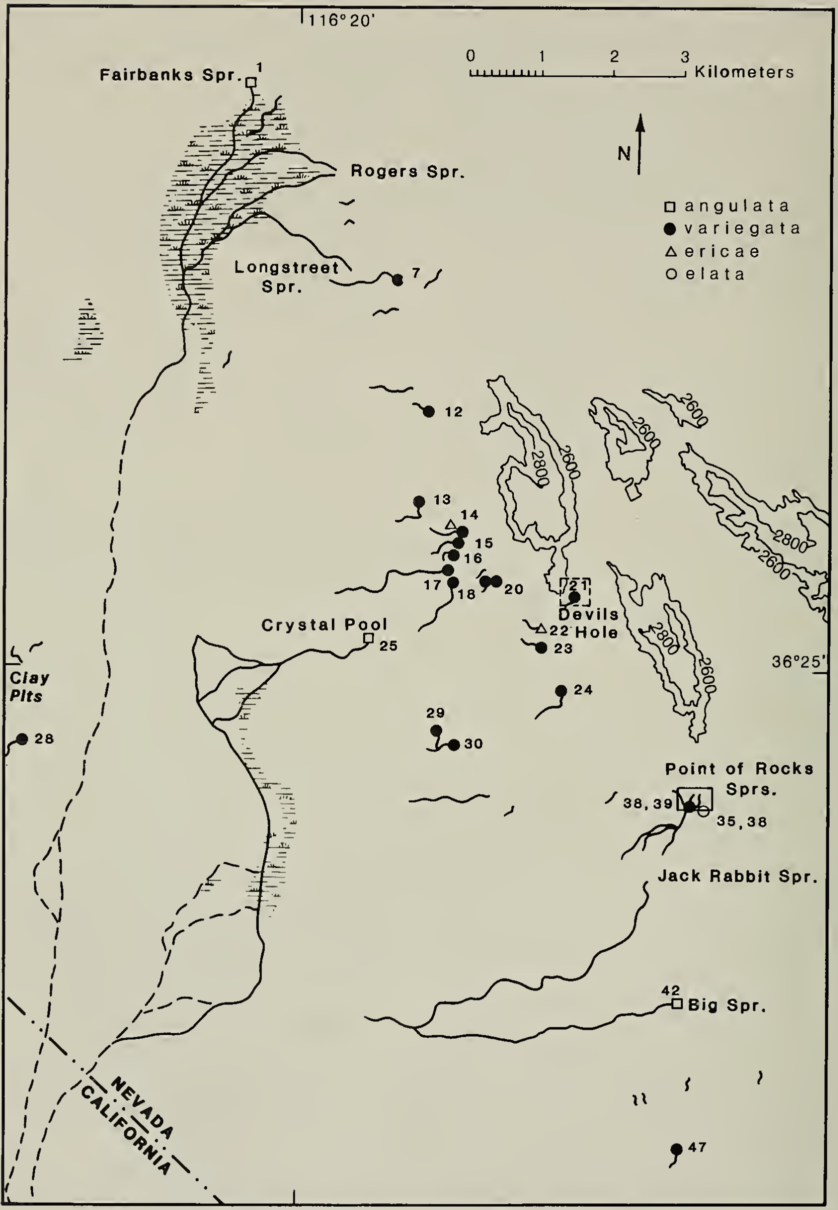


Fig. 44. Map showing distribution of *Tryonia* spp. in Ash Meadows.

COUNTY: Shoshone Spring (Shoshone), T22N, R7E, NW corner sec. 30, 12 Mar 1985.—Spring by Grimshaw Lake (Tecopa), T21N, R7E, NE corner sec. 9, 13 Mar 1985.

Diagnosis.—A variably-sized species (medium to large), with high-spired, turriform-aciculate shell. Aperture moderately sinuate. Central radular teeth with 2 pairs of basal cusps. Penis with 3 or 4 papillae on inner curvature (all but 1 distal); outer curvature occasionally with basal papilla.

Description.—Shell (Figs. 39e–g, 45–48) 2.8–7.5 mm high, more than twice as tall as wide. Whorls, 5.25–9.75, slightly to moderately convex, with slightly impressed su-

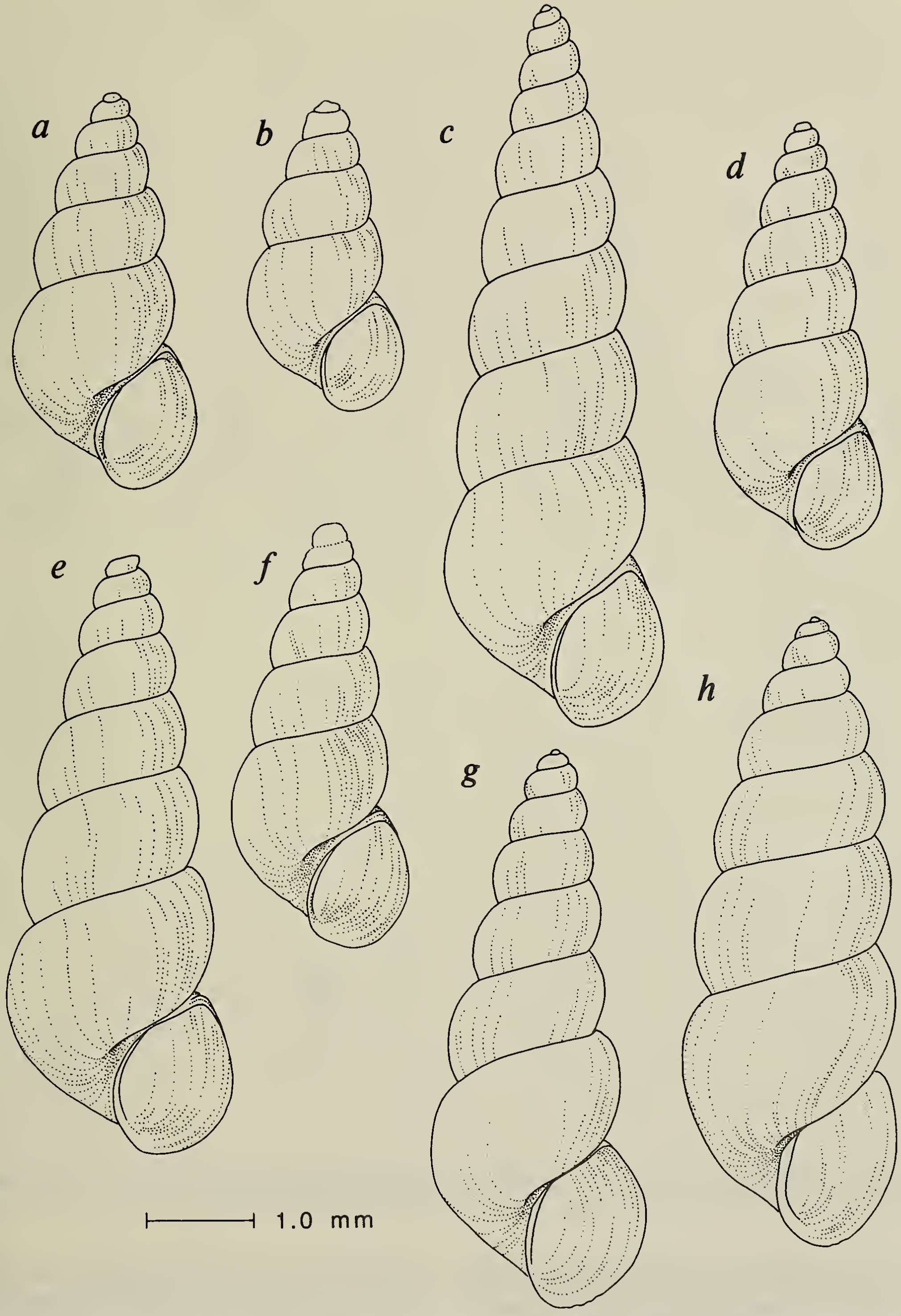


Fig. 45. Shells of *T. variegata*: a, b, Paratypes, USNM 859166, Five Springs; c, d, USNM 859168, Chalk Spring; e, f, USNM 859169, Mary Scott Spring; g, h, USNM 859175, North Scruggs Spring.

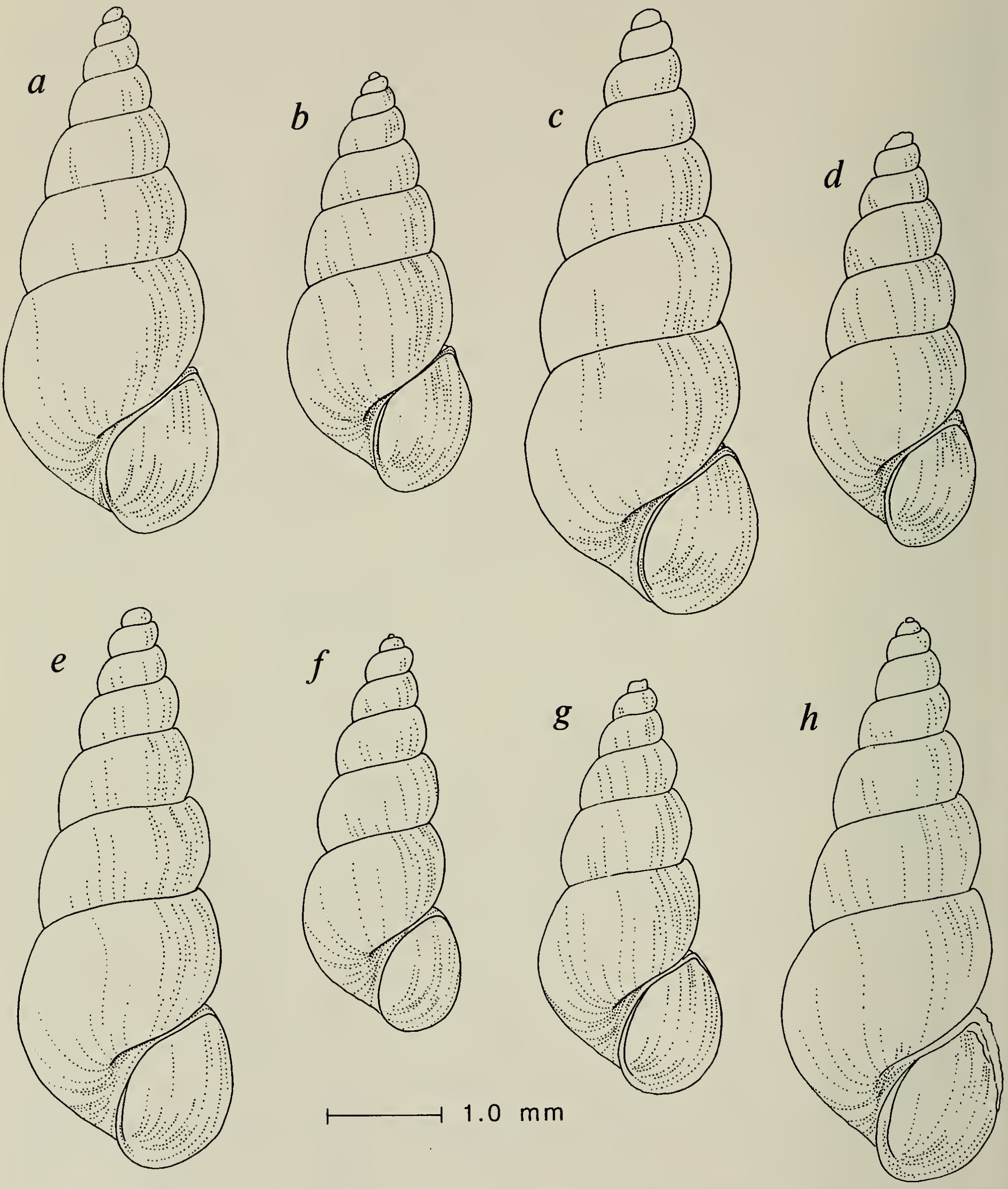


Fig. 46. Shells of *T. variegata*: a, b, USNM 859170, South Scruggs Spring; c, d, USNM 859171, Marsh Spring; e, f, USNM 859172, North Indian Spring; g, h, USNM 859173, School Spring.

tures. Elongation of shell reflected in high values of T varying from 5.3–21.7 (averaging 9.7). Whorls sometimes slightly shouldered; whorl outline unusually asymmetrical in one population (Figs. 39f, 48a, b), with abaxial point well below (rather than at) mid-point of whorl. Spire convex, with middle portion sometimes near-straight due

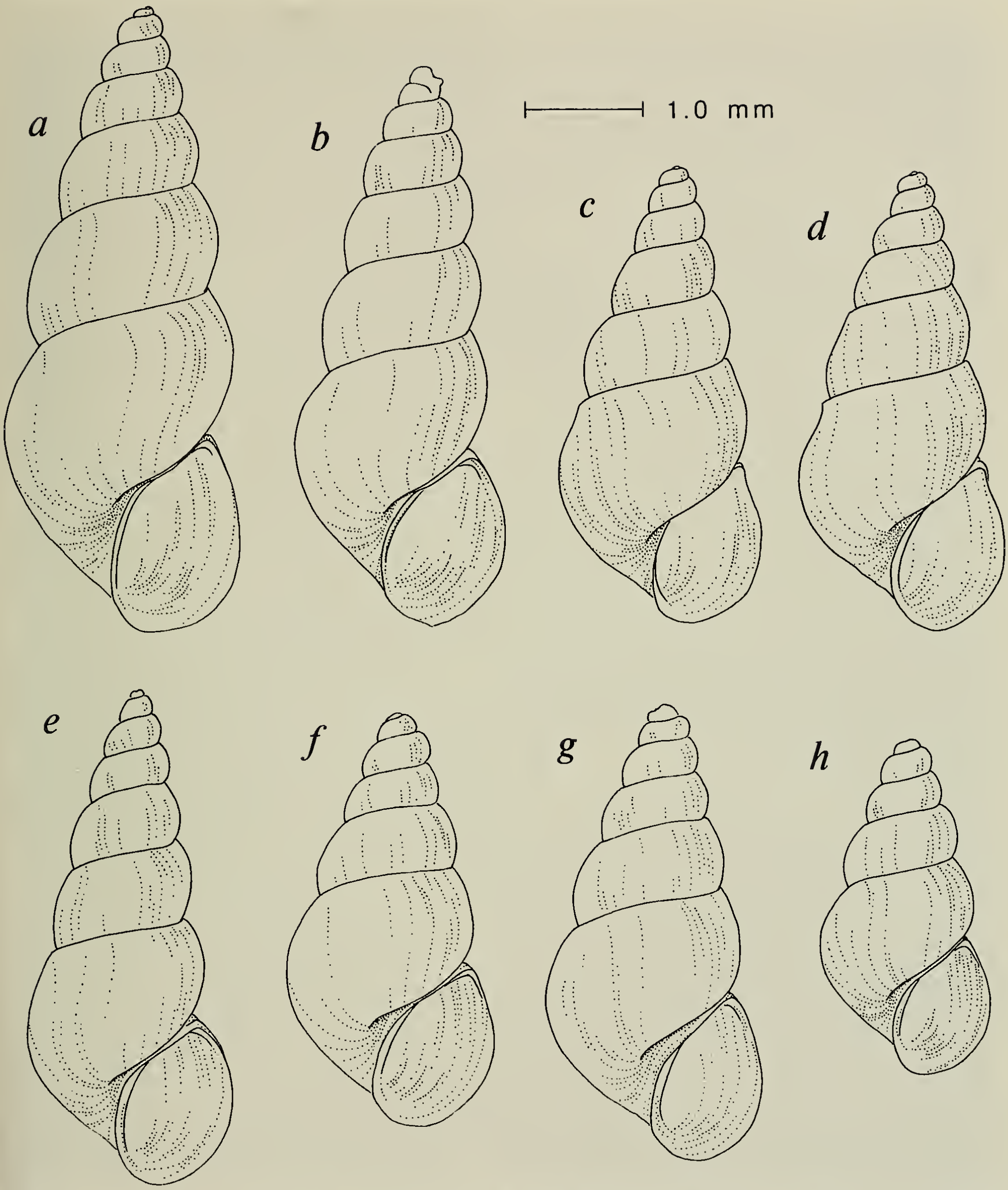


Fig. 47. Shells of *T. variegata*: a, b, USNM 859174, spring (western) near Crystal Reservoir; c, d, USNM 859176, spring (eastern) near Crystal Reservoir; e, f, USNM 859177, Point of Rocks Springs (Locality 38); g, h, USNM 859178, Point of Rocks Springs (Locality 39).

to little whorl expansion; apex often eroded. Body whorl ca. 50% of shell height. Shell colorless, transparent; periostracum thin, light brown. Aperture narrowly ovate, slightly angled above, often slightly loosened from body whorl (or with short adnate section). Inner lip slightly thickened, reflected below; outer lip thin. Umbilicus chink-

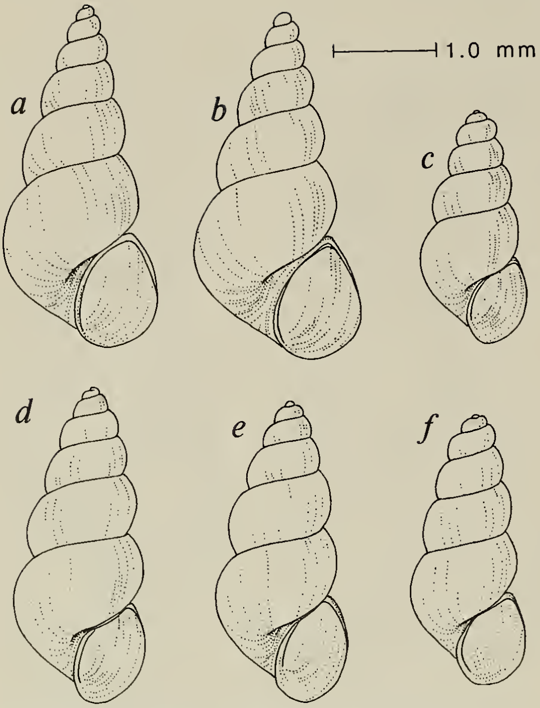


Fig. 48. Shells of *T. variegata*: a, b, USNM 859155, Devils Hole; c, d, USNM 859157, Collins Ranch Spring; e, f, USNM 859158, spring (southern) N of Collins Ranch Spring.

like to open. Growth lines pronounced; weak collabral threads or costae sometimes present.

Visceral coil darkly pigmented with melanin, especially on digestive gland and stomach. Snout and sides of head/foot usually darkly pigmented. Operculigerous lobe darkly pigmented internally. Penis frequently with small, distal pigment patch (Fig. 42b, e, h).

Radular (Figs. 49–52) formula: (4-7)-1-(4-7)/2-2, (3)4-1-5, 17–29, 22–30; width of central tooth, 0.023 mm. Penis (Fig. 42b, e, g, h) large: third distal papilla occasionally present on inner penial curvature. Median distal papilla often small, and likely representing an addition to common pattern of 2 distal lobes.

Type locality.—Five Springs, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Occurs in at least 19 small springs in Ash Meadows, Nye County, Nevada (Fig. 44), and in a few similar springs at Shoshone and Tecopa, Inyo County, California. Common at virtually all sites. Found on macrophytes, in detritus-covered areas, or on travertine blocks in springpools; and on travertine and in soft sediment along sides of upper portions of stream outflows.

Syntopic with *T. ericae,* n. sp. (described below) in North Scruggs Spring, and with *T. elata,* n. sp. (described below) in small spring at Point of Rocks.

Etymology.—From Latin *variegatus,* of different sorts, referring to variable shell of this species.

Comparisons.—Shell similar in general aspect to *T. protea* (Gould), but never exhibiting sculptural features characteristic of that species. Among Ash Meadows congeners, most similar to *T. angulata* (see above).

Remarks.—Species may be polytypic, as distinctive forms are found in Devils Hole (see above, Fig. 48a, b), in springs near Crystal Reservoir (shells highly aciculate, with collabral sculpture, Fig. 47a–d) and in a spring N of Collins Ranch Spring (unusually small-sized shells, Fig. 47c–f).

Tryonia ericae, new species
Minute Tryonia
Figs. 39c, d, 42f, i, 44, 53a–d, 54, 55

Minute slender Tryonia.—Sada and Mozejko, 1984: fig. 5.

Minute slender tryonia.—Taylor in Williams et al., 1985:43.

Material examined.—NEVADA, NYE COUNTY: North Scruggs Spring, 859162 (holotype), 859163 (paratypes), UF 93962 (paratypes), 850312, 9 Nov 1985.—Spring (northern) N of Collins Ranch Spring, 859165, 850313, 9 Nov 1985.

Diagnosis.—A very small-sized species with elongate-conic to turriform shell. Central teeth with 1 or 2 pair(s) of basal cusps.

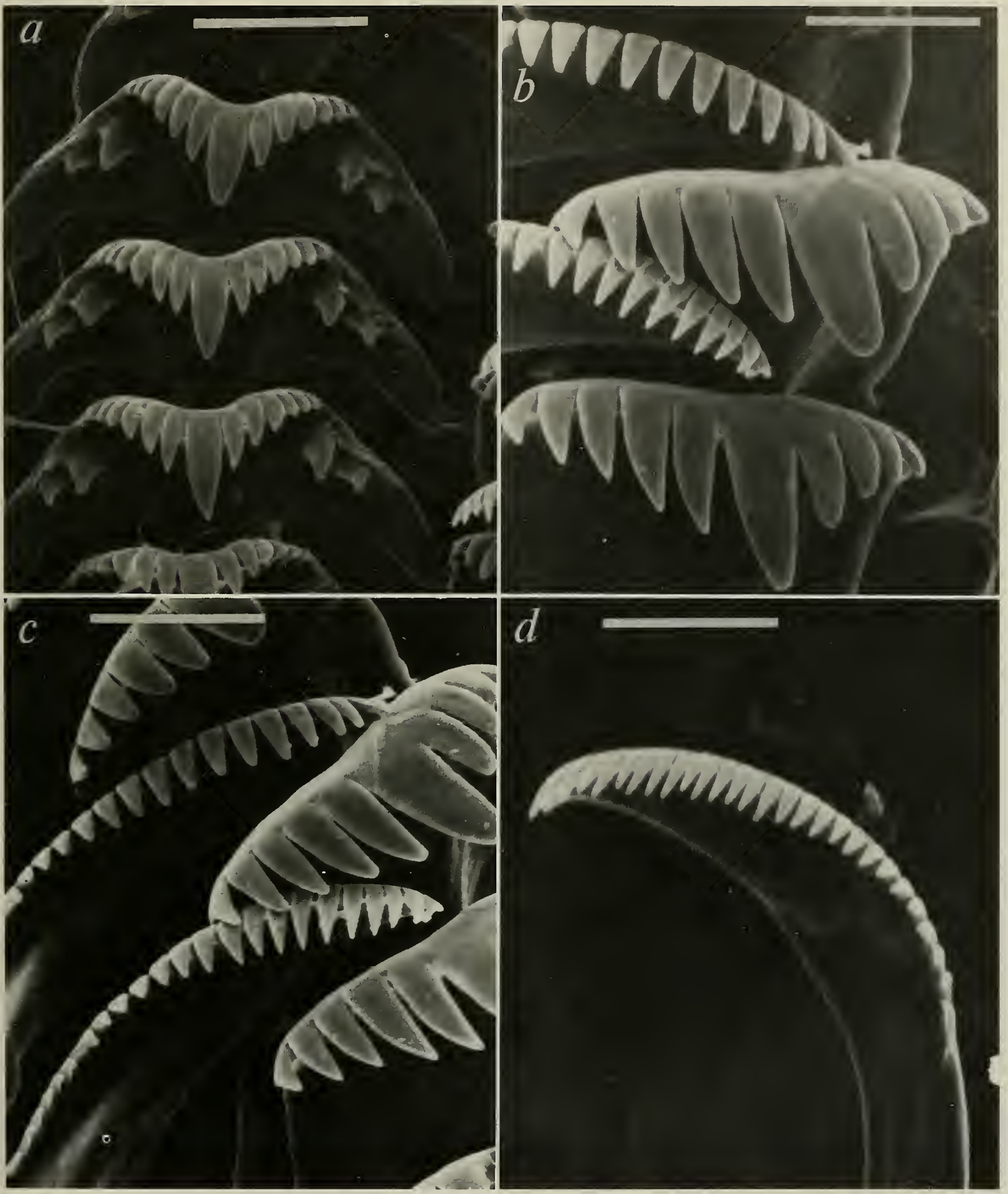


Fig. 49. Radula of *T. variegata,* USNM 850314, Five Springs: a, Centrals (bar = 7.5 μm); b, Laterals and inner marginals (bar = 5.0 μm); c, Laterals and inner marginals (bar = 6.0 μm); d, Outer marginal (bar = 4.3 μm).

Penis small, with 3 papillae (2 distal) on inner curvature.

Description.—Shell (Figs. 39c, d, 53a–d) 1.2–1.9 mm high, slightly less than twice as tall as wide. Whorls, 3.75–6.0 well-rounded, with deeply impressed sutures. Whorls sometimes shouldered below sutures. Translation rate moderate, ca. 5.8. Spire

Fig. 50. Radula of *T. variegata,* USNM 850325, spring (western) near Crystal Reservoir: a, Centrals (bar = 8.6 μm); b, Laterals (bar = 7.5 μm); c, Inner marginal (bar = 6.0 μm); d, Inner and outer marginals (bar = 6.0 μm).

slightly convex. Body whorl ca. 65% of shell height. Shell colorless, transparent; periostracum very faint, light brown. Aperture ovate, slightly angled above, usually slightly separated from body whorl. Inner lip thickened, slightly reflected; outer lip thin, straight or very slightly convex. Umbilicus chink-like. Growth lines moderately pronounced.

Fig. 51. Radula of *T. variegata,* USNM 850303, Devils Hole: a, Centrals (bar = 10 μm); b, Laterals and inner marginal (bar = 7.5 μm); c, Laterals and inner marginals (bar = 10 μm); d, Outer marginals (bar = 6 μm).

Visceral coil darkly pigmented. Head/foot usually lightly pigmented with grey-black melanin. Operculigerous lobe dark. Distal tip of penis with pigment patch.

Radular (Figs. 54, 55) formula: 6-1-6/(1)2-(1)2, 4-1-4(5), 20–25, 20–22; width of central tooth, 0.015 mm. Outer marginals with relatively few cusps (Figs. 54d, 55d). Distal penial papillae sometimes enlarged (Fig. 42f) relative to proximal papilla.

Fig. 52. Radula of *T. variegata,* USNM 850305, Collins Ranch Spring: a, Centrals (bar = 7.5 μm); b, Laterals and inner marginals (bar = 5 μm); c, Laterals and inner marginals (bar = 7.5 μm); d, Outer marginals (bar = 5 μm).

Type locality.—North Scruggs Spring, Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Endemic to two small springs, North Scruggs Spring and spring (northern) N of Collins Ranch Spring, within four km of one another at ca. 708 m elevation in Ash Meadows (Fig. 44). Common in small springpool of former, on various macrophytes, and in stream outflow of latter, on loose travertine bits and algal mats.

Etymology.—Named after spouse of senior author.

Comparisons.—Distinguished from *T. angulata* and *T. variegata* by much smaller size. Overlaps in adult size with *T. elata,* n. sp. (described below) and shares with this probable sister species unusual character-states of small penis (relative to body size), and (occasional in former) single pair of basal cusps on central radular teeth. Separable from *T. elata* by typically smaller size, less elongate shell, and more rounded whorls.

Tryonia elata, new species
Point of Rocks Tryonia
Figs. 39b, 42c, 44, 53e–h, 56

Material examined.—NEVADA, NYE COUNTY: Point of Rocks Springs (Locality 35), 859159 (holotype), 859160 (paratypes), UF 93963 (paratypes), 850309, 8 Nov 1985.—Point of Rocks Springs (locality 38), 850310, 859161, 8 Nov 1985.

Diagnosis.—A small-sized species, with narrow, turriform shell. Central teeth with single pair of basal cusps. Penis with 3 papillae (2 distal) on inner curvature.

Description.—Shell (Figs. 39b, 53e–h) 1.8–2.9 mm high, slightly more than twice as tall as wide. Whorls, 5.25–6.75, moderately rounded with impressed sutures and prominent shoulders below sutures. Translation rate high, averaging 8.9. Spire slightly convex, with middle whorls often exhibiting little expansion; apex often eroded. Body whorl about half shell height. Shell colorless, transparent; periostracum very faint, light brown. Aperture ovate, slightly angled above. Inner lip slightly thickened, reflected, either broadly adnate (above) to or slightly separated from body whorl; outer lip straight or very slightly sinuate. Umbilicus chink-like to open. Faint spiral lines often on second whorl. Growth lines well-developed, with periodic elevated lines common.

Visceral coil darkly pigmented. Head/foot variably dusted with epithelial melanin. Operculigerous lobe lightly pigmented internally. Distal penis with pigment patch.

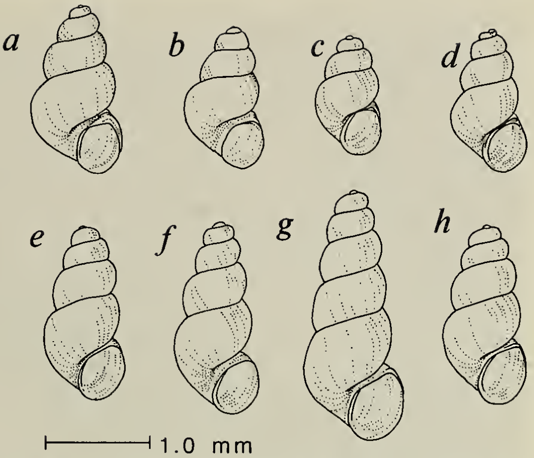


Fig. 53. Shells of *Tryonia* spp.: a–d, *T. ericae* (a, b, paratypes, USNM 859163, North Scruggs Spring; c, d, USNM 859165, spring (northern) N of Collins Ranch Spring); e–h, *T. elata* (e, f, paratypes, USNM 859160, Point of Rocks Springs [Locality 35]; g, h, USNM 859161, Point of Rocks Springs [Locality 38]).

Radular (Fig. 56) formula: 6-1-6/1-1, 4-1-4, 19, 23; width of central tooth, 0.015 mm. Penial lobation undistinctive (Fig. 42c).

Type locality.—Point of Rocks Springs (Locality 35), Ash Meadows, Nye County, Nevada.

Distribution and habitat.—Endemic to two small springs on travertine mound at Point of Rocks, Ash Meadows (Fig. 44). Common in stream outflows in silted areas.

Etymology.—From Latin *elatus,* exalted or high, referring to endemism of species on elevated mound at Point of Rocks.

Comparisons.—Most similar to *T. ericae* (see above).

Morphometrics

Significant heterogeneity among species occurred in all three groups for each standard shell measurement used (ANOVA, $P < 0.05$). However, for two of three groups several Raupian parameters did not vary significantly among species (Group II; T, AS, W, $P > 0.08$; Group III, D, W, $P > 0.27$).

Fig. 54. Radula of *T. ericae,* USNM 850312, North Scruggs Spring: a, Centrals (bar = 6 μm); b, Laterals (bar = 4.3 μm); c, Laterals, inner and outer marginals (bar = 5 μm); d, Outer marginals (bar = 3 μm).

Results of discriminant analyses are in Tables 4–6. Overall classification was 86–93% in analyses using standard shell measurements. In analyses using Raupian parameters, classification was 71% for Groups I and II, but only 48% for Group II. If classification of individual species is considered, classification based on standard measurements was higher (often by >20%) in every case, with values exceeding 80% for every species except *P. crystalis,* in which one of three shells measured was misclassified (67%

Fig. 55. Radula of *T. ericae,* USNM 850313, spring (northern) N of Collins Ranch Spring: a, Centrals (bar = 7.5 μm); b, Laterals and inner marginal (bar = 4.3 μm); c, Laterals (worn) and inner marginals (bar = 5 μm); d, Outer marginals (bar = 3 μm).

classification). Significant ($P < 0.05$) separation of closest groups was achieved in all three analyses using standard measurements, but only in one of three (for *Tryonia* spp.) using Raupian parameters.

For this local example, standard shell measurements were obviously superior to Raupian parameters in discriminating among the taxa concerned. Poor performance by the latter suggests that size or size-

Fig. 56. Radula of *T. elata,* USNM 850309, Point of Rocks Springs (Locality 35): a, Centrals (bar = 6.7 μm); b, Centrals and laterals (bar = 6.7 μm); c, Laterals and inner marginals (bar = 7.5 μm); d, Outer marginals (bar = 4 μm).

correlated features (as quantified by standard measurements) vary more among species involved than shape (alone) as quantified by Raupian parameters. Translation (T) and whorl expansion (W) rates, responsible for much shape variation among gastropods (Raup 1966), were not even selected in two of three stepwise discriminant analyses. In the analysis of *Tryonia* spp., T was incorporated into the discriminant equation

Table 3.—List of species groups with number of specimens and populations used in discriminant analyses. Mean shell height (mm) is given for each species.

Group and species	$\overline{SH}$	Number of specimens	Number of populations
I—*Pyrgulopsis fairbanksensis*	2.84	14	1
P. crystalis	2.04	3	1
P. erythropoma	2.09	68	5
II—*P. nanus*	1.82	43	3
P. pisteri	2.41	31	2
P. isolatus	2.94	13	1
III—*Tryonia variegata*	4.53	180	14
T. angulata	3.29	39	3
T. elata	2.10	30	2
T. ericae	1.47	19	2

and used to separate species differing in shell elongation. We feel that our determination of Raupian parameters was accurate enough to have discerned variation among species except in the possible case of W, although the simplified estimate used was able to detect differences between the two genera involved (see Tables 1 and 2).

Discussion

The uniformly high percentage of correct classification of species using standard shell measurements lends support to our species level decisions. *Pyrgulopsis* species are also distinguished by anatomical features (mostly penial morphology), with *Tryonia* species exhibiting lesser variation. Significant differentiation within the three groups can also be demonstrated by comparing shell variation among species with variation within *P. micrococcus*, a widespread species in Ash Meadows (not used in discriminant analyses). This was done by generating F values for each character, using variance among species as numerator and variance within *P. micrococcus* as denominator (data from ANOVA). For each group, significant heterogeneity of all variables occurred (F test, $P < 0.01$).

Clear morphological separation of species is also indicated in two cases of syntopy involving *T. variegata* and either of two congeners, *T. ericae* (North Scruggs Spring) and *T. elata* (spring at Point of Rocks). In each case, syntopic species differ significantly in size (shell height) and number of whorls (t test, $P < 0.05$), and there was no misclassification of specimens of either in discriminant analyses.

Origins of Ash Meadows springsnails are largely conjectural at this time not only because the regional fauna remains unstudied,

Table 4.—Results of discriminant function analyses on Group I (*Pyrgulopsis fairbanksensis, P. crystalis, P. erthropoma*) using standard and Raupian shell parameters. Variables listed in order of entry during analysis. Percent correct classification is given in parentheses.

Variables	Discriminant fn. coefficients		Standardized coefficients		Correlations	
	Fn. 1	Fn. 2	Fn. 1	Fn. 2	Fn. 1	Fn. 2
Standard (86)						
SW	−0.01	0.26	−0.62	3.34	0.88	0.46
LBW	0.01	−0.10	0.81	−1.46	0.96	0.16
AW	0.11	−0.22	0.82	−1.64	0.95	0.20
(Constant)	−7.48	−3.14				
C. correlation	0.70	0.36				
Raupian (71)						
D	−14.60	14.81	−0.71	0.72	−0.58	0.82
AS	12.06	8.55	0.82	0.58	0.71	0.70
(Constant)	−15.36	−9.24				
C. correlation	0.44	0.26				

Table 5.—Results of discriminant function analyses on Group II (*Pyrgulopsis nanus, P. pisteri, P. isolatus*) using standard and Raupian shell parameters. Variables listed in order of entry during analysis. Percent correct classification is given in parentheses.

Variables	Discriminant fn. coefficients		Standardized coefficients		Correlations	
	Fn. 1	Fn. 2	Fn. 1	Fn. 2	Fn. 1	Fn. 2
			Standard (93)			
LBW	0.01	−0.18	0.56	−1.35	0.94	−0.14
AW	0.01	0.36	0.02	1.61	0.83	0.51
AL	0.10	−0.01	0.50	−0.06	0.93	0.14
(Constant)	−13.44	−2.41				
C. correlation	0.92	0.44				
			Raupian (48)			
D	−11.39	13.94	−0.63	0.78	−0.59	0.81
AS	11.36	8.28	0.81	0.59	0.77	0.63
(Constant)	−13.40	−8.73				
C. correlation	0.30	0.14				

but also because phyletic relationships among taxa involved are not easily elucidated solely on the basis of morphological data provided by such phenotypically conservative snails. The highly endemic Ash Meadows fauna is probably an old one, with progenitors entering the area along with fishes during late Pliocene–early Pleistocene (Hubbs and Miller 1948, Smith 1978, Minckley et al. 1986). Faunal antiquity coupled with occurrence in a region having complex drainage history further clouds zoogeographic inquiry. Minckley et al. (1986:565) commented in this regard (while discussing fishes of the region), "It is important to understand that available time has provided ample opportunity for aquatic connections through most unlikely areas and that bits of evidence for such events may not be contemporaneous."

We recognize at least three lineages in the fauna, which includes apparent species flocks

Table 6.—Results of discriminant function analyses on Group III (*Tyronia* spp.) using standard and Raupian shell parameters. Variables listed in order of entry during analysis. Percent correct classification is given in parentheses.

Variables	Discriminant fn. coefficients		Standardized coefficients		Correlations	
	Fn. 1	Fn. 2	Fn. 1	Fn. 2	Fn. 1	Fn. 2
			Standard (86)			
SH	−0.01	−0.06	−1.35	2.43	0.55	0.74
WBW	−0.01	−0.11	0.97	−1.10	0.83	0.43
LBW	0.01	−0.10	0.93	−1.45	0.79	0.51
AL	0.01	0.10	0.23	0.86	0.85	0.48
(Constant)	−9.71	1.79				
C. correlation	0.89	0.62				
			Raupian (71)			
AS	4.95	−7.61	0.56	−0.86	0.65	−0.74
T	0.36	0.31	0.87	0.75	0.76	0.50
D	6.85	2.40	0.46	0.16	−0.07	−0.06
(Constant)	−10.14	8.76				
C. correlation	0.63	0.36				

(sensu Greenwood 1984:18) of *Pyrgulopsis* and *Tryonia* that may have arisen from local evolution. Local *Pyrgulopsis* is separable into (at least) two lineages, corresponding to endemic and non-endemic components. *Pyrgulopsis micrococcus,* restricted to Amargosa basin, has affinities with similar-shelled, undescribed forms occurring in Death Valley and other basins to the west. All other Ash Meadows *Pyrgulopsis* belong to an informal *Fluminicola*-like group. No known members of this group occur west of Amargosa basin and affinities of Ash Meadows forms apparently lie with fauna of either Amargosa or Colorado River drainage. Monophyly of this endemic component may be indicated by shared absence of fleshy penial crests (contrasting with taxa from southwestern Nevada). However, conflicting groupings based on shell form and habitat type versus soft-part and radular morphology suggest a more complex situation.

Ash Meadows *Tryonia,* including three endemic species plus *T. variegata* (which also occurs elsewhere in Amargosa drainage), are separable from other nominal congeners by penial lobation pattern, but quite similar to undescribed taxa from Death Valley. Given their morphological uniformity, local endemics are probably monophyletic and possibly derived from *T. variegata.*

Ash Meadows springsnails thus parallel local fish fauna in having affinities with taxa from both Death Valley System and Colorado River drainage: *Empetrichthys,* now extinct in Ash Meadows, also occurred in nearby Pahrump Valley, and is related to *Crenichthys* from southeastern Nevada; Ash Meadows pupfish (*Cyprinodon*) are related to forms occurring in lower Amargosa drainage and in Death Valley; local speckled dace (*Rhinichthys*) are members of a widespread species occurring in Amargosa and Owens Valleys (Soltz and Naiman 1978, Miller 1981, Minckley et al. 1986).

Springsnail distribution in Ash Meadows reflects divergent habitat utilization as well as possible local allopatric speciation. Most taxa occur in small springs and outflows although several *Fluminicola*-like *Pyrgulopsis* and *Tryonia angulata* are restricted to large spring pools. The former are obviously specialized for clinging to hard substrate in strong current (present at spring orifices).

The two nonendemic species are widespread in Ash Meadows, while endemics are more narrowly distributed (Figs. 25, 44). Distribution of closely related endemics suggests that local differentiation of taxa has occurred largely among disjunct habitats having a narrow range of altitude (note *Pyrgulopsis* of large springs [Fig. 25] and small-sized *Tryonia* spp. [Fig. 44]). Such a pattern is in contrast to that seen for local pupfishes, in which species are zoned by elevation. The Devils Hole pupfish, *Cyprinodon diabolis,* is endemic to the highest spring in Ash Meadows (741 m); Warm Springs pupfish, *C. nevadensis pectoralis,* occur in springs isolated at a lower elevation of 715 m; and Ash Meadows Amargosa pupfish, *C. n. mionectes,* occur in springs at elevations of 683–695 m elevation. Miller (1948) suggested that this pattern reflects local differentiation that occurred as springs at these elevations became progressively isolated as pluvial wetland receded, with the highly divergent Devils Hole pupfish having been isolated for the longest time period. Among springs, only the presumed sister species pair of *P. isolatus* and *P. nanus* (Fig. 25) provide a possible example of such differentiation along an altitudinal gradient. Distribution of springsnails in Ash Meadows must be interpreted with caution, however, given probable alteration of historical patterns due to extensive modification of aquatic habitats in the area.

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Appendix 1

Collection localities, numbered as in Figs. 5 and 6. Data (in parentheses, with subsets lacking for some sites) include location (from Ash Meadows Quadrangle, Nevada–California [1952], USGS 15 minute series [topographic]), water temperature, conductivity, dissolved oxygen, discharge, and elevation of site. Discharge estimated or from Dudley and Larson (1976) or Garside and Schilling (1979). Capsule habitat descriptions are provided, with notes on condition of site, springsnail deployment, and presence of native fishes and introduced biota.

1. Fairbanks Spring (NE ¼ Sec. 9, T17S, R50E; 27°C, 700 micromhos/cm, 3.5 mg/liter, 6500 liters/min, 695 m). Large limnocrene tributary to outflows from Rogers, Soda, Longstreet, and Five Springs in Carson Slough. Spring enlarged by heavy equipment; springpool now circular, approximately 15 m in diameter and four meters deep. Bordering vegetation a mixture of mesquite and salt grass. Submergent vegetation absent in springpool; cattails bordering much of pool perimeter and common in outflow. *Pyrgulopsis fairbanksensis* common, clinging to travertine at spring orifice; *T. angulata* common in soft substrate of outflow. Ash Meadows Amargosa pupfish present; speckled dace and poolfish extinct. Mosquito fish, red-rim melania, and crayfish abundant.

2. Soda Spring (NW ¼ Sec. 10, T17S, R50E, 22°C, 290 liters/min, 695 m). Moderate-sized, disturbed spring consisting of seemingly stagnant pool heavily

overgrown by salt cedar, willow, and mesquite. Seasonally tributary to outflow from Fairbanks Spring. Springsnails absent. Mosquito fish and red-rim melania abundant.

3. Rogers Spring (NE ¼ Sec. 15, T17S, R50E; 28°C, 700 micromhos/cm, 2.0 mg/liter, 2700 liters/min, 695 m). Deep limnocrene seasonally tributary to outflows from Soda, Longstreet, Fairbanks, and Five Springs in Carson Slough. Spring pool and outflow altered by heavy equipment; outflow contained in man-made channels. Springpool without submerged vegetation, but cattails and rushes dense along pool perimeter and in outflow. Springsnails absent. Ash Meadows Amargosa pupfish present in springpool, less common in outflows. Ash Meadows speckled dace and Ash Meadows poolfish extinct. Mosquito fish, crayfish, and red-rim melania present.

4. Spring 0.2 km S of Rogers Spring (SE ¼ Sec. 15, T17S, R50E; 12°C, 560, 4.3 mg/liter, <10 liters/min, 695 m). Northern-most of many small seeps (two containing springsnails) located along north-south bluff extending almost to Longstreet Spring. Spring isolated. Flow not evident, but small stringer maintained for approximately 75 m. Heavily overgrown by rushes. *Pyrgulopsis micrococcus* rare in soft mud at springsource.

5. Spring 0.3 km S of Rogers Spring (SE ¼ Sec. 15, T17S, R50E; 17°C, 780 micromhos/cm, 7.3 mg/liter, <10 liters/min, 695 m). Small, isolated seep similar to above, located along same bluff. Flow not evident, but discharge maintaining moist area of about 30 × 50 m. Heavily overgrown by rushes and saw grass. *Pyrgulopsis micrococcus* restricted to source area, moderately common.

6. Longstreet Spring (NE ¼ Sec. 22, T17S, R50E; 27°C, 700 micromhos/cm, 4.3 mg/liter, 4700 liters/min, 701 m). Large limnocrene impounded by meter high dike diverting outflow in two directions; both outflow channels man-made. Submergent vegetation absent in impoundment and outflows, but latter with dense cattails. Impoundment periphery dominated by salt grass, salt ceder, and cattail, with occasional mesquite. Springsnails absent. Ash Meadows Amargosa pupfish common; speckled dace extinct. Bullfrogs, mosquito fish, crayfish, and red-rim melania common.

7. Five Springs (NW ¼ Sec. 23, T17S, R50E; 32°C, 820 micromhos/cm, 3.1 mg/liter, 546 liters/min, 716 m). Complex of at least eight small springs; discharges combining to form outflow extending three kilometers to west. All springs channelized and diverted into earthen canals by heavy equipment. *Chara* sp. primary submergent vegetation; cattail dominant emergent. Salt grass and rushes border springs and outflows. *Pyrgulopsis nanus* and *T. variegata* common on all substrates in restricted small area of stream isolated from lower segment (having red-rim melania) by 0.75 m vertical drop probably created by equipment during spring development. Ash Meadows Amargosa pupfish and mosquito fish present.

8. Purgatory Spring (SW ¼ Sec. 14, T17S, R50E; 32°C, 820 micromhos/cm, 7.0 mg/liter, 87 liters/min [from well casing], 722 m). Small, isolated seep badly disturbed by wild horse activity. Discharge contained in narrow, shallow channel for about 10 m before spreading over area of about 75 × 75 m. Emergent vegetation, salt grass and rushes. *Pyrgulopsis micrococcus* restricted to and rare in submergent *Chara* sp. lining a small gauging box having cool (25°C) water.

9. Spring 1.0 km S of Five Springs (SW ¼ Sec. 23, T17S, R50E; 29°C, 740 micromhos/cm, 3.3 mg/liter, <10 liters/min, 716 m). Isolated seep with broad, shallow outflow extending about a kilometer. Disturbance minimal, although source likely deepened. Densely covered by rushes; bordered by salt grass. *Pyrgulopsis micrococcus* moderately common upstream, in soft substrate within dense rushes.

10. Cold Spring (SE ¼ Sec. 21, T17S, R50E; 284 liters/min, 683 m). Small spring on eastern border of and tributary to Carson Slough. Springsnails absent. Crayfish abundant.

11. Shaft Spring (NW ¼ Sec. 26, T17S, R50E; 26°C, 650 micromhos/cm, 3.2 mg/liter, 600 liters/min [est.], 719 m). Isolated spring with broad outflow densely covered by rushes and cattail. Flows for about 1.5 km to west. Appearance pristine although small abandoned mine near source. *Pyrgulopsis micrococcus* common on all substrates.

12. Chalk Spring (NW ¼ Sec. 26, T17S, R50E; 18.5°C, 700 micromhos/cm, 3.9 mg/liter, <10 liters/min, 719 m). Small isolated spring, located about 200 m S of Shaft Spring. Outflow less than 100 m long, spreading to cover area of about 25 × 75 m. Disturbed but restabilized: now covered by dense rushes and wild grape. *Tryonia variegata* and *P. micrococcus* common in soft substrate at source.

13. Mary Scott Spring (NW ¼ Sec. 35, T17S, R50E; 27°C, 750 micromhos/cm, 4.5 mg/liter, 600 liters/min [est.], 704 m). Isolated spring discharging from deep pool about 0.75 m in diameter and 1.0 m across. Spring diverted in past. Outflow channel well defined, extending 1.5 km; densely covered by shrub and mesquite. Rushes cover open areas. *Tryonia variegata* common in soft substrates in backwaters upflow; *P. nanus* common on travertine bits.

14. North Scruggs Spring (NE ¼ Sec. 35, T17S, R50E; 32°C, 810 micromhos/cm, 2.8 mg/liter, 227 liters/min, 710 m). Moderate-size spring located about 30 m from South Scruggs Spring: springs connected by man-made channels. Springpool and upper 50 m of deeply incised outflow overgrown by salt grass; lower areas modified and impounded. A two meter wide outflow channel extends 3 km to west. Channel densely covered by rushes and bordered by mesquite, ash trees, and shrub. *Pyrgulopsis pisteri* and *T. variegata* abundant near

source in vegetated areas. Warm Springs pupfish present.

15. South Scruggs Spring (NE ¼ Sec. 35, T17S, R50E; 32°C, 800 micromhos/cm, 2.8 mg/liter, 230 liters/min [est.], 710 m). Moderate-size spring with broad (1.5 m), shallow outflow densely vegetated by rushes. Spring manipulated and badly trampled by wild horses. Outflow extending three kilometers to west. Spring source with sparsely scattered rushes, bordered by salt grass. *Tryonia variegata* common in soft substrate and on submerged *Chara* sp. Warm Springs pupfish and mosquito fish present.

16. Marsh Spring (SE ¼ Sec. 35, T17S, R50E; 30°C, 700 micromhos/cm, 2.7 mg/liter, 600 liters/min [est.], 710 m). Isolated spring. Sourcepool 4.0 m across and 2.0 m deep. Source and upper 30 m of outflow undisturbed; below a small dike impounds flow, producing wet area about 50 × 30 m. Bordering vegetation primarily salt grass with some saw grass. Rushes sparse in stream; impoundment densely covered by cattails. *Tryonia variegata* abundant in soft substrate and *P. pisteri* common on travertine in areas with current. Warm Springs pupfish and bullfrogs present.

17. North Indian Spring (SE ¼ Sec. 35, T17S, R50E; 27°C, 780 micromhos/cm, 3.3 mg/liter, 400 liters/min [est.], 710 m). Moderate size spring: sourcepool 0.8 m wide and 0.3 m deep. Old diversion structures indicate past manipulation. Spring now restabilized and flowing in isolated, well-defined channel for about 3.0 km. Dense ash tree/mesquite thicket covers much of outflow; rushes thick in exposed areas of stream. *Tryonia variegata* common in soft substrate of uppermost 60 m of outflow. Warm Springs pupfish present. Mosquito fish restricted to lower reaches of stream.

18. South Indian Spring (SE ¼ Sec. 35, T17S, R50E; 28°C, 790 micromhos/cm, 3.8 mg/liter, 200 liters/min [est.], 710 m). Small spring with narrow outflow channel. Located 150 m south of North Indian Spring; springs isolated from one another. Disturbance not apparent, but proximity to above suggests probable past alteration. Outflow densely covered by rushes, with scattered ash trees, mesquite, and shrub. Seepage from Indian Springs maintaining one of few remaining ash tree/mesquite bosques in Ash Meadows. *Tryonia variegata* common in soft substrates of outflow channel. Warm Springs pupfish and mosquito fish present.

19. Mexican Spring (SE ¼ Sec. 35, T17S, R50E). Formerly a small pool that largely dried in 1973 (Soltz and Naiman 1978). Heavily overgrown by rushes; open water absent. Springsnails absent; Warm Springs pupfish extinct.

20. School Spring (SE ¼ Sec. 35, T17S, R50E; 32.5°C, 710 micromhos/cm, 3.2 mg/liter, 75 liters/min [est.], 715 m). Moderate size spring: sourcepool 1.0 m across and 3 cm deep. Current strong in narrow outflow. Spring altered in 1970's to increase pool habitat for Warm Springs pupfish. Additional pools constructed in 1981. Mesquite and shrub now reestablished at site. Rushes, cattail, and *Chara* sp. dense in springpool and outflow. *Tryonia variegata* common in soft sediments at spring source. Above common and *P. pisteri* rare in soft substrate of large (7.0 m across), cool (22°C) observation pond below spring. Warm Springs pupfish present.

21. Devil's Hole (SE ¼ Sec. 35, T17N, R50E; 32°C, 820 micromhos/cm, 3.2 mg/liter, no discharge, elevation, 741 m). A 4 × 17 m pool, deep to one side, without outflow. Lies 15 m below surrounding terrain in limestone cavern. Surrounding and emergent vegetation absent. Submergent vegetation on shallow shelf includes several species of filamentous algae. Water level temporarily lowered during period of local groundwater mining during 1970's. *Tryonia variegata* moderately common on large travertine blocks in shelf. Devils Hole pupfish and Devils Hole Warm Spring riffle beetle endemic to site.

22. Spring N of Collins Ranch Spring (NE ¼ Sec. 1, T18S, R50E; 31°C, 800 micromhos/cm, 3.1 mg/liter, 100 liters/min [est.], 710 m). Small spring with shallow outflow extending westward from north-south bluff originating near Collins Ranch Spring. Isolated from nearby Locality 23. Nearby rusted pipes suggest past alteration. Outflow a well defined channel bordered by shrub and ash trees, extending ca. 1.0 km. Rushes dense in sun-exposed areas. *Tryonia ericae* common in soft sediments and on algal mats.

23. Spring N of Collins Ranch, about 150 m S of Locality 22 (SE ¼ Sec. 1, T18S, R50E; 27°C, 650 micromhos/cm, 5.4 mg/liter, 75 liters/min [est.], 710 m). Small spring with shallow outflow extending 1.0 km to west. Spring and outflow densely covered by rushes, shrub, and wild grape; ash trees scattered along length. Scattered debris suggest past disturbance. *Tryonia variegata* and *P. micrococcus* common in soft mud beneath dense rushes, *P. nanus* rare.

24. Collins Ranch Spring (SW ¼ Sec. 1, T18S, R50E; 25.5°C, 700 micromhos/cm, 4.3 mg/liter, 40 liters/min, 707 m). Several small springs on ranch, but only eastern-most seep occupied by springsnails. Diversion structures and nearby building foundations indicate past modifications. Broad, shallow outflow densely covered by rushes, flowing 75 m. Scattered ash trees, shrub, and mesquite provide little shade. *Pyrgulopsis nanus* and *T. variegata* common in mud and on travertine bits along outflow margins.

25. Crystal Pool (NE ¼ Sec. 3, T18S, R50E; 27°C, 870 micromhos/cm, 3.9 mg/liter, 11,000 liters/min, 668 m). Large limnocrene about 5.0 m deep and 15 m across. Although pumped during 1970's for irrigation, springpool appears undisturbed. Outflow channelized and impounded. Historically tributary to Carson Slough and therefore seasonally connected to outflows from Fairbanks, Rogers, Longstreet, Five, Big, and Jack Rabbit Springs. Springpool bordered by rushes, sedges (primarily *Scirpus robustus*), and salt grass. Outflow

heavily overgrown with cattails. Submergent vegetation, filamentous algae. *Pyrgulopsis crystalis* extremely rare, located on less than 1 m^2 of travertine in strongly voided water at orifice. *Tryonia angulata* abundant in soft substrate throughout springpool. Ash Meadows Amargosa pupfish present, Ash Meadows speckled dace and Ash Meadows poolfish extinct. Bullfrogs, mosquito fish, sailfin mollies, crayfish, and red-rim melania abundant in spring and outflow.

26. Spring N of Clay Pits (SE ¼ Sec. 6, T18S, R50E; 10°C, 580 micromhos/cm, < 10 liters/min [est.], 652 m). Isolated small seep in west side of Carson Slough, flowing to east for about 50 m. Some evidence of past alteration by heavy equipment to enhance discharge. Densely covered by rushes. Several mesquite shrubs scattered along outflow. *Pyrgulopsis micrococcus* common in mud.

27. Spring at Clay Pits (SW ¼ Sec. 6, T18S, R50E; 13°C, 500 micromhos/cm, 50 liters/min [est.], 658 m). Isolated spring lying in 70 × 150 m pit created for clay mining. Wetland vegetation supported by spring and outflow includes salt grass, cattail, and rushes. Outflow extending 1.0 km to north. *Pyrgulopsis micrococcus* common on *Chara* sp. in outflow channel.

28. Spring S of Clay Pits (NE ¼ Sec. 7, T18S, R50E; 7°C, 430 micromhos/cm, 400 liters/min [est.], 658 m). Isolated spring W of Carson Slough. Discharge from large, 50 × 50 m area enclosed in (artificial?) pit surrounded by 2.0 m high travertine walls. Character of site seemingly natural, although slightly impacted by grazing horses. Outflow extends to south for 100 m before spreading to form a 0.5 ha wetland. Spring source bordered by salt grass and rushes; *Chara* sp. abundant. Emergent cattails in outflow; wetland vegetated by bunch grass. *Pyrgulopsis isolatus* moderately common along pool perimeters in spring area, extremely common on rocks in outflow, absent from wetland; *P. micrococcus* rare.

29. Spring near Crystal Reservoir (NW ¼ Sec. 11, T18S, R50E; 16°C, 700 micromhos/cm, 3.0 mg/liter, 200 liters/min [est.], 665 m). Marshy area watered by discharge from well casing atop a spring-mound densely covered by rushes. Scattered debris indicates past disturbance. Outflow tributary to that of Locality 30, and extending 1.0 km to south and then west toward Crystal Reservoir. *Tryonia variegata* common and *Pyrgulopsis micrococcus* very rare in soft substrate.

30. Spring 200 m east of Locality 30 (NW ¼ Sec. 11, T18S, R50E; 19°C, 730 micromhos/cm, 4.4 mg/liter, 400 liters/min [est.], 665 m). Habitat similar to above; outflows combine to create 2.0 ha wetland dominated by rushes and sedges. Spring source altered by heavy equipment during agricultural development. Outflow channel 2.0 m wide and shallow. *Pyrgulopsis micrococcus* common on watercress; *T. variegata* common in soft sediments.

31. Bradford Springs (SE ¼ Sec. 11, T18S, R50E; 21.5°C, 850 micromhos/cm, 3.2 mg/liter, 1700 liters/min [est.], 684 m). Site includes three adjacent springs formerly flowing westward. Springs now altered and connected by earthen canal capturing flow from Point of Rocks Springs (Localities 34–40) and extending southward to spread over land cleared and leveled for agriculture. Site remains badly degraded. Spring sources populated by cattails; canal with filamentous algae. Springsnails absent from single (middle) spring examined. Ash Meadows Amargosa pupfish and Ash Meadows speckled dace present in springs and canal. Bullfrogs, mosquito fish, sailfin mollies, red-rim melania, and crayfish abundant.

32. Tubbs Spring (SW ¼ Sec. 12, T18S, R50E; 600 liters/min [est.], 684 m). Small springpool lying 2.0 m below surrounding terrain; outflow tributary to Bradford Springs through small pipe. Spring altered during clearing of land for agriculture: surrounding vegetation now consisting of weeds. Cattails surrounding springpool. Although not sampled, site's degraded condition suggests absence of springsnails.

33. Forest Spring (SW ¼ Sec. 7, T18S, R51E; 22°C, 660 micromhos/cm, 6.8 mg/liter, 0.0 liters/min, 698 m). Spring greatly altered during agricultural development, now surrounded by salt cedar. Springsnails absent. Ash Meadows Amargosa pupfish, Ash Meadows speckled dace, and Ash Meadows poolfish extinct. Bullfrogs, mosquito fish, sailfin mollies, red-rim melania, and crayfish present.

Point of Rocks Springs (Localities 34–40; SE ¼ Sec. 7, T18S, R51E). Site altered a number of times during agricultural and municipal development. Many small springs now inundated by series of four ponds constructed in 1982, with Localities 35–40 representing springs remaining above impoundments. Discharge from Point of Rocks Springs historically flowed for 3.0 km in braided channels to southwest through a mesquite bosque, without surface connection to other springs. Outflows from Localities 34–37 now combined in ponds, which feed King's Pool and then connect with Bradford Springs via artificial channel.

34. King's Pool (30°C, 810 micromhos/cm, 3.1 mg/liter, 4500 liters/min, 701 m). Largest and westernmost of Point of Rocks Springs with single discrete orifice at SE corner of pool. Size, depth, and configuration of pool changed several times during agricultural and municipal development. Surrounding vegetation primarily salt cedar and cattails; mesquite and yerba mansa (*Anemopsis californica*) also present. Submergent vegetation, filamentous green algae. *Pyrgulopsis erythropoma* restricted to small area at orifice, abundant on travertine. Ash Meadows Amargosa pupfish present; Ash Meadows speckled dace and Ash Meadows poolfish extinct. Bullfrogs, sailfin mollies, mosquito fish, red-rim melania, and crayfish present.

35. Spring about 150 m east of King's Pool (32°C, 810 micromhos/cm, 5.0 mg/liter, 450 liters/min [est.], 705 m). Small rheocrene emerging from crevice and flowing southward through limestone trough before

cascading down 15 m embankment and entering artificial pond. Habitat appears pristine. Outflow 0.5 m wide, several centimeters deep; bordered by salt grass and rushes. *Pyrgulopsis erythropoma* common on travertine; *T. elata* common in soft sediments in limestone trough.

36. Spring about 60 m east of Locality 35 (29°C, 790 micromhos/cm, 6.0 mg/liter, 450 liters/min [est.], 705 m). Similar, pristine-appearing rheocrene also cascading southward down narrow channel into artificial pond. Channel 0.2 m wide, 15 m long, several centimeters deep; bordered by saw grass, salt grass, and rushes. *Pyrgulopsis erythropoma* abundant on stones.

37. Spring 30 m east of Locality 36 (30°C, 680 micromhos/cm, 6.6 mg/liter, 450 liters/min [est.], 705 m). Very swiftly flowing rheocrene. Outflow 15 m long and 0.2 m wide, cascading southward into artificial pond. Outflow disturbed during pond construction in 1982, but habitat regained natural character. Bordering vegetation similar to that found at Localities 35 and 36, with addition of scattered mesquite. *Pyrgulopsis erythropoma* abundant on travertine.

38. Seep 100 m N of Locality 35 (28°C, 700 micromhos/cm, 7.1 mg/liter, <10 liters/min [est.], 707 m). Seep watering area of 2 × 10 m. Site modified by backhoe in past; currently impacted by wild horse activity. Rushes and *Chara* sp. dominate as emergent and submergent vegetation, respectively. Salt grass, scattered mesquite, and wild grape enclose downflow portions of site (and those of Localities 39 and 40). *Tryonia elata* and *T. variegata* common in mud; *P. erythropoma* rare.

39. Spring 4.0 m N of Locality 38 (30°C, 780 micromhos/cm, 6.5 mg/liter, 75 liters/min [est.], 707 m). Seep with small outflow extending 5.0 m to west; densely covered by rushes. Site regained stability following past backhoe disturbance. *Tryonia variegata* common in mud; *P. erythropoma* rare on travertine.

40. Spring 7.0 m N of Locality 39 (32°C, 810 micromhos/cm, 6.1 mg/liter, 45 liters/min [est.], 707 m). Swiftly flowing rheocrene; outflow a well defined channel extending 5.0 m. Site in good condition despite past alteration by heavy equipment. Bordering vegetation matches that for Localities 37–39. *Pyrgulopsis erythropoma* abundant on travertine.

41. Jack Rabbit Spring (NW ¼ Sec. 18, T18S, R51E; 27°C, 870 micromhos/cm, 3.9 mg/liter, 2500 liters/min, 692 m). Large limnocrene temporarily dried by pumping during early 1970's. Outflow extending about 5.0 km in well defined channel before converging with that from Big Spring. Will seasonally connect with waters from Fairbanks, Rogers, Longstreet, Soda, Five Springs, and Crystal Pool in Carson Slough. Ash Meadows Amargosa pupfish and Ash Meadows speckled dace now reestablished. Bullfrogs, red-rim melania, and crayfish present (Williams and Sada 1985).

42. Big Spring (NE ¼ Sec. 19, T18S, R51E; 26°C, 850 micromhos/cm, 3940 liters/min, 683 m). Large limnocrene about 20 m across and 7.0 m deep. Outflow channelized and used for irrigation, but spring otherwise undisturbed. Bordering vegetation includes salt grass, saw grass, and bunch grass. Mesquite and salt cedar scattered along outflow. Filamentous green algae moderately common in springpool and outflow; cattails also in latter. *Tryonia angulata* scarce in springpool and outflow. Ash Meadows Amargosa pupfish and Ash Meadows speckled dace present; Ash Meadows poolfish extinct. Bullfrogs, mosquito fish, sailfin mollies, and crayfish present (Williams and Sada 1985).

43. Brahma Spring (NW ¼ Sec. 29, T18S, R51E; 50 liters/min [est.], elevation, 693 m). Isolated site badly degraded by horse grazing to point of no longer resembling natural spring. Springsnails absent.

44. Bole Spring (NE ¼ Sec. 30, T18S, R51E; 45 liters/min [est.], 686 m). Spring in same condition as above. Springsnails absent; crayfish present.

45, 46. Frenchy Springs (NW ¼ Sec. 30, T18S, R51E; 16°C, 410 micromhos/cm, < 10 liters/min [est.], 686 m). Six isolated seeps occupying area in which small ponds (about 1.5 m deep and 2.5 m^2 area) created by heavy equipment. Site trampled by wild horses. Mesquite, salt grass, and rushes border seeps; ponds covered by duck weed (*Lemmna* sp.). *Pyrgulopsis micrococcus* present and moderately common in two seeps, in mud of shallows well vegetated by rushes.

47. Last Chance Spring (Center Sec. 30, T18S, R51E; 16°C, 520 micromhos/cm, 3.9 mg/liter, <10 liters/min, 684 m). Seep flowing about 5.0 m before entering dense wild grape/mesquite thicket. Site badly trampled by wild horses. *Pyrgulopsis micrococcus* and *T. variegata* common in mud and on emergent vegetation.

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STUDIES IN THE *LEPIDAPLOA* COMPLEX (VERNONIEAE: ASTERACEAE). III. TWO NEW GENERA, *CYRTOCYMURA* AND *EIRMOCEPHALA*

Harold Robinson

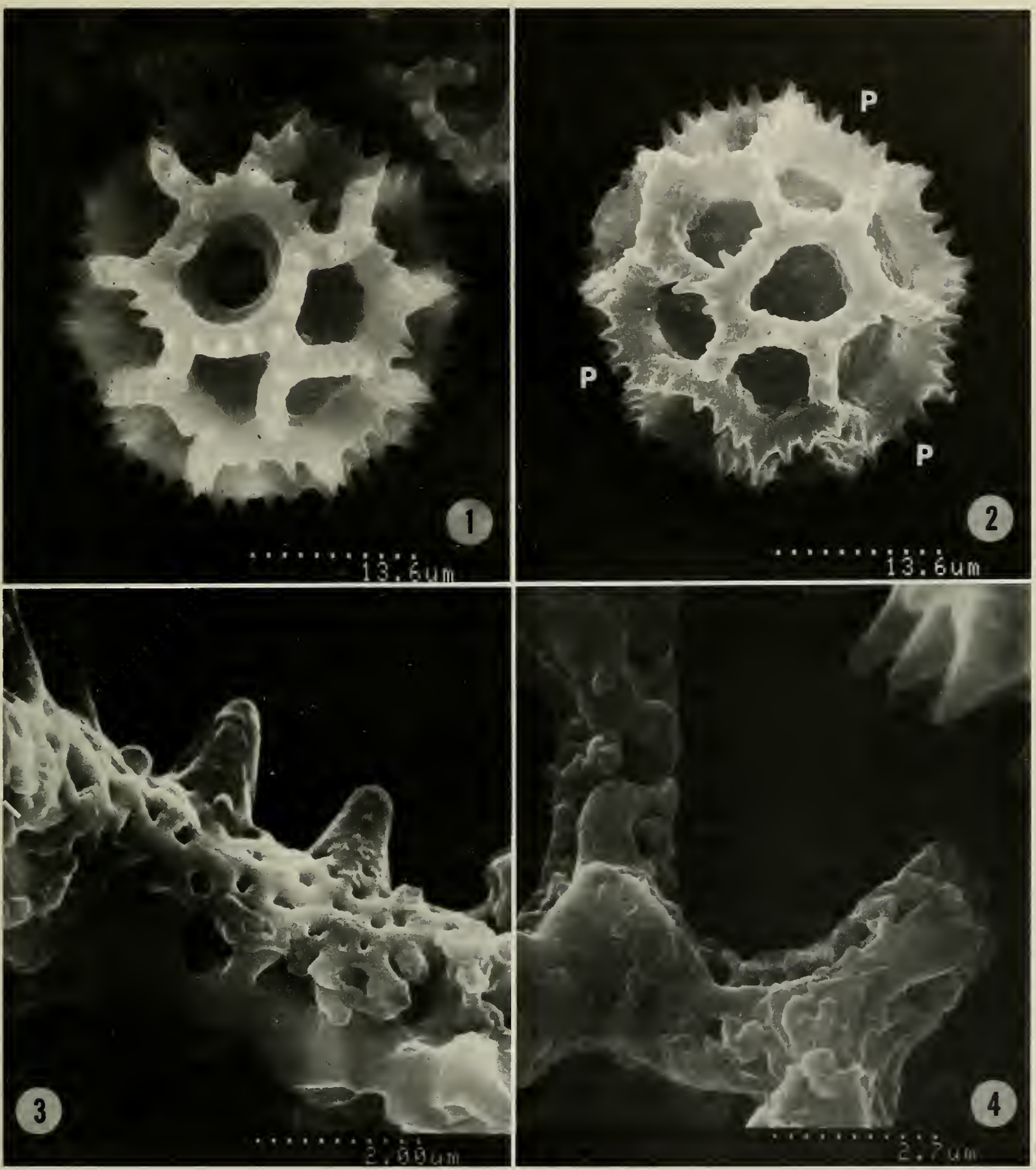
Abstract.—The *Vernonia* series *scorpioides* proves to consist of at least three distinct elements. The elements showing strongly scorpioid tips on their cymes are recognized as two new genera, the *V. scorpioides* group as *Cyrtocymura* and the *V. brachiata* group as *Eirmocephala.* The two differ in the bases of their leaves, persistence of their heads, structure of their pappus bristles, elaboration of the bases of their anther thecae, and surface of their achenes. The latter genus also shows an isolated occurrence of rhizomatous lophate pollen in one species. The rejection of the previous arbitrary selection of *V. scorpioides* as lectotype of *Lepidaploa* is confirmed.

The present paper continues a series of studies aimed at the resolution of the *Lepidaploa* group in the tribe Vernonieae. This study deals with a group that has been consistently associated with *Lepidaploa* due to its scorpioid cymes, and which is also nomenclaturally entwined with the latter genus. One of the species also shows the rhizomatous lophate pollen form that is otherwise unique to the *Lepidaploa* complex. The actual interrelationships of the scorpioid group need careful revision, and some of the species concepts have proven to need correction.

Historically the scorpioid group has been closely tied to the name *Lepidaploa. Vernonia scorpioides* was one of the seven species included by Cassini in 1823 in his subgenus *Lepidaploa.* Unfortunately, *V. scorpioides* was the first listed. In spite of the fact that it is generically distinct from the other species and is very unrepresentative of the series, four of which form a related group, it was later arbitrarily and rather incidentally selected as lectotype of the genus by Gleason (1906:162). The lectotypification was overturned and the more appropriate *V. albicaulis* Pers. was selected by Robinson et al. (1980). Many lectotypifications such as that made by Gleason have had to be overturned because they were made strictly on the basis of first-listed even if they were totally unrepresentative of the original concept. In the present concept, *V. scorpioides* is not the lectotype of *Lepidaploa,* or congeneric with the latter genus, and it is the type of a new and distinct genus of Vernonieae.

Both the names *Lepidaploa* and *Scorpioideae* have become widely used for subgroups of *Vernonia,* the former as the broader concept with *Scorpioideae* as a subgroup. Both concepts were applied so widely as to be undefinable, as seen in Baker (1873), where the *Scorpioideae* included such diverse species as *V. geminata* Less., *V. platensis* Less., *V. tweedieana* Baker, *V. westiniana* Less., *V. mariana* Mart., and *V. eupatoriifolia* DC.

The refined concept of the series *Scorpioides* of Jones (1979), provided the first sound basis for discussion of the group. The species included are *V. cainarachiensis* Hieron., *V. diffusa* Less., *V. ignobilis* Less., *V. megaphylla* Hieron., and *V. scorpioides* (Lam.) Pers. cited with type A pollen (Figs. 5–12), and *V. brachiata* Benth. cited with type D pollen (Figs. 1–4), using the pollen



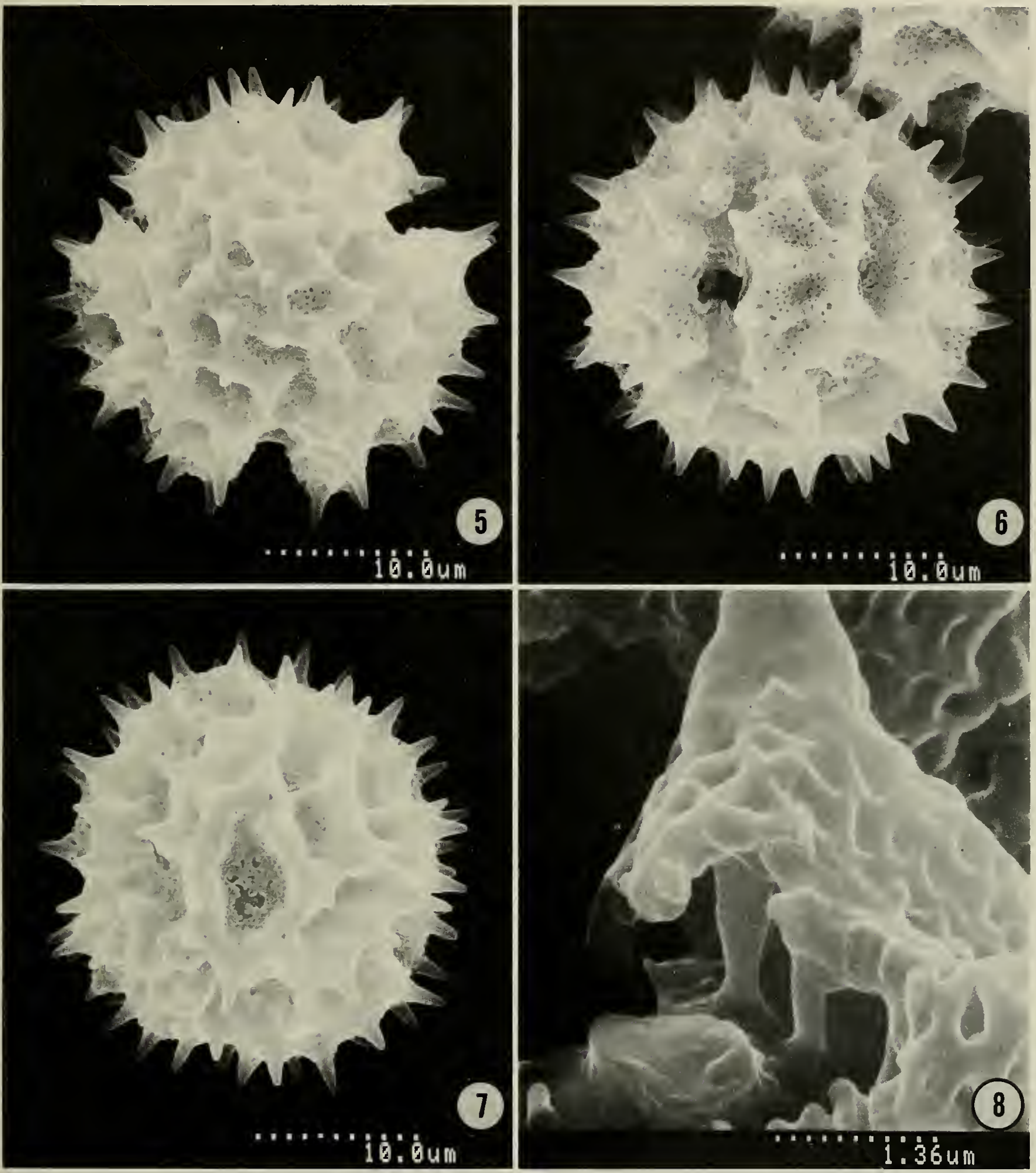
Figs. 1–4. Pollen of *Eirmocephala brachiata* (Bentham ex Oersted) H. Robinson. 1, 2, Dotted lines = 13.6 μm; 3, dotted line = 2 μm; 4, dotted line = 2.7 μm. 1, Whole grain showing colpus with crosswalls above and below pore; 2, Polar view showing polar areole, P marks positions of pores; 3–4, Crests of exine stripped from foot layer showing rhizome and weak basal attachments.

types defined by Jones (1979). With the exception of the unrelated *V. ignobilis,* all the species listed show the uninterrupted cymose branches that have lost all trace of their basically proliferated nature. All of these have reason to be considered as a possibly closely related group.

The seriate-cymose condition is particularly well-developed in the general section *Lepidaploa,* and reaches its extreme in the present series. This character has been the primary reason for the continuing close association between the groups. In both groups the cymose branches have to be recognized as an evolutionary derivative of a repeatedly proliferating branching series, each segment of the branch being technically a lateral innovation from below the preceding head. Only in this way is the sequence of maturation of the heads maintained from the base upward. In true *Lepidaploa* the original form is more obvious and some deflection of the branch at each head is often evident. This is true even in such species as *V. geminata,* which has the subtending bracts reduced and only partially displaced laterally. In the more restricted *Scorpioides* group all trace of the innovating basic structure is lost, and the subtending bracts are shifted almost completely to one side. The two rows of heads are nearly fused into one. The branch appears as one continuous rachis and the tip is sometimes truly scorpioid as in a Boraginaceous inflorescence. The inflorescence of the scorpioid group must be considered one of the most highly derived forms in the Vernonieae; it is undoubtedly derived from the more generalized type of *Lepidaploa* inflorescence, which is distributed more widely in the tribe than the immediate *Lepidaploa* complex.

The series *Scorpioides* has one marked distinction from the true *Lepidaploa* complex in its pollen. The character presents several problems in interpretation, but the *Lepidaploa* complex is one of the largest groups in the Vernonieae that has almost consistently lophate-pollen, while the series *Scorpioides* has type A pollen in all but one species. The one example is not particularly close in any other character to *Lepidaploa* and does nothing to support the idea of close relationships between the groups. The least specialized of the species listed by Jones (1979) is *V. diffusa,* and that species has type A pollen like the large related series containing such species as *V. patens* H.B.K., *V. tweedieana, V. brasiliana* Druce, and *V. polyanthes* Less. If the type A pollen is a reversion type as now seems likely in the Vernonieae (Robinson and Kahn 1986), the reversion seems to have occurred before the origin of the series *Scorpioides.*

The one example of type D pollen in the series *Scorpioides* does require an explanation. The pollen of *V. brachiata* is not just lophate (Figs. 1, 2), but is the rhizomatous type that otherwise seems to be restricted in the tribe to the true *Lepidaploa* complex (Figs. 3, 4). The pollen type will be discussed more fully in the treatment of *Lepidaploa.* The pollen is totally unlike that seen in other members of the series *Scorpioides,* such as *V. megaphylla* (Figs. 5–8) and *V. scorpioides* (Figs. 9–12). This occurrence of rhizomatous lophate pollen in *V. brachiata* cannot be a relict, but other explanations also encounter difficulties. The general distribution of pollen types in the group does not suggest the degree of instability of types that is found in such genera as *Distephanus* (Robinson and Kahn 1986), although something certainly caused instability within the limited relationship of *V. brachiata.* Hybridization is personally regarded as a major factor in the evolution of the American Vernonieae. However, *V. brachiata* does not show the degree of difference from its close relatives, especially *V. megaphylla,* that would be expected if hybridization with a remote relative were involved in one species and not the others. The present conclusion is that the group of three species shares a hybrid history between an ancestor more like *V. diffusa* and one that was a *Lepidaploa.* The resulting hybrid could have the instability of pollen characters that on further evolution distributed differently to the derived species. There are many members of *Lepidaploa* in the geographical area of the *V. brachiata* group that could have furnished the genes for rhizomatous lophate pollen with polar areoles (Figs. 1–4). SEM views of the pollen of *V. megaphylla,* although it is type A, give further support to the hybrid ancestry for the



Figs. 5–8. Pollen of *Eirmocephala megaphylla* (Hieron.) H. Robinson. 5–7, Whole grains, dotted lines = 10 μm; 5, Polar view showing irregularity and areole at pole; 6, Colpar view showing variable sizes of areoles in adjacent intercolpus; 7, Oblique view showing intercolpus, pole at lower end of large areole; 8, Broken surface, dotted line = 1.36 μm, showing two smaller basal columellae and large scar of central columella of missing spine.

group by showing structures interpreted as polar areoles (Fig. 5). The latter character is found in the regularly lophate grains of *V. brachiata,* but is lacking from the type A grains of *V. scorpioides* (Fig. 9) of the nonhybrid group. Light microscope examination of some *V. cainarachensis* pollen also shows evidence of such irregular polar areoles.

The probable existence of a hybrid ancestry with *Lepidaploa* for only part of the series *Scorpioides* raises the question of other possible evidence of disunity in that group. Initially it can be noted that the differences between the two main groups of the series, recognized here as genera, the *V. scorpioides* group (*Cyrtocymura*) and the *V. brachiata* group (*Eirmocephala*), cannot be accounted for simply by the hybridization of the latter with *Lepidaploa.* It should also be noted that the third group involved, *V. diffusa* shows clear evidence of relationship to the large and widespread *V. patens-V. brasiliana* group. Finally it must be noted that the *V. brachiata* (*Eirmocephala*) and *V. scorpioides* (*Cyrtocymura*) groups each show more characters in common with the *V. diffusa* than with each other. The characters involved include the leaf bases, persistence of heads, corolla form, anther bases, resiniferous cells on the achene surface, carpopodium, and pappus.

In *Eirmocephala,* in all but a few specimens of *E. cainarachiensis,* the lamina of the leaf extends as a wing to the base of the petiole. Even where it is narrowed at the base it broadens again at the insertion. This differs from both *Cyrtocymura* and *V. diffusa,* where the petiole is always distinct and often long. This is one character in *Eirmocephala* that may trace to a *Lepidaploa* parentage. The leaves of the latter genus are characteristically sessile or short-petiolate, although not with the winged or pseudopetiolate form seen in *Eirmocephala.*

The tendency for whole older heads on the cymose branches to dehisce is restricted in the groups under discussion to *Cyrtocymura.* The older branches ultimately become completely bare except for the single small bract at the base of each head. The loss of heads limits the ability to check old receptacles on the specimens. The condition is regarded as a specialized characteristic of the genus.

The corolla lobes of *Cyrtocymura* seem characteristically more erect and less distorted than those of the other groups under discussion. *Eirmocephala* and the *V. diffusa* group seem to have more recurved or distorted lobes on the open corollas. The corolla lobes of *Cyrtocymura* also have rather distinctive sericeous pilosity on the outer surface in all but one species, the latter being an evident reversion.

In *Eirmocephala* the bases of the anther thecae are sclerified and form dentate appendages. In this respect the genus falls outside the technical limits of traditional *Vernonia,* but the character has been widely ignored by previous students of the tribe. The anther bases of *Eirmocephala* may relate the genus to *V. diffusa,* where strongly developed sclerified appendages are also present. Similar basal appendages also occur in close relatives of *V. diffusa,* such as *V. discolor* Less. and *V. piresii* H. Robinson, but they do not occur in most other members of that group, such as *V. patens* or *V. brasiliana.* There are no sclerified cells at the base of the thecae in *Cyrtocymura.* In contrast, the tissue is very indistinct at the base and more like the condition found in most Vernonieae.

In *Vernonia diffusa* and its relatives, and in *Cyrtocymura,* the surface of the achene bears distinct specialized cells that are referred to here as resiniferous. These are idioblasts that seem to contain some special substance, but they have no obvious structure such as a raphid inside. In *Cyrtocymura* the cells are intermixed with other cells that seem similarly shaped and mamillose but are not enlarged or colored. In contrast, *Eirmocephala* has no resiniferous cells on the surface. Raphids are present in other cells of the achene walls. They are elongate in *Eirmocephala,* short-oblong in *Cyrtocymura,* and very short in *V. diffusa.*

The carpopodium in two species of *Eirmocephala* is greatly enlarged and has very thick-walled oblong cells. In spite of the larger size, the detailed structure of the carpopodia is similar to that of *V. diffusa* and its relatives. The third species of *Eirmocephala, E. megaphylla,* has a shorter annuliform carpopodium with essentially quadrate cells. The narrow, small-celled form of carpopodium seen in *Cyrtocymura* is undoubtedly neotic in its unenlarged, usually thin-walled cells, but it is clearly less developed than the unexpanded form of *Eirmocephala* carpopodium seen in *E. megaphylla.*

The pappus of *Cyrtocymura* differs from others in the series *Scorpioides* by the structure of both the bases and the tips. The bases have a longer, narrow, fragile area with numerous transverse walls, and the tips are more spreading-scabridulous with no evident clavate enlargement. The capillary bristles of the *Cyrtocymura* type can be easily distinguished from the clavate, erectly scabridulous and somewhat more persistent types of *Eirmocephala* and the *V. diffusa* group. No intergrading forms have been seen.

The variations in pollen within *Eirmocephala* would seem to be greater than the variations between members of that genus and *Cyrtocymura,* and the presence of type A pollen in both genera would be expected to minimize the possibility of meaningful differences. The most common type of substructure is found under the spines of both genera, a large central post with a few additional small basal columellae (Figs. 8, 12). Nevertheless, the genera seem to differ by the presence of polar areoles in *Eirmocephala* (Figs. 2, 5), even in the type A grains, and their lack in *Cyrtocymura* (Fig. 9). The pollen in *Eirmocephala* also shows variations in size that contrast with the apparent uniformity in *Cyrtocymura.* The pollen of the latter genus measures between ca. 35–37 μm in fluid in all species that have been examined. *Eirmocephala* also has grains that size, but *E. megaphylla* shows pollen that may be one of the consistently smallest in the tribe at ca. 30 μm in fluid. The sizes are smaller in SEM preparations than in fluid, but the comparative differences are still evident (Figs. 5–7, 9–11).

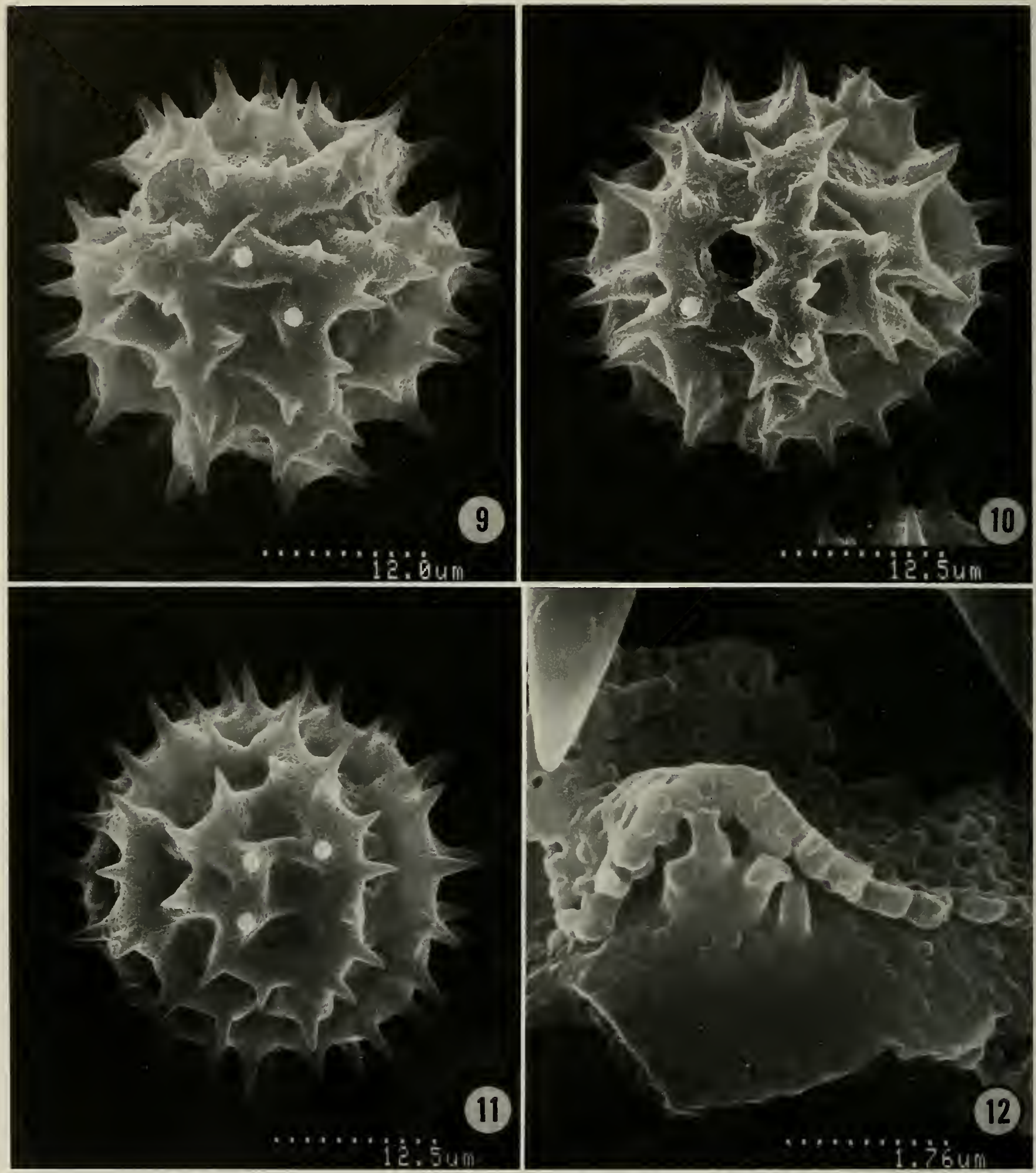
The evidence of the above characters indicates that the members of the series *Scorpioides* are generically distinct from the true *Lepidaploa* complex, and that they, in addition, form three distinct elements among themselves. The superficially similar extreme development of the scorpioides cymes in *Cyrtocymura* and *Eirmocephala* proves misleading since each of those groups proves to be related separately to a form more like *V. diffusa* or even more remote elements among the South American Vernonieae with type A pollen. The relationship of *V. diffusa* is left for treatment at a future time. The two other elements of the series *Scorpioides* are here described as the new genera *Cyrtocymura* and *Eirmocephala.*

Key to the Genera *Cyrtocymura* and *Eirmocephala*

1. Leaves distinctly petiolate with narrow insertions onto the stem; older heads at bases of cymes deciduous leaving only reduced subtending bracts on branch; pappus bristles not clavate distally, distinctly scabridulous at tip; anther thecae without sclerified dentate basal appendages; achene surface with bulging enlarged resiniferous cells . . *Cyrtocymura*
1. Leaves almost always broadly winged to the base, broadly inserted at base on the stem; older heads at bases of cymes not deciduous, with at least outer involucral bracts persistent; pappus bristles distinctly broadened near tips, with erect nonspreading indistinct scabridulae; anther thecae with sclerified basal appendages; achene surface without differentiated resiniferous cells . . . . *Eirmocephala*

Cyrtocymura H. Robinson, gen. nov.

Plantae herbaceae perennes laxe ramosae 0.1–1.5 (–3.0) altae. Caules teretes vel leniter angulati. Folia alterna petiolata base anguste inserta; laminae late ovatae vel late



Figs. 9–12. Pollen of *Cyrtocymura scorpioides* (Lam.) H. Robinson. 9–11, Whole grains; 9, dotted line = 12 μm; 10, 11, dotted lines = 12.5 μm; 9, Polar view showing lack of polar areole; 10, Colpar view showing part of intercolpar region; 11, Intercolpar view; 12, Broken spine, dotted line = 1.76 μm, showing branching of central columella and one nearby smaller basal columella.

lanceolatae integrae vel dentatae subtus leniter vel dense tomentosae et glandulo-punctatae. Inflorescentiae terminales in ramis elongatis seriate cymosis scorpioideis divaricate proliferatae. Capitula in seriebus subduplicibus densis lateralibus sessilia demum decidua; bracteae involucri ca. 20–30 subimbricatae ca. tri-seriatae inaequilongae graduatae in apice breviter acutae vel filiforme attentuatae. Flores in capitulo 14–30;

corollae inferne plerumque glabrae, lobis plerumque erectis et plerumque sericeopilosulis; thecae antherarum base non appendiculatae non scleroideae, cellulis endothecialibus in scutis scleroideis multo noduliferae; appendices apicales antherarum glabrae; basi stylorum discoideo-nodati. Achaenia 10-costata inter costam dense sericeo-setulifera, raphidis elongatis, cellulis superificialibus mamillosis et saepe in partibus resiniferis; carpopodia anguste annulata, cellulis subquadratis in parietibus leniter incrassatis; setae pappi interiores capillares facile deciduae in partibus basilaribus transversaliter septatis elongatae apice non clavatae distincte scabridulae, squamae pappi exteriores lineares. Grana pollinis in diametro ca. 40 μm non vel leniter lophata (typus A).

Type: *Conyza scorpioides* Lamarck.

The genus includes six species, four concentrated in eastern Brasil and adjacent Bolivia, and a fifth widely distributed as far north as Mexico. A sixth species is in the West Indies.

Key to the Species of *Cyrtocymura*

1. Involucres covered by a dense, whitish tomentum; bracts without hairs inside at the apex; bases of leaf blades truncate, leaf apex obtuse or rounded, the margins distinctly crenate or crenate-serrate . . . *C. harleyi*
1. Involucres appearing brownish, without a dense, whitish tomentum; bracts with hairs on inner surface at the apex; bases of leaf blades obtusely to acuminately angled; leaf apex acute or acuminate, the margins remotely serrulate to dentate, not crenate 2
2. Tips of inner involucral bracts and the persistent bract at the base of the head subulate to short acuminate 4
3. Leaves rounded-ovate with shortly apiculate tips; petioles 5 mm or less long, terminating rather abruptly at the rounded base of the leaf blade . . . . *C. saepia*
3. Leaves ovate with acute tips; petioles up to 10 mm long, terminating distally in the acuminate base of the blade . . . . *C. scorpioides*
2. Tips of all involucral bracts and the persistent bract at the base of the head flagelliform 3
4. Stems and branches of the inflorescence with a short pubescence, yellowish in younger parts; heads mostly 5–6 mm high; corolla lobes with few or no long hairs; leaf blades serrulate . . . . *C. mattos-silvae*
4. Stems and branches of the inflorescence with a deep grayish or whitish tomentum; heads mostly 7–9 mm high; corolla lobes with many sericeous hairs on the outer surface . . 5
5. Leaf blades with rounded bases, abruptly narrowly decurrent on the petiole, the margins remotely serrulate to strongly serrate or dentate . . . . *C. lanuginosa*
5. Leaf blades narrowly acute or acuminate at the base, the margins closely serrulate . . . . *C. cincta*

Cyrtocymura cincta (Griseb.) H. Robinson, comb. nov.

Vernonia cincta Griseb., Symb. Fl. Argent. 162. 1879.

Cacalia cincta (Griseb.) Kuntze, Rev. Gen. Plant. 3(2):138. 1898.

Vernonia scorpioides var. *cincta* (Griseb.) Cabrera, Darwiniana 6:338. 1944.

Argentina, Bolivia.

The species is restricted to the eastern slopes of the Andes in Bolivia from Santa Cruz southward into northern Argentina. As in the case of all the close relatives of *C. scorpioides*, the present species has been reduced to varietal level (see Cabrera above). Some specimens of *C. scorpioides* seem intermediate in the tips of their involucral bracts, but they are easily assigned on the basis of their darker and less dense pubescence and by their more nearly entire leaves. The species distinctions seem strongest in the Bolivian material.

Cyrtocymura harleyi (H. Robinson)
H. Robinson, comb. nov.

Vernonia harleyi H. Robinson, Phytologia 44:287. 1979.

Brazil (Bahia).

The species is the only member of the genus sufficiently distinct to avoid any broadened concept of *V. scorpioides.* The appearance of the leaves is totally different and the involucral bracts have no hairs on the inner surface at the tip.

Cyrtocymura lanuginosa (Gardn.)
H. Robinson, comb. nov.

Vernonia lanuginosa Gardn., Lond. J. Bot. 5:219. 1846.

Brazil (Minas Gerais).

The species was originally distinguished from *C. scorpioides* by the more acuminated and 3-nerved involucral bracts, the glabrous receptacle, and the shorter more paleaceous external pappus (Gardner 1846). An isotype (US) also shows a thicker pubescence on the stems, leaf undersurfaces, and involucres, a condition that was evidently the basis of the species name. The species was subsequently reduced to synonymy by Baker (1873) under *Vernonia sororia* DC. which was treated as a variety of *V. scorpioides.* The species was resurrected and extended to include in its synonymy *V. mattos-silvae* of Bahia by Robinson (1980). At present, in spite of failure of some of the original distinctions such as the receptacle character, the species is regarded as distinct from *V. scorpioides, V. sororia,* and *V. mattos-silvae,* being restricted to Minas Gerais. Although related to *C. mattos-silvae* in the flagelliform tips of its bracts and in its closely serrulate leaf margins, it is distinct in the deeper, more grayish pubescence, the more truncate base of its leaf blades, and the presence of numerous hairs on the corolla lobes. The species is actually more closely related to *C. cincta* of Argentina and Bolivia, from which it differs in the leaf base and margin. The older species with which it has been synonymized, *V. sororia* DC., proves in microfiche to be a totally different entity, matching in its type locality of Rio de Janeiro, its nearly sessile leaves, and its sparser heads that sometimes have small foliose bracts, the later described *V. coulonii* Sch. Bip. ex Baker, which is a true *Lepidaploa.*

Cyrtocymura mattos-silvae (H. Robinson)
H. Robinson, comb. nov.

Vernonia mattos-silvae H. Robinson, Phytologia 44:288. 1979.

Brasil (Bahia).

The species was originally described (Robinson 1979) in ignorance of the existence of *V. lanuginosa* Gardn. which was then in synonymy under a variety of *V. scorpioides.* Discovery of the latter caused an over-reaction, with reduction of the new species to synonymy (Robinson 1980). The species is accepted here on the basis of the attenuate bases of its leaf blades, its shorter pubescence, its smaller heads, and its nearly or completely hairless corolla lobes. The species is the only member of the genus lacking numerous hairs on the corolla lobes. The descriptions consistently refer to the corollas as violet, but in most of the specimens the corollas seem to dry with a more reddish or orange color.

Cyrtocymura scorpioides (Lamarck)
H. Robinson, comb. nov.

Conyza scorpioides Lamarck, Encycl. Méthod. 2:88. 1786.

Vernonia scorpioides (Lamarck) Pers., Syn. Plant. 2:404. 1807.

Vernonia subrepanda Pers., Syn. Plant. 2: 404. 1807.

Vernonia tournefortioides H.B.K., Nov. Gen., folio ed. 4:27. 1818.

Lepidaploa scorpioides (Lamarck) Cassini, Dict. Sci. Nat. 26:16. 1823, comb. inval. due to author's failure to recognize *Lepidaploa* at generic rank at the time.

Chrysocoma repanda Vellozo, Fl. Flum. 8: pl. 13. 1825.

Vernonia centriflora Link & Otto, Ic. Plant. Select. pl. 55. 1828 Dec/or Jan 1829.

Staehelina solidaginoides Willd. ex Lessing, Linnaea 4:281. 1829.

Vernonia longeracemosa Martius ex DC., Prodr. 5:42. 1836, nom. inval. in synon.

Vernonia flavescens Lessing, Linnaea 6:657. 1831.

Cacalia scorpioides (Lamarck) Kuntze, Rev. Gen. Plant. 1:971. 1891.

First described from Brazil. Widely distributed in South America from Argentina north to Trinidad and Tobago, and in Central America north to Mexico.

The species has been interpreted widely by most recent taxonomists, with *C. cincta, C. lanuginosa,* and *C. saepia* being reduced to its synonymy. The present concept shows a comparative lack of regional variation in spite of its wide distribution. The species overlaps geographically with all other members of the genus except *C. saepia* of Hispaniola.

Cyrtocymura saepia (Ekman) H. Robinson, comb. nov.

Vernonia saepia Ekman Ark. för Bot. 17(7): 63. 1921, as "*saepium.*"

Haiti.

The species has been reduced to synonymy under *Vernonia scorpioides* by Keeley (1978), and geographical considerations might at first seem to support the idea. It is the only species of the genus to be found entirely outside the center of diversity in eastern Brazil and Bolivia. Still, there are precedents for such distribution patterns in such groups as the Eupatorieae, and bird flight paths could explain such a northward extension from a Brasilian center. In any case, the species is distinctively densely foliate without intermediate forms, and it is geographically isolated in the Greater Antilles.

Eirmocephala H. Robinson, gen. nov.

Plantae herbaceae perennes saepe suffrutescentes vel subarborescentes laxe ramosae ad 1.5–3.0 (–6) m altae. Caules angulati. Folia alterna base alata vel breviter pseudopetiolata in caulibus late inserta; lamina ovata vel lanceolata margine serrata variabiliter pubescentia et subtus glandulopunctatae. Inflorescentiae terminales in ramis numerosis elongatis seriate cymosis divaricate proliferatae interdum apice scorpioideae. Capitula in seriebus subduplicibus lateralibus sessilia demum plerumque persistentia; bracteae involucri ca. 24–65 dense subimbricatae multiseriatae inaequilongae in apicibus late scariosae. Flores in capitulo 7–35; corollae inferne glabrae, lobis tenuibus distaliter pauce glanduliferis et interdum pauce piliferis; thecae antherarum base distincte scleroideae et dentatae; cellulae endotheciales in scutis scleroideis multo noduliferae; appendices apicales antherarum glanduliferae vel non glanduliferae; basi stylorum discoideo-nodati. Achaenia 10-costata intercostate erecto-patentiter setulifera base glandulifera, raphidis minutis breviter oblongis, cellulis superficialibus resiniferous nullis; carpopodia annuliformia vel gongyliformia; setae pappi interiores capillares subpersistentes in partibus basilaribus transversaliter septatis abbreviatae apice distincte latiores dense ascendentiter scabridulae, squamae pappi exteriores lineares. Grana pollinis in diametro ca. 30–45 μm lophata et rhizomatifera vel non lophata (typi A et C).

Type: *Vernonia brachiata* Benth. ex Oersted.

The genus contains three species that are distributed geographically from Costa Rica and Colombia in the north to Bolivia in the south.

Key to the Species of *Eirmocephala*

1. Branches of inflorescence densly tomentose, the surface not visible; heads containing ca. 60 involucral bracts and 35 flowers, the inner bracts of the involucre linear, with long narrowly acute tips; achenes with narrow, annuliform carpopodia; apical anther appendages narrowly rounded at the tip .... *E. megaphylla*
1. Branches of inflorescence with costae obvious, not completely covered by pubescence; heads containing 24–45 involucral bracts and ca. 7–21 flowers, the inner involucral bracts with rounded or shortly pointed tips; achenes with large, swollen carpopodia; apical anther appendages sharply acute at the tip 2
2. Involucres mostly wider than high, the pale or rarely reddish bracts bearing a dark median costa, acute or apiculate at the apex; heads containing ca. 45 involucral bracts and 21 flowers; apical anther appendages glabrous .... *E. brachiata*
2. Involucres as high as wide or higher, the dark bracts lacking a darker median line, usually rounded at the apex, sometimes mucronate; heads containing 24–28 involucral bracts and 7–15 flowers; apical anther appendages glanduliferous .... *E. cainarachiensis*

Eirmocephala brachiata
(Bentham ex Oersted)
H. Robinson, comb. nov.
Figs. 1–4

Vernonia brachiata Bentham ex Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852:67. 1852. Costa Rica, Panama, Colombia, Venezuela, northwestern Ecuador (Manabí).

Eirmocephala cainarachiensis (Hieron.)
H. Robinson, comb. nov.

Vernonia cainarachiensis Hieron., Verh. Bot. Vereins. Prov. Brandenburg 48:196. 1906. Peru, Ecuador (Napo).

Eirmocephala megaphylla (Hieron.)
H. Robinson, comb. nov.
Figs. 5–8

Vernonia megaphylla Hieron., Verh. Bot. Vereins Prov. Brandenburg 48:195. 1906.
Vernonia digitata Rusby, Bull. New York Bot. Gard. 8:125. 1912.

The species has been placed in the synonymy of *Vernonia brachiata* in the recent treatment of the Peruvian species by Jones (1980), in spite of the previous observation by Jones (1979) that the two species differ in the form of their pollen. The species differ additionally in the density of the pubescence on their inflorescence branches and involucres, the shape of the involucral bracts, the numbers of bracts and flowers in the heads, the shape of the apical anther appendages, and the expansion of the carpopodia. Also, the outer squamae of the pappus in the present species are longer (often over 1 mm). In the carpopodia and the shape of the anther appendage the northern *E. brachiata* shows a closer relationship to *E. cainarachiensis* than to *E. megaphylla.* The two species that were synonymized are completely separated geographically. The present species occurs only in Peru and Bolivia.

Acknowledgments

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Kahn of the Smithsonian Museum of Natural History SEM Laboratory using a Hitachi S-570 scanning electron microscope.

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REVISIONS IN CLASSIFICATION OF GAMMARIDEAN AMPHIPODA (CRUSTACEA), PART 3

J. L. Barnard and G. S. Karaman

Abstract.—The following new families are described or revived: Cardenioidae, Clarenciidae, Pseudamphilochidae, and Bolttsiidae (the latter two are companion families); the Ochlesidae are incorporated into the Acanthonotozomatidae. The following new genera are described: *Meraldia* in Acanthonotozomatidae (Ochlesinae); *Abdia, Manerogeneia, Membrilopus, Nasageneia,* and *Whangarusa* in Eusiridae; *Geniculophotis* in Isaeidae; *Isipingus* in Liljeborgiidae; *Bruunosa, Cedrosella, Cicadosa, Galathella, Lepiduristes,* and *Rimakoroga* in Lysianassidae; *Stegosoladidus* in Stegocephalidae; *Aurometopa, Knysmetopa, Torometopa, Vonimetopa,* and *Zaikometopa* in Stenothoidae; *Hystriphlias* in Temnophliantidae. The following change in nomenclature is proposed: *Valettiella* formerly in Lysianassidae is removed to *Gammarella* in the Nuuanuids (Pherusanids).

We continue our series of expositions on new genera and nomenclatural changes necessary to realign various Amphipoda preparatory to our completion of a new compendium of genera in Gammaridea. Parts 1 and 2 are Karaman and Barnard (1979) and Barnard and Karaman (1982).

As we have indicated before, the promulgation of new taxa and substantive changes in others from the literature alone is not the most desirable of methods. We are trying to keep these changes to the minimum, but in order to write keys to genera and otherwise to define genera as precisely as possible it becomes necessary to remove certain species from selected genera or certain genera from selected families and to create new taxa. We base these changes on extensive review of the world literature in each taxonomic group. We recognize that many other taxonomists are engaged in revisions of various taxonomic groups and have left them the task of realigning those.

We frequently list species for each genus we change; for each species we list principal references and distribution in the style we propose to use in our forthcoming generic compendium. The distribution is cited as a three-digit number in brackets which can be determined from the list on pages 184–203 of Barnard and Barnard (1983). The method of description and citation of relationships follows the pattern of the aforementioned monograph.

Any genus lacking reference can be found in J. L. Barnard (1969a).

Acanthonotozomatidae (Ochlesinae), new combination, new rank

Remarks.—New taxa recently described provide the intergradation necessitating amalgamation of Ochlesidae with Acanthonotozomatidae. We retain Ochlesinae at subfamily level temporarily, although we have little conviction that any gross differences are to be found. Ochlesinae are simply apomorphic acanthonotozomatids with loss of articles on the maxillipedal palp. One species of *Ochlesis* is so distinctive that it is relegated to a new genus, *Meraldia.*

Diagnosis.—Body massive, compressed; anterior coxae acuminate or oddly shaped. Head short, tall, partially enveloped by pereon. Accessory flagellum absent. Mouthparts grouped conically. Mandibular rakers absent, molar very small, poorly triturative or simple. Palp of maxilliped 0–2-articulate. Gnathopods feeble, gnathopod 1 simple, hand of gnathopod 2 simple, otherwise gnathopod 2 carpo- or merochelate. Urosomites separate. Uropod 3 ordinary. Telson entire or weakly slit.

See Lysianassidae.

Description.—Rostrum large. Eyes ordinary. Lateral cephalic lobes well developed. Antennae cuspidate or not; antennal flagella sparsely articulate. Labrum elongate. Left mandible with spiniform lacinia mobilis, right lacinia mobilis absent, palp article 1 elongate. Mandibular lobes of labium acuminate, inner lobes weak or absent. Inner plate of maxilla 1 small, outer plate subconical, spines mostly fused to base, palp vestigial or absent. Maxilla 2 elongate. Inner plate of maxilliped acuminate, outer operculiform. Coxae variable. Articles 3–6 of gnathopod 1 elongate, apical setae strap-shaped or grossly feathered; articles 4–6 of gnathopod 2 elongate. Article 2 of pereopods 5–7 well or weakly expanded, with even or deeply sinuate posteroventral lobe. Pereopodal dactyls variable in length. Pleopods ordinary. Epimera toothed or not. Outer ramus of uropod 3 shortened. Body narrowing dorsally to thin continuous keel, one or more segments usually with large dorsal tooth.

Gills 2–?, narrow, strap-shaped and clavate or apically geniculate; oostegites narrow and broad together in same species, thus narrow on coxae 2 and 5 but broad on coxae 3–4 or also broad on coxa 2 in another species.

Variables.—Peduncle of antenna 1 with large teeth (*Ochlesis* type) or not (*Ochlesis eridunda*); dactyls of pereopods 3–7 elongate (*Ochlesis innocens*), short (*Ochlesis lenticulosus*).

Relationship.—Of the suborder Gammaridea, only the Ochlesinae and the genus *Danaella* (see also *Thoriella* and *Chevreuxiella*) in the Lysianassoidea lack a palp on the maxilliped. This lack is characteristic of all members of the Hyperiidea but Ochlesinae appear in other respects to be related closely to Gammaridea; and *Ochlesodius* has a 2-articulate palp and thus shows a close connection to the Acanthonotozomatidae. The large coxae are especially characteristic of gammarideans but the general body shape resembles that of Acanthonotozomatidae and Astyridae (=Stilipedidae).

Assumed to be apomorphs of Acanthonotozomatidae.

Key to the Genera of Ochlesinae

1. Palp of maxilliped 2-articulate ... . *Ochlesodius*
– Palp of maxilliped 0–1-articulate .. 2
2. Body keel dorsally flattened, with plaques, pereonites with lateral plaques, telson linguiform, lateral margins curled upward ..... *Meraldia*
– Body keel dorsally knife-like, pereonites smooth laterally, telson flat ... 3
3. Palp of maxilliped absent .... *Ochlesis*
– Palp of maxilliped 1-articulate ... . *Curidia*

Curidia Thomas

Curidia Thomas, 1983:127 (*Curidia debrogania* Thomas, 1983, monotypy).

Diagnosis.—As in key.

Species.—*debrogania* Thomas, 1983 [362].

Marine, Belize to Biscayne Bay, Florida, 2–20 m, 1 species.

Meraldia Barnard and Karaman, new genus

Type species.—*Ochlesis meraldi* (J. L. Barnard, 1972a, original designation).

Diagnosis.—As in key.

Species.—*meraldi* (J. L. Barnard, 1972a) [785].

Marine, Pearson Islands, South Australia, 35 m, 1 species.

Ochlesis Stebbing

Ochlesis Stebbing, 1910:581 (*Ochlesis innocens* Stebbing, 1910a, monotypy).

Diagnosis.—As in key.

Removal.—*O. meraldi* to *Meraldia.*

Species.—*alii* J. L. Barnard, 1970a (?*innocens* ID of Pirlot, 1936 and ?Schellenberg, 1938) [381 + ?640];

eridunda J. L. Barnard, 1972a [785];
innocens Stebbing, 1910 [781];
lenticulosus K. H. Barnard, 1940 (Griffiths 1974b, c, 1975) [743];
levetzowi Schellenberg, 1953 (Griffiths 1974a, c) [743].

Marine, Indo-Pacific from Hawaii to southern Australia and southern Africa, 0–200 m, 5 species.

Ochlesodius Ledoyer

Ochlesodius Ledoyer, 1982:48 (*Ochlesodius spinicornis* Ledoyer, 1982, original designation).

Diagnosis.—As in key.

Species.—*spinicornis* Ledoyer, 1982 [698].

Marine, Madagascar, 26 m, 1 species.

Cardenioidae, new family

Type genus.—*Cardenio* Stebbing, 1888.

Diagnosis.—Gammaridean with nongaleate head (though probably derived from such); accessory flagellum of antenna 1 uniarticulate but large; antenna 2 lacking facial spines on article 4; upper lip fleshy, ventrally rounded; mandibles with 3-articulate palp, article 3 short, thick, weakly bevelled apically, all setae apical, molar medium to large, triturative, spine row present; lower lip with mandibular lobes broad but not projecting, inner lobes present and separate from each other, no extraordinary wide space between outer lobes; maxillae 1–2 well developed, inner lobes strongly setose medially, palp of maxilla 1 biarticulate; plates of maxilliped well developed, palp 3-articulate; coxae poorly setose, coxa 1 tiny and hidden by large following coxae; gnathopod 1 present, essentially 6-articulate (dactyl vestigial), carpus large and lobate, propodus small and simple, gnathopod 2 very slender, elongate, carpus dominant, dactyl vestigial or absent; pereopods 3–4 with dactyls vestigial, of pereopods 5–6 small, of pereopod 7 absent; pereopod 6 dominant, pereopods generally fossorial; uropods 1–3 present, strongly biramous; telson elongate, deeply cleft.

Relationship.—Sharing many characters of Synopiidae but head not distinctly galeate and coxa 1 strongly reduced. Characters shared with Synopiidae include the short article 3 of the mandibular palp, fossorial pereopods, rather slender though reduced antenna 1 and shape of the gnathopods.

Formerly in the old concepts of Haustoriidae-Pontoporeiidae but not now in those groups because of the non-fossorial antennae, non-haustorioid but otherwise well developed lanceolate rami on uropod 3, and elongate poorly setose telson.

The diagnosis of *Cardenio* below follows that of Synopiidae for comparisons.

Cardenio Stebbing

Cardenio Stebbing, 1888:806 (*Cardenio paurodactylus* Stebbing, 1888, monotypy); 1906:125.

Diagnosis.—Forehead not protuberant, lateral cephalic lobe not sharp, eyes present; mandible with palp, molar of medium size and not dominating mandible, moderately triturative; articles 1–2 of antenna 1 basic, article 3 as long as 1 (longer than 2), no teeth; dactyl of maxilliped vestigial or absent; coxa 1 strongly reduced; coxae 3–4 not pelagont; gnathopods simple, gnathopod 1 stout, carpus thick, lobate, with serrate spines; gnathopod 2 slender, carpus long, not lobate, without serrate spines, dactyl obsolescent or absent; pereopods 5–7 elongate, dactyls elongate, pereopod 6 dominant; article 2 of pereopod 7 strongly expanded, subtruncate ventrally; pleonites 1–3 denticulate; uropod 3 not grossly exceeding uropod 1, peduncle elongate, uropod 2 short; telson elongate, deeply cleft.

Species.—*paurodactylus* Stebbing, 1888, 1906 (K. H. Barnard 1932, Stephensen 1947, Thurston 1974b) [835, 890].

Antiboreal and Antarctic islands, 0–70 m, 1 species.

Clarenciidae, new familly

Type genus.—*Clarencia* K. H. Barnard, 1931.

Diagnosis.—Peduncle of antenna 1 short, stubby, accessory flagellum absent. Mandibular molar simple, conical. Plates of maxilliped of medium size. Gnathopod 2 enlarged and chelate, article 3 short. Uropods and telson [unknown].

See Sebidae; Lysianassidae; Eusiridae and allies.

Description.—Body compressed, dorsally carinate and toothed, urosomites 1 and 2 free, first elongate and crested [urosomite 3 unknown]. Head subcuboidal, rostrum obsolescent, lateral lobes undeveloped; eyes absent.

Antennae [broken], but peduncle of antenna 1 short and articles 1–3 progressively shorter, article 1 shorter than head, article 3 produced and almost as long as article 2, article 1 of primary flagellum ordinary [remainder broken]; antenna 2 much longer than 1 [but missing from middle of article 5].

Epistome and labrum [?separate, ?labrum dominant, ?broader than long, ?epistome unproduced], labrum apically rounded. Mandibular incisor ordinary, toothed, lacinia mobilis [?present], rakers 5, molar simple, subconical, palp attached opposite molar, article 3 shorter than 2, subfalciform, strongly setose, setae = DE. Labium with appressed outer lobes, with weak fused appressed inner lobes. Inner plate of maxilla 1 medium, with 4 marginal setae, outer plate with 9 spines, palp long, 2-articulate, article 1 short; plates of maxilla 2 moderately narrow, moderately setose, outer longer than inner; plates of maxilliped of medium size, poorly armed, palp stout, 4-articulate, dactyl long, unguiform.

Coxae 1–4 medium, coxa 4 scarcely largest, coxa 1 weakly expanded, coxa 3 weakly tapering, coxa 4 scarcely lobate and scarcely excavate, coxa 5 slightly shorter than 4. Gnathopod 1 small, carpus not lobate, propodus of medium length, as long as carpus, palm transverse; gnathopod 2 enlarged, carpus tiny, cryptic, propodus huge, palm chelate, dactyl fitting palm.

Pereopods short to medium, 3–4 ordinary, article 2 of pereopods 5–7 expanded, weakly lobate, [scarcely setulate?]. Pleopods [?ordinary, each ramus with ? articles]. Urosome elongate, epimera ordinary, urosome elongate [but urosome missing from 2 onward, uropods 1–3 missing, telson missing].

Gills [2–?], simple; oostegites [unknown].

Sexual dimorphism.—Unknown [specimen immature].

Remarks.—Apices of antennae, urosomites, and all of uropods and telson missing.

Relationship.—Differing from Sebidae (see J. L. Barnard 1969a) in the short stubby peduncle of antenna 1, and the absence of the accessory flagellum.

Differing from Lysianassidae in the enlargement of gnathopod 2 with short article 3. Differing from Eusiridae in the combination of short peduncle on antenna 1 and chelate gnathopod 2.

Vaguely resembling Acanthonotozomatidae but only coxa 4 scarcely acuminate, gnathopod 2 huge and chelate.

Clarencia K. H. Barnard

Clarencia K. H. Barnard, 1931:428 (*Clarencia chelata* K. H. Barnard, 1931, original designation); 1932:155.

Species.—*chelata* K. H. Barnard, 1931, 1932 [871B].

Marine, South Shetland Islands, 342 m, 1 species.

Eusiridae

Abdia Barnard and Karaman, new genus

Type species.—*Atylopsis latipalpus* Walker and Scott, 1903, here designated.

Etymology.—From the type locality, "Abd-el-Kuri." Feminine.

Body ordinary, compressed, smooth. Rostrum [?large], lateral cephalic lobes ordinary, anteroventral margin of head not produced. Eyes ovate.

Antenna 1 longer than 2, peduncular articles of antenna 1 progressively shorter, article 2 shorter than head, article 3 not produced; article 1 of primary flagellum short, accessory flagellum absent.

Labrum [?entire, ?subrounded, ?broader than long, ?epistome unproduced]. Molar triturative, columnar, article 2 of mandibular palp unlobed, article 3 shorter than 2. Labium: [?inner lobes absent].

Maxilla 1: inner plate with 3 medial setae, palp long, article 1 slightly elongate. Maxilla 2: [?inner plate not broader nor longer than outer, ?plates narrow, ?inner plate without facial row of setae and other medial setae]. Maxilliped: inner plate relatively long, outer plate slightly shorter than inner; palp of 4 articles, 4 slightly shorter than 3, 3 unlobed, 4 not spinose along inferior margin.

Coxae ordinary, coxa 1 not produced anteriorly nor expanded ventrally, coxa 4 with posterior lobe, excavate.

Gnathopods diverse, small (female), of similar size, subchelate, not eusirid, carpus of both scarcely shorter than propodus, of second only with strong posterodistal lobe extending distad, carpus of both without numerous long posterior setae.

Pereopods 3–7 ordinary, simple, dactyls simple, article 2 not anteriorly lobate. Coxal gills heavily pleated as in Atylidae. Epimeron 3 not serrate. Urosomites distinct. Outer rami of uropods 1–2 shortened; rami with lateral and dorsal spines. Uropod 3 ordinary, not extended beyond uropod 1, peduncle without large process, rami lanceolate. Telson ordinary, cleft, apices without long apical armaments.

Assumption.—If *Pontogeneia barnardi* Rabindranath (1972) is a synonym of *Atylopsis latipalpus* then the rostrum of *Abdia* is large like that of *Tethygeneia* (see J. L. Barnard 1972a) and *Nasageneia* (see below).

Relationship.—Differing from the freshwater Australia *Pseudomoera* in the presence of carpal lobes only on gnathopod 2.

Differing from *Tethygeneia* in the seriate, not anthurial, calceoli.

Not Atylidae because urosomites separate. See *Nasageneia.*

Species.—*latipalpus* (Walker and Scott, 1903) (Sivaprakasam 1968) (?=*barnardi* Rabindranath, 1972) [690].

Marine, India to Abd-el-Kuri, sublittoral, 1 species.

Manerogeneia, new genus

Type species.—*Pontogeneiella maneroo* J. L. Barnard 1972a, here designated.

Etymology.—From the type species, "maneroo," and "geneia," a common suffix in this family. Feminine.

Body ordinary, compressed, smooth. Rostrum large, lateral cephalic lobes ordinary, anteroventral margin of head not produced. Eyes round.

Antenna 1 longer than 2, peduncular articles progressively shorter, article 1 shorter than head, article 3 weakly produced; article 1 of primary flagellum as long as article 3 of peduncle; accessory flagellum absent.

Labrum entire, subrounded, broader than long; epistome unproduced. Molar triturative, columnar, article 2 of mandibular palp unlobed, article 3 as long as 2. Labium: inner lobes present. Maxilla 1: inner plate with many medial setae, palp long, article 1 short. Maxilla 2: inner plate not broader nor longer than outer, inner plate with facial row of many setae and other medial setae. Maxilliped: inner plate relatively short, outer plate not longer than inner; palp of 4 articles, 4 slightly shorter than 3, 3 unlobed, 4 weakly setulate along inferior margin.

Coxae ordinary, coxa 1 not produced anteriorly nor expanded ventrally, coxa 4 not quite twice as long as 1, excavate, with posterior lobe. Gnathopods alike, medium, but 1 scarcely larger than 2, subchelate, not eusirid, carpus of both shorter than propodus, with weak or no posterior lobe not extending distad, carpus without numerous long posterior setae, propodi rectangular.

Pereopods 3–7 ordinary, simple, dactyls strongly toothed or bifid on inferior margins, article 2 not anteriorly lobate. Epimeron 3 smooth.

Outer rami of uropods 1–3 shortened; rami with lateral and dorsal spines. Uropod 3 ordinary, not extended beyond uropod 1, peduncle without large process, rami lanceolate. Telson slightly elongate, entire, linguiform, without long apical armaments.

Relationship.—Noted among its relatives for the bifid dactyls of pereopods 5–7. Closest to *Tylosapis* Thurston (1974a) but back smooth, telson not emarginate, medial margin of inner plate on maxilla 1 strongly setose, and gnathopod 1 slightly enlarged; also like *Atylopsis* but outer ramus of uropod 3 shortened. Differing from *Prostebbingia* and *Gondogeneia* (see J. L. Barnard 1972a, b) in the uncleft telson; from *Bovallia* in the short article 1 of antenna 1; from *Halirages* in the unserrate epimeron 3, short outer ramus of uropod 3 and non-emarginate telson.

See *Apherusa, Haliragoides, Membrilopus* (below).

Species.—*maneroo* (J. L. Barnard, 1972a) [775].

Marine, New Zealand, intertidal, 1 species.

Membrilopus, new genus

Type species.—*Metaleptamphopus membrisetata* J. L. Barnard, 1961, here designated.

Etymology.—"Membri," from the type species, and L., "lopho," comb. Masculine.

Body ordinary, compressed, smooth. Rostrum medium, lateral cephalic lobes ordinary, anteroventral margin of head scarcely produced. Eyes reniform.

Antenna 1 longer than 2, peduncular articles progressively shorter, article 1 shorter than head, article 3 not produced; article 1 of primary flagellum short, accessory flagellum 1-articulate, barrel-shaped.

Labrum entire, subrounded, broader than long, epistome unproduced. Molar triturative, columnar, article 2 of mandibular palp unlobed, article 3 as long as 2. Labium: inner lobes absent. Maxilla 1: inner plate with many medial setae, palp long, article 1 short. Maxilla 2: inner plate not broader nor longer than outer, plates narrow, inner without facial row of setae but with 2 other medial setae. Maxilliped: inner plate relatively short, outer plate slightly longer than inner; palp of 4 articles, 4 slightly shorter than 3, 3 unlobed, 4 spinose along inferior margin.

Coxae ordinary, coxa 1 not produced anteriorly nor expanded ventrally, coxa 4 almost twice as long as 1, with posterior lobe, excavate.

Gnathopods alike, medium, subchelate, not eusirid, carpus of both nearly as long as propodus, with weak posterior lobe not extending distad, with numerous long posterior setae, propodi weakly inflated, trapezoidal.

Pereopods 3–7 scarcely elongate, simple, dactyls strongly pectinate on inferior margins, article 2 not anteriorly lobate.

Epimeron 3 smooth.

Outer rami of uropods 1–3 not or slightly shortened; rami with lateral and dorsal spines. Uropod 3 ordinary, not extended beyond uropod 1, peduncle without large process, rami lanceolate, outer shortened. Telson ordinary, entire, linguiform, without long apical armaments.

Relationship.—Like *Metaleptamphopus* but lobes of maxilla 2 narrow, inferior side of pereopodal dactyls 3–7 ornamented (not superior side), accessory flagellum present, enlarged gnathopods with short lobed carpi, articles 2–3 of maxillipedal palp normally shorter and uropod 3 neither extended well beyond uropod 1 nor bearing elongate peduncle.

Differing from *Prostebbingia* in the uncleft telson; from *Haliragoides* in the short carpi of the gnathopods and the absence of truly facial setae on maxilla 2; from *Manerogeneia* (see above) in the absence of inner lobes on the lower lip, absence of facial setae on maxilla 2, and the pectinate dactyls of the pereopods (bifid only in *Manerogeneia*). Very close to *Atylopsis* but lacking a process on article 3 of antenna 1, lacking inner lobes on the lower lip and bearing pectinate dactyls on the pereopods. Also very close to *Paracalliopiella* Tzvetkova and Kudrjaschov (1975) but differing in the pectinate dactyls and lack of inner lobes on the lower lip. Close to *Tylosapis* Thurston (1974a) but inner plate of maxilla 1 strongly setose medially. Differing from *Lopyastis* Thurston (1974a) in the short outer ramus of uropod 3 and the pectinate dactyls of the pereopods.

See *Harpinioides.*

Species.—membrisetatus (J. L. Barnard, 1961) (Griffiths 1974a) [416B].

Marine, southwest Africa, 537 m, 1 species.

Nasageneia, new genus

Type species.—Pontogeneia nasa J. L. Barnard, 1969b, here designated.

Etymology.—"Nasa," from the type species, and "geneia," a common suffix in this family. Feminine.

Body slender, compressed, smooth. Rostrum large, lateral cephalic lobes ordinary, anteroventral margin of head scarcely produced. Eyes reniform.

Antennae subequal, peduncular articles of antenna 1 progressively shorter, article 1 shorter than head, article 3 weakly produced; article 1 of primary flagellum ordinary to short, accessory flagellum absent.

Labrum entire, subrounded, broader than long; epistome unproduced. Molar triturative, columnar, article 2 of mandibular palp unlobed, article 3 shorter than 2. Labium: inner lobes absent. Maxilla 1: inner plate with 1 medial and 2 apical setae, palp long, article 1 short. Maxilla 2: inner plate not broader but slightly longer than outer, inner plate without facial row of setae but with other medial setae, few, large, at least one slightly submarginal. Maxilliped: inner plate not relatively long, outer plate slightly shorter than inner; palp of 4 articles, 4 slightly shorter than 3, 3 unlobed, 4 not spinose along inferior margin.

Coxae ordinary to short, coxa 1 not produced anteriorly nor expanded ventrally, coxa 4 without posterior lobe, excavate.

Gnathopods diverse, medium, of similar size, subchelate, not eusirid, medium, carpus of both shorter than propodus, only gnathopod 2 with strong posterior lobe extending distad, carpus without numerous long posterior setae, propodi rectangular in female, inflated in male, in latter with posterior spines outside limits of oblique palm.

Pereopods 3–7 ordinary, simple, dactyls simple, article 2 not anteriorly lobate. Epimeron 3 serrate.

Outer rami of uropods 1–2 shortened; rami with lateral and dorsal spines. Uropod 3 ordinary, not extended beyond uropod 1, peduncle with small process, rami lanceolate. Telson ordinary, weakly cleft, apices without long armaments.

Relationship.—Like *Tethygeneia* J. L. Barnard (1972a) but epimeron 3 serrate and propodi of male gnathopods with posterior spines well outside palmar limits as in *Gondogeneia.* Calceoli tending to be much more strongly anthurial than in *Tethygeneia,* with one lobe quite linguiform.

Differing from *Abdia* (see above) in the serrate epimeron 3 and presence of many spines on the propodi of the gnathopods outside of the palmar area.

See *Antarctogeneia* Thurston (1974a), *Pseudomoera.*

Species.—*nasa* (J. L. Barnard, 1969b, 1979) [370]; *quinsana* (J. L. Barnard, 1964b, 1969b, 1979) [370].

Marine, warm temperate California and Mexico, 0–1 m, 2 species.

Whangarusa, new genus

Type species.—*Panoploea translucens* Chilton, 1884, here designated.

Etymology.—Composed of parts of "Whangaparoa" (Peninsula) and "translucens." Feminine.

Body ordinary, compressed, smooth. Rostrum very small, lateral cephalic lobes ordinary, anteroventral margin of head not produced. Eyes ovate.

Antenna 1 longer than 2, peduncular articles progressively shorter, article 1 shorter than head, article 3 weakly produced; article 1 of primary flagellum ordinary, accessory flagellum absent.

Labrum [?entire, subrounded, broader than long]; epistome unproduced. Molar triturative, columnar, article 2 of mandibular palp unlobed, article 3 almost as long as 2. Labium: inner lobes small. Maxilla 1: inner plate with many medial setae, palp long, article 1 short. Maxilla 2: inner plate not broader nor longer than outer, inner plate with full facial row of setae and other medial setae. Maxilliped: inner plate not relatively long, outer plate slightly longer than inner; palp of 4 articles, 4 slightly shorter than 3, 3 unlobed, 4 not spinose along inferior margin.

Coxae ordinary, coxa 1 not produced anteriorly nor expanded ventrally, coxa 4 with posterior lobe, excavate.

Gnathopods alike, large, 1 larger than 2, subchelate, not eusirid, carpus of both in male much shorter than propodus, with weak posterior lobe not extending distad, carpus without numerous long posterior setae, gnathopods 1–2 of female much more slender, carpus as long as propodus.

Pereopods 3–7 ordinary, simple, dactyls simple, article 2 not anteriorly lobate. Epimeron 3 smooth.

Outer rami of uropods 1–2 shortened; rami with lateral and dorsal spines. Uropod 3 ordinary to small, not extended beyond uropod 1, peduncle without large process, rami lanceolate.

Telson ordinary, entire, almost pointed, without long apical armaments.

Relationship.—Differing from *Gondogeneia* J. L. Barnard (1972a, b) in the uncleft telson. Differing from *Atylopsis, Laothoes, Apherusa,* and *Halirages* in the grossly enlarged male gnathopod 1, both gnathopods with very short carpus and large propodi.

Species.—*translucens* (Chilton, 1884, 1921) (J. L. Barnard, 1972b) [775].

Marine, New Zealand, intertidal, 1 species.

Isaeidae

Cheiriphotis Walker

Cheiriphotis Walker, 1904:283 (*Melita megacheles* Giles, 1885, monotypy).

Photis geniculata K. H. Barnard (1935) is transferred to this genus.

Liljeborgiidae

Key to the Genera of Liljeborgiidae

1. Article 1 of mandibular palp short .... *Idunella*
– Article 1 of mandibular palp elongate 2
2. Wrist of gnathopods 1–2 strongly produced, slender and elongate, one or both dactyls of gnathopods 1–2 deeply serrate or toothed 3
– Wrist of gnathopods 1–2 weakly produced, slender or thick or short, neither gnathopodal dactyl deeply serrate nor toothed 4
3. Coxa 1 enlarged, posteroventrally lobate and enveloping reduced coxae 2–3, each lobe of telson with 4+ spines .... *Isipingus*

– Coxa 1 ordinary, not lobate, coxae 2–3 of ordinary length and not enveloped by coxa 1, each lobe of telson with 1 spine .... *Liljeborgia*

4\. Mandibular molar triturative, gnathopod 2 propodus and carpus setose anteriorly .... *Sextonia*

– Mandibular molar simple, gnathopod 2 propodus and carpus naked anteriorly .... *Listriella*

Isipingus, new genus

Type species.—*Liljeborgia epistomata* K. H. Barnard, 1932, original designation.

Etymology.—From "Isipingo," a beach in southern Africa. Masculine.

Diagnosis.—Article 2 of peduncle on antenna 1 [?short], accessory flagellum 4+-articulate. *Epistome hugely produced.* Article 1 of mandibular palp elongate. In male, coxa 1 greatly enlarged, posteroventrally lobate, this lobe encompassing much reduced coxae 2–3; coxa 4 much smaller than coxa 1, abnormally narrowed and anteriorly bevelled. Wrists of gnathopods 1–2 strongly produced, dactyls deeply toothed. Outer ramus of uropod 3 [?uniarticulate]. Each lobe of telson with 4–5 apical spines.

Relationship.—Differing from *Liljeborgia* in the large epistomal process, enlarged coxa 1 enveloping reduced coxae 2–3 and the multispinose lobes of the telson.

Species.—*epistomata* (K. H. Barnard, 1932, 1940, 1955) [743].

Marine, South Africa, 44–124 m, 1 species.

Lysianassidae

We are aware that our colleagues are revising this family; we have many new genera to describe but are delaying these as long as possible to allow our colleagues, who have better information than we, time to publish; the following five genera, however, are needed in print urgently by one of us (Barnard) to service a paper in press on amphipods from thermal vents.

Bruunosa, new genus

Type species.—*Tryphosa bruuni* Dahl, 1959, here designated.

Etymology.—From roots of the type species. Feminine.

Mouthparts forming quadrate bundle. Labrum and epistome differentially produced, not prominent, separate, labrum slightly dominant in size and projection, blunt. Incisor ordinary, molar triturative, large, palp attached opposite molar. Inner plate of maxilla 1 weakly (2) setose; palp biarticulate, large. Inner and outer plates of maxilliped well developed, palp slightly exceeding outer plate, dactyl well developed.

Coxa 1 large and visible, slightly tapering or rounded below. Gnathopod 1 short, subchelate, palm oblique, article 5 slightly longer than 6, dactyl large; article 6 of gnathopod 2 much shorter than article 5, ordinary, propodus subchelate, dactyl thick and stubby.

Inner ramus of uropod 2 with large notch. Uropod 3 ordinary, peduncle elongate, inner ramus strongly shortened, outer ramus 2-articulate. Telson elongate, deeply cleft.

Additional characters.—Article 1 of accessory flagellum elongate and flattened; outer plate of maxilla 2 much broader than inner; outer plate of maxilliped with large articulate spines (versus *Cicadosa* and *Anonyx*); coxa 4 posteroventral lobe weak and blunt (versus *Anonyx* and *Cicadosa*); dactyl of gnathopod 2 especially thick; telson with dorsal spines but none terminal.

Relationship.—Differing from *Cicadosa* in the large articulate spines on outer plate of maxilliped, subchelate gnathopod 1, and slightly rounded, not expanded coxa 1.

From *Anonyx* in large spines on outer plate of maxilliped, slightly rounded, not expanded coxa 1, incised inner ramus of uropod 2, and dorsal spines on telson.

From *Tryphosella* in triturative molar, slightly dominant labrum, and dorsal not terminal telsonic spines.

From *Ambasiopsis, Cedrosella, Galathella,* and *Schisturella* in the non-reduced coxa 1; in addition, from *Cedrosella* and *Galathella* by the incised inner ramus of uropod 2.

Species.—*bruuni* Dahl, 1959 [714A].

Marine, Kermadec Trench, 6660–6770 m, 1 species.

Cedrosella, new genus

Type species.—*Ambasiopsis* (?) *fomes* J. L. Barnard, 1967, here designated.

Etymology.—From "Cedros," the type locality of the type species, and "ella" L. diminutive suffix. Feminine.

Mouthparts forming quadrate bundle. Labrum and epistome differentially produced, not prominent, separate, labrum slightly dominant in size and projection, blunt. Incisor ordinary, molar weakly triturative, large, also setulose, palp attached opposite molar. Inner plate of maxilla 1 weakly (2) setose; palp biarticulate, large. Inner and outer plates of maxilliped well developed, palp strongly exceeding outer plate, dactyl well developed.

Coxa 1 strongly shortened and partly covered by coxa 2, tapering. Gnathopod 1 short, strongly subchelate, palm transverse, article 5 shorter than 6, dactyl large; article 6 of gnathopod 2 much shorter than article 5, ordinary, propodus minutely chelate.

Inner ramus of uropod 2 without notch. Uropod 3 ordinary, peduncle ordinary, inner ramus slightly shortened, outer ramus 2-articulate. Telson ordinary, short, deeply cleft.

Additional characters.—Head lacking sinus for antenna 2; antennae very short; basalmost inner seta of maxilla 2 largest; apex of outer plate on maxilliped with 2 thick spines; dactyl of gnathopod 1 lacking inner tooth; pereopods 5–7 very short.

Relationship.—Differing from *Ambasiopsis* in: lack of carina on article 1 of peduncle on antenna 1; D-setae occupying less than half of mandibular palp article 3 (but also true of *Ambasiopsis tumicornis*); 10 spines on outer plate of maxilla 1; apex of outer plate on maxilliped with strong apical spines (but also weakly in *Ambasiopsis tumicornis*); article 5 of gnathopod 1 shorter than article 6, dactyl without inner tooth, palm transverse; no process on urosomite 1.

From *Schisturella* in lack of notch on inner ramus of uropod 2, small antennae, weaker molar, small head without sinus for antenna 2 and short pereopods 5–7.

From *Galathella* in the slightly reduced and setulose molar, and the narrow and serrate apex of the palp on maxilla 1 (versus broad and armed with articulate bead-like spines).

Species.—*fomes* (J. L. Barnard, 1967) [309A].

Marine, Cedros Trench, Pacific Mexico, 3705–3745 m, 1 species.

Cicadosa, new genus

Type species.—*Anonyx cicadoides* Stebbing, 1888, here designated.

Etymology.—From "cicadoides" and "osus," L. suffix denoting quality of, for example, fullness. Feminine.

Mouthparts forming quadrate bundle. Labrum and epistome separate, differentially produced, labrum slightly dominant in size and projection, subsharp. Incisor ordinary, molar simple, large, weakly conicolaminate, subconical, setulose; palp attached strongly distal to molar. Inner plate of maxilla 1 weakly (2) setose; palp biarticulate, large. Inner and outer plates of maxilliped well developed, palp strongly exceeding outer plate, dactyl well developed.

Coxa 1 large and visible, not tapering. Gnathopod 1 simple or poorly subchelate, palm oblique, article 5 shorter than 6, dactyl large; article 6 of gnathopod 2 greatly shorter than article 5, ordinary, propodus with minute palm.

Inner ramus of uropod 2 with large notch. Uropod 3 ordinary, peduncle slightly elongate, inner ramus slightly shortened, outer ramus 2-articulate. Telson elongate, deeply cleft.

Sexual dimorphism.—Male antennae 1–

2 calceolate, flagellum of antenna 2 elongate, peduncle with anterior male tufts.

Relationship.—Differing from *Anonyx* in the simple gnathopod 1, slightly elongate article 3 of gnathopod 1 and the slightly shorter palp of the maxilliped.

Differing from *Tryphosella* in the expanded coxa 1 and notched inner ramus of uropod 2.

From *Tmetonyx* in the notched inner ramus of uropod 2 and weakness of elongation on article 3 of gnathopod 1.

From *Tryphosites* in the dominant labrum.

See *Bruunosa* above.

Species.—*cicadoides* (Stebbing, 1888, as *Anonyx*) (Schellenberg 1926, Bellan-Santini and Ledoyer 1974) [851].

Marine, Kerguelen Island, 3–228 m, 1 species.

Galathella, new genus

Type species—*Schisturella galatheae* Dahl, 1959, here selected.

Etymology.—From "galatheae" and "ella" L. diminutive suffix. Feminine.

Mouthparts forming quadrate bundle. Labrum and epistome not differentially produced, not prominent, separate, neither dominant, blunt. Incisor ordinary; molar triturative, large, palp attached opposite molar. Inner plate of maxilla 1 weakly (2) setose; palp biarticulate, large. Inner poorly and outer plates of maxilliped well developed, palp strongly exceeding outer plate, dactyl well developed.

Coxa 1 slightly shortened, tapering, and partly covered by coxa 2. Gnathopod 1 short, subchelate, palm oblique, articles 5 and 6 subequal, dactyl large; article 6 of gnathopod 2 slightly shorter than article 5, ordinary, propodus subchelate.

Inner ramus of uropod 2 without notch. Uropod 3 ordinary, peduncle elongate, inner ramus slightly shortened, outer ramus 2-articulate. Telson ordinary, deeply cleft.

Relationship.—Differing from *Schisturella* in the unproduced upper lip and lack of notch on the inner ramus of uropod 3.

Species.—*galatheae* (Dahl, 1959) [715A].

Marine, Kermadec Trench, 6960–7000 m, 1 species.

Lepiduristes, new genus

Type species.—*Uristes* (?) *lepidus* J. L. Barnard, 1964a, here selected.

Etymology.—Based on the old name of the taxon, *Uristes lepidus.* Masculine.

Article 1 of antenna 1 thickened and carinate. Mouthparts forming quadrate bundle. Labrum and epistome separate, not produced, epistome slightly dominant in size. Incisor ordinary, molar weakly triturative, large, palp attached opposite molar. Inner plate of maxilla 1 weakly (?2) setose; palp biarticulate, large. Inner and outer plates of maxilliped well developed, palp strongly exceeding outer plate, dactyl well developed.

Coxa 1 tapering, slightly shortened and partly covered by coxa 2. Gnathopod 1 poorly subchelate, palm oblique, article 3 elongate, article 5 scarcely longer than 6, dactyl large, gnathopod 2 scarcely subchelate, propodus slightly longer than article 5.

Inner ramus of uropod 2 without notch. Uropod 3 ordinary, peduncle ordinary, inner ramus slightly shortened, outer ramus 2-articulate. Telson ordinary, deeply cleft.

Sexual dimorphism.—Unstudied.

Relationship.—Differing from *Uristes, Lepidepecreum,* and *Tryphosella,* and most other similar lysianassids in the elongate article 3 of gnathopod 1. The almost complete loss of ventral cephalic integrity is not sufficient for generic differentiation because this is a feature of *Uristes perspinis* and is found moderately well developed in most of the taxa formerly assigned to *Tryphosa* or *Tryphosella.* The attachment of antenna 2 into a strong anteroventral cephalic notch is typical of most lysianassids but in the *Uristes-Tryphosa-Tryphosella* complex this cephalic support is weakened or lost and the base of antenna 2 is shoved posteriorly and has only weak cephalic envelopment.

Species.—*lepidus* (J. L. Barnard, 1964a) [404A].

Marine, Caribbean Sea, 5419–5497 m, 1 species.

Rimakoroga, new genus

Type species.—*Pseudokoroga rima* J. L. Barnard, 1964b, here selected.

Etymology.—From the name of the type species. Feminine.

Mouthparts forming quadrate bundle. Labrum and epistome prominent, separate, epistome slightly dominant in size and projection, blunt. Incisor ordinary, molar weakly triturative, of medium size, also setulose; palp attached strongly proximal to molar. Inner plate of maxilla 1 [?weakly (2) setose]; palp biarticulate, large. Inner and outer plates of maxilliped well developed, palp strongly exceeding outer plate, dactyl well developed.

Coxa 1 large and visible, not tapering. Gnathopod 1 in male strongly enlarged, strongly subchelate, palm transverse, article 5 much shorter than 6, lobate, dactyl large; article 6 of gnathopod 2 much shorter than article 5, ordinary, propodus minutely chelate.

Inner ramus of uropod 2 without notch. Uropod 3 ordinary, peduncle ordinary, inner ramus slightly shortened, outer ramus 2-articulate. Telson ordinary, weakly to deeply cleft.

Additional characters.—Primary flagellum of antenna 1 with 5 articles only; terminal male gnathopod 1 with carpus very short, lobe thin, propodus enormous, palm and hind margin continuous (as in *Ischyrocerus*), dactyl immense and folding back on false palm; epimeron 3 weakly serrate.

Sexual dimorphism.—Female gnathopod 1 small but thick, carpus short and lobate, propodus subrectangular, palm almost transverse, dactyl fitting palm; otherwise antennae, eyes and uropod 3 similar between the sexes.

Relationship.—Differing from *Pseudokoroga* in the cleft telson and unconstricted inner ramus of uropod 2.

From *Orchomene* in the inflated article 6 of male gnathopod 1, in the terminal male this propodus developing massively, palm and hind margin contiguous, dactyl huge and folding back on false palm.

From *Koroga* in the cleft telson, strongly transformed gnathopod 1 of the terminal male and the better developed molar.

Species.—*rima* (J. L. Barnard, 1964b, c, 1966) [370].

Marine, southern California and west Mexico, 2–30 m, 1 species.

Nuuanuids (Pherusanids, Gammarellids)

This family group cannot bear a name until some person asks the ICZN to determine its spelling. There is already a family Gammarellidae Bousfield (1977), based on the unrelated genus *Gammarellus.*

Gammarella Bate, new synonymy

Pherusa Leach, 1814:432 (homonym, Polychaeta) (*Pherusa fucicola* Leach, 1814, monotypy).

Gammarella Bate, 1857:143 (*Gammarella orchestiformis* Bate, 1857, monotypy, =*Pherusa fucicola* Leach).—Barnard and Barnard, 1983:637.

Pherusana J. L. Barnard, 1964d:62 (new name for *Pherusa,* same type species).

Nuuanu J. L. Barnard, 1970:166 (*Nuuanu amikai* J. L. Barnard, original designation).

Cottesloe J. L. Barnard, 1974:27 (*Cottesloe berringar* J. L. Barnard, 1974, original designation).

Valettiella Griffiths, 1977:116 (*Valettiella castellana* Griffiths, 1977, original designation).

Valettiella is a synonym of *Gammarella* and is not a genus of the Lysianassidae.

Pseudamphilochidae

Pseudamphilochidae Schellenberg, 1931:92.

Diagnosis.—Like Amphilochidae but coxae 1–4 ordinary, coxa 1 expanded ventrally and broader than coxa 2, coxa 4 of medium size and well excavate posteriorly. Telson cleft.

Relatively good plesiomorph of other amphilochids because of strong rostrum, round eye, mouthparts, hammer-like small gnathopods of general form, elongate (but split) telson.

Description.—Antennae longer than in other amphilochids but individual articles of similar dimensions. Accessory flagellum obsolescent. Antenna 2 longer than antenna 1, article 4 of peduncle longer than article 5. Upper lip scarcely incised (unusual). Mandibular incisor of ordinary width, toothed, lacinia mobilis present, raker row sparse (unusual), molar simple and obsolescent, palp stout (unusual). Lower lip with well developed unnotched outer lobes bearing ordinary blunt mandibular lobes, outer lobes widely separated by well developed unfused inner lobes. Inner plate of maxilla 1 small, with 1 seta, outer plate with 9 spines, palp thin, 2-articulate. Plates of maxilla 2 broad but outer much narrower than inner, latter naked medially. Maxilliped ordinary but inner plate slightly broader than normal.

Gnathopods small, alike, carpi short, weakly lobate, propodi longer, moderately expanded, palm almost transverse. Pereopods 3–7 ordinary.

Outer ramus of uropod 1 strongly, of uropod 2 scarcely shorter than inner; peduncle of uropod 3 not greatly elongate (unusual), inner ramus half as long as outer (unusual). Telson elongate, leaf-like, apex sharp but telson split more than one third its length (unusual).

See Bolttsiidae (below).

Relationship.—The unusual characters marked above spoil a tight definition of amphilochoidids. The type genus needs extensive study. Though coxa 1 is broadened, *Pseudamphilochus* differs from Astyridae (=Stilipedidae) in the propodi of the gnathopods being larger than the carpi and is not a member of Acanthonotozomatidae because no anterior coxa is acuminate.

Pseudamphilochus Schellenberg

Pseudamphilochus Schellenberg, 1931:92 (*Pseudamphilochus shoemakeri* Schellenberg, 1931, monotypy). With the characters of the family.

Species.—*shoemakeri* Schellenberg, 1931 [833].

Marine, South Georgia, 12–15 m, 1 species.

Bolttsiidae, new family

Type genus.—*Bolttsia* Griffiths, 1976.

Diagnosis.—Like Amphilochidae but coxae 1–4 of ordinary size, coxa 1 not expanded ventrally and not broader than coxa 2; coxa 4 of medium size, broader than coxa 3, posterodorsal excavation small. Telson entire.

Relatively good plesiomorph of other amphilochids but probably a distinct side branch from ancestors of Pseudamphilochidae because of poorly developed excavation on coxa 4, uncleft telson and unexpanded coxa 1.

Description.—Antennae short and similar to those of amphilochids. Antenna 2 slightly shorter than antenna 1, article 5 longer than 4. Accessory flagellum obsolescent. Upper lip scarcely incised (unusual), molar large but simple, setulose, palp of medium stoutness. Lower lip with well developed unnotched outer lobes bearing ordinary blunt mandibular lobes, outer lobes widely separated by well developed unfused inner lobes. Inner plate of maxilla 1 small, naked, outer plate with 7 spines, palp thin, 2-articulate. Plates of maxilla 2 of medium width, subequal in width, inner without large medial setae. Maxilliped ordinary, inner plates thin, apical spine of dactyl very strong.

Gnathopods moderately enlarged, alike, carpi short, weakly lobate, propodi longer, well expanded, palms almost transverse. Pereopods 3–7 ordinary.

Outer ramus of uropods 2–3 shortened; peduncle of uropod 3 elongate, rami naked and shorter than peduncle. Telson elongate, leaf-like, entire, apically rounded.

Pleonites 1–3 with dorsal tooth.

Relationship.—Differing from Amphilochidae in the large coxa 1.

From Pseudamphilochidae in the short antennae, uncleft telson, thin inner plate of maxilliped, presence of 7 (versus 9) spines on the outer plate of maxilla 1, and regular uropod 3 with elongate peduncle.

Bolttsia Griffiths

Bolttsia Griffiths, 1976:12 (*Bolttsia minuta* Griffiths, 1976, original designation). With the characters of the family.

Species.—*minuta* Griffiths, 1976 [743].

Marine, coastal disjunct lagoon (Sibaya Lake), South Africa near Mozambique border, 1 species.

Stegocephalidae

Stegosoladidus, new genus

Type species.—*Andaniotes simplex* K. H. Barnard, 1930, here designated.

Etymology.—From root of Stegocephalidae, "sol" L. sun, "idus" L. having the nature of.

Body smooth. Article 1 of flagellum on antenna 1 [?longer than peduncle]. Article 4 of peduncle on antenna 2 [?longer than article 5].

Labrum [?ordinary, ?elongate, ?very broad, ?asymmetrically incised]. Mandibular incisor smooth. Labium very short, with gaping extended lobes, with [?1 or 2 bidigitate distal fingers]. Maxilla 1 ordinary, palp 1-articulate (slender relative to *Andaniotes corpulentus*). Outer plate of maxilla 2 ordinary, spines without hooks. Inner plate of maxilliped not reaching base of palp article 1, palp 3-articulate (articles 1–2 coalesced), article 2 unproduced.

Dactyls of gnathopods simple. Pereopods 3–4 simple. Article 2 of pereopod 6 expanded. Pereopod 7 with 7 articles.

Uropod 3 biramous, outer ramus [?2-articulate, peduncle ?longer than rami]. Telson [?as broad as long], incised.

Relationship.—Like *Andaniotes* but plates of maxilliped very short, palp with only 3 articles, apparently articles 1–2 of primordial palp fused (or article 4 lost and article 1 elongate).

Species.—*simplex* (K. H. Barnard, 1930) [779].

Marine, New Zealand, Three Kings Islands, 183 m, 1 species.

Stenothoidae

Aurometopa, new genus

Type species.—*Metopoides aurorae* Nicholls, 1938, here designated.

Etymology.—From the type species, *aurorae* and the genus *Metopa.* Feminine.

Antenna 1 lacking nasiform process on article 1. Accessory flagellum [not discerned]. Palp of mandible 3-articulate; palp of maxilla 1 biarticulate. Inner plate of maxilla 2 ordinary. Inner plates of maxillipeds well separated. Gnathopods 1–2 subchelate, scarcely different from each other in shape, gnathopod 1 small, palm oblique and shorter than posterior margin of propodus; article 4 not incipiently chelate; article 5 short, lobed; article 6 expanded. Gnathopod 2 enlarged, palm strongly oblique, article 5 short, lobed. Pereopod 5 with rectolinear article 2, pereopod 7 with expanded lobate article 2; pereopod 6 with intermediate article 2. Pereonite 4 ordinary. Pleonites 4–6 free; pleonite 3 lacking dorsal process; pleonite 4 not weakly extended posterodorsally. Telson ordinary, flat.

Relationship.—Differing from *Metopoides* and *Proboloides* in the relatively short and weakly lobate carpus of gnathopod 1 with unexpanded elongate propodus.

From *Torometopa* in the perfectly rectolinear article 2 of pereopod 5.

Aurometopa also has article 2 of pereopod 6 differing from pereopod 7 unlike the other genera mentioned.

Species.—*aurorae* (Nicholls, 1938) (J. L. Barnard 1972b) [850].

Marine, Macquarie Island, 0 m, 1 species.

Knysmetopa, new genus

Type species.—*Parametopa grandimana* Griffiths, 1974c, here designated.

Etymology.—From "Knysma," a town near the type locality, and the classic genus *Metopa.* Feminine.

Antenna 1 lacking nasiform process on article 1. *Antenna 2 half as long as antenna 1.* Accessory flagellum absent. Palp of mandible absent; palp of maxilla 1 biarticulate. Inner plate of maxilla 2 ordinary. Inner plates of maxillipeds well separated. *Coxa 2 not bevelled anteriorly.* Gnathopods 1–2 subchelate, strongly different from each other in size and shape, gnathopod 1 small, subchelate, palm oblique and as long as posterior margin of propodus; article 4 chelate and freely projecting, article 5 elongate, unlobed; article 6 slightly expanded. Gnathopod 2 greatly enlarged, palm strongly oblique, articles 4–5 short, lobed. Pereopod 5 with rectolinear article 2, pereopods 6–7 with expanded and lobate article 2. Pereonite 4 ordinary. Pleonites 4–6 free; pleonite 3 lacking dorsal process; pleonite 4 not extended posterodorsally. Telson ordinary, flat.

Variables.—Coxa 4 adze-shaped and pointing posteriorly as in *Stenothoe.*

Relationship.—Differing from *Stenothoe* in the short antenna 2 and non-bevelled anteroventral angle of coxa 2.

From *Wallametopa* in the subchelate gnathopod 1.

From *Parametopa* in the absence of a nasiform process on antenna 1, huge enlargement of gnathopod 2 and rearward pointing adze-shaped coxa 4.

Species.—*grandimana* (Griffiths, 1974c) [743].

Marine, South Africa, 200 m, 1 species.

Torometopa, new genus

Type species.—*Metopa crenatipalmata* Stebbing, 1888, here designated.

Etymology.—From "torus," protuberance, and the genus *Metopa.* Feminine.

Antenna 1 lacking nasiform process on article 1. Accessory flagellum 0–2-articulate. Palp of mandible 3-articulate; palp of maxilla 1 biarticulate. Inner plate of maxilla 2 ordinary. Inner plates of maxillipeds well separated. Gnathopods 1–2 different from each other in size and shape, gnathopod 1 small, almost simple or weakly subchelate, palm oblique and shorter than posterior margin of propodus; article 4 incipiently chelate; article 5 elongate, unlobed; article 6 long, weakly expanded. Gnathopod 2 enlarged, palm strongly oblique, article 5 short, lobed. Pereopod 5 with rectolinear article 2 bearing posteroventral lobe, pereopods 6–7 with expanded and lobate article 2. Pereonite 4 ordinary. Pleonites 4–6 free; pleonite 3 lacking dorsal process; pleonite 4 not weakly extended posterodorsally. Telson ordinary, flat.

Variables.—Inner plate of maxilliped adze-shaped (*perlata*); gnathopod 1 elongate, sublinear (*aequalis, carinata, dentimana, perlata*); pleonite 3 with dorsal tooth (*carinata*).

Relationship.—Differing from *Metopoides* and *Proboloides* in the lobation on article 2 of pereopod 5.

Species.—*aequalis* J. L. Barnard, 1962 [416A];

antarctica Walker, 1906, 1907 (K. H. Barnard, 1932) [871];

carinata (Schellenberg, 1931) (K. H. Barnard, 1932) [833 + B];

crenatipalmata (Stebbing, 1888) (K. H. Barnard, 1932) (Bellan-Santini, 1972a) [867 + 731 + B];
compacta Stebbing, 1888 (Schellenberg, 1931) [867 + B];
crassicornis Schellenberg, 1931 [831];
dentimana Nicholls, 1938 (Bellan-Santini, 1972a, b) [870 + B];
palmata Ruffo, 1949 [802B];
parallelocheir (Stebbing, 1888) (Schellenberg, 1931) (K. H. Barnard, 1932) [867];
perlata K. H. Barnard, 1930 [893];
porcellana K. H. Barnard, 1932 [831];
stephenseni Ruffo, 1949 [802B].

Marine, Antarctica and antiboreal, N. to Tristan da Cunha and Magellan area, into deep southern basins, 10–4986 m, 12 species.

Vonimetopa, new genus

Type species.—*Metopella dubia* Shoemaker, 1964, here selected.

Etymology.—From *Somateria voniger,* duck from which this species was found in stomach and classic genus *Metopa.* Masculine.

Antenna 1 lacking nasiform process on article 1. Accessory flagellum absent. Palp of mandible 1-articulate; palp of maxilla 1 uniarticulate. Inner plate of maxilla 2 ordinary. Inner plates of maxillipeds well separated. Gnathopod 1 small, simple, article 4 incipiently chelate; article 5 short, unlobed; article 6 elongate, linear. Gnathopod 2 weakly enlarged, palm strongly oblique, article 5 short, lobed. Pereopods 5–7 with rectolinear article 2. Pereonite 4 ordinary. Pleonites 4–6 free; pleonite 3 lacking dorsal process; pleonite 4 not weakly extended posterodorsally. Telson ordinary, flat.

Relationship.—Differing from *Metopelloides* in the elongate simple propodus and short lobed carpus of gnathopod 1; and the fully separated inner plates of the maxillipeds.

See *Zaikometopa.*

Species.—*barnardi* Gurjanova, 1938, 1951 [280];
brazhnikovi Gurjanova, 1948, 1951 (Kudrjaschov and Zujagintsev 1975) [280];
dubia Shoemaker, 1964 [277];
schellenbergi Gurjanova, 1938, 1951 [391];
shoemakeri Gurjanova, 1938, 1951 (Kudrjaschov 1979) [280];
zernovi Gurjanova, 1948, 1951 [391].

Marine, Bering Sea, Okhotsk Sea, Japan Sea, shallow to 5 m, 6 species.

Zaikometopa, new genus

Type species.—*Metopelloides erythrophthalmus* Coyle and Mueller, 1981, here selected.

Etymology.—From the paratype locality, "Zaikov Bay," Alaska, and the classic genus, *Metopa.* Feminine.

Antenna 1 bearing nasiform process on article 1. Accessory flagellum absent. Palp of mandible 1-articulate; palp of maxilla 1 biarticulate. Inner plate of maxilla 2 ordinary. Inner plates of maxillipeds mostly fused together. Coxa 2 small and hidden by coxa 3. Gnathopod 1 small, simple, article 4 incipiently chelate; article 5 short, unlobed; article 6 elongate, linear. Gnathopod 2 enlarged, palm parachelate, article 5 short, lobed. Pereopods 5–7 with rectolinear article 2. Pereonite 4 highly elongate. Pleonites 4–6 free; pleonite 3 lacking dorsal process; pleonite 4 strongly carinate posterodorsally. Telson ordinary, flat.

Relationship.—Differing from *Metopelloides* and *Vonimetopa* in the nasiform lobe on article 1 of antenna 1, the mostly fused inner plates of the maxillipeds and the carinate urosomite 1.

From *Metopelloides* also in the short lobed carpus and elongate simple propodus of gnathopod 1; and the unusually small coxa 2 hidden by coxa 3.

Species.—*erythrophthalmus* Coyle and Mueller, 1981 [272].

Marine, Gulf of Alaska westward along Alaskan Peninsula, 0 m, 1 species.

Temnophliantidae

Temnophliidae Griffiths, 1975:171.

Latinists inform us the family name should be emended to the spelling of our center heading.

Diagnosis.—Head slightly reduced in size; basal fusion of antenna 2 [unknown (but probably fused)]; urosomal fusion unknown; pleon small and flexed below body; thorax depressed, very broad and flat or triquetrous, segments laterally discontiguous and produced into pleurae; coxae, though small, splayed outwards. Eyes small, ommatidial. Antennae short. Accessory flagellum absent. Mandible lacking palp, molar degraded, styliform; maxillae feeble. Gnathopods simple. Peduncles of pleopods expanded. Uropods 1–2 with one ramus, uropod 3 without ramus. Telson entire, laminar or appearing weakly fleshy, pyriform.

See Phliantidae; Eophliantidae; Plioplateidae.

Description.—Head with thorn-like rostrum. Antennal flagella 1–2-articulate. Right lacinia mobilis absent; rakers sparse. Inner lobes of lower lip absent. Inner plate and palp of maxilla 1 absent, outer plate with 4–5 spines. Maxilla 2 poorly setose. Maxillipeds short, stout, plates ordinary, palp 2-articulate. Coxae rectangular, bifid, or trifid. Gnathopods and pereopods either simple or prehensile. Article 2 of pereopods 5–7 unexpanded. Body smooth dorsally or elevated in triquetral fashion with processes on head, pereon and pleonites 1–2. Rami of pleopods well developed. Rami of uropods 1–2 very short. Oostegite form and count and gill formulas [unknown]; gills slender; setae of oostegites curl-tipped.

Relationship.—Differing from Phliantidae, Eophliantidae, and Plioplateidae (see J. L. Barnard 1978) in the presence of pereonal pleurae. Similarity in body form between *Hystriphlias* and Plioplateidae suggests descent through common ancestor.

Key to the Genera of Temnophliantidae

1. Body flat, lacking dorsal processes, coxae simple, all thoracic legs simple .... *Temnophlias*
– Body triquetrous, with dorsal processes, coxae bifid or trifid, all thoracic legs prehensile ...... *Hystriphlias*

Hystriphlias, new genus

Type species.—*Temnophlias hystrix* K. H. Barnard, 1954, here selected.

Etymology.—From the old name of the taxon, *Temnophlias hystrix.* Neuter?

Diagnosis.—Body triquetrous, with dorsal processes, coxae bifid or trifid, all thoracic legs prehensile.

Species.—*hystrix* (K. H. Barnard, 1954) (Griffiths 1975) [743].

Marine, South Africa, littoral, 1 species.

Temnophlias K. H. Barnard

Temnophlias K. H. Barnard, 1916:158 (*Temnophlias capensis* K. H. Barnard, 1916, monotypy).—Griffiths, 1975:172.

Diagnosis.—Body flat, lacking dorsal processes, coxae simple, all thoracic legs simple.

Species.—*capensis* K. H. Barnard, 1916, 1954 (Griffiths 1975) [743].

Marine, South Africa, littoral, 1 species.

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OSTRACODA FROM THE SKAGERRAK, NORTH SEA (MYODOCOPINA)

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Abstract.—*Doloria sarsi,* new species, is described and illustrated, and a supplementary description is presented of *Philomedes lilljeborgii* (Sars, 1865) from specimens collected in 1865 in the Skagerrak. The synonymy for *P. lilljeborgii* is comprehensive. A key is presented to certain species of *Philomedes.*

The Skagerrak is a broad arm of the North Sea bounded by the southeastern coast of Norway on the northeast, Denmark on the south, and the western end of Sweden on the east. While preparing a paper on the Myodocopina of the Bay of Biscay (in press), I borrowed for comparative purposes from the Naturhistoriska Riksmusset, Stockholm, Sweden, two vials of specimens collected in the Skagerrak that had been referred to *Philomedes lilljeborgii* by Skogsberg (1920:410). Some of the specimens of *lilljeborgii* that I examined from the vials had fewer bristles on the endopodite of the 2nd antenna, the mandible, and 7th limb than on the specimens described by Skogsberg. The differences, as well as some additional characters not mentioned by Skogsberg, are presented herein in a supplementary description. One of the vials, which contained about 130 specimens of *P. lilljeborgii,* also had an adult female of a new species of *Doloria.* Although only the single specimen of the new species was available, its distinctiveness warranted its description. All specimens have been returned to Dr. A. Andersson, Naturhistoriska Riksmuseet, Stockholm, Sweden.

Extensive collections of ostracodes in the Skagerrak by Elofson (1941) contained only four species in three genera of Myodocopina: *Prionotoleberis norvegica* (Sars, 1869), *Philomedes brenda* (Baird, 1850), *P. lilljeborgii* (Sars, 1865), and *Vargula norvegica* (Baird, 1860). Thus, the new species, *Doloria sarsi,* increases the number of species known from the Skagerrak to five, and the number of genera to four.

One of the common species in the Skagerrak, *Philomedes brenda,* was reported [as *P. globosa*] at station 1101 in the Mediterranean Sea by Granata and Caporiacco (1949: 38). Because of some discrepancies in that paper discussed by me in a previous paper (Kornicker 1982:5), I referred the specimens collected at station 1101 to *Philomedes* species indeterminate (Kornicker 1982:5). I later wrote enquiring about the sample to Dr. Christian Carpine, Conservateur des Collections, Institut Océanographique, Monaco, where the specimens reported by Granata and Caporiacco are deposited. She informed me (in litt., 7 May 1986) that *Philomedes globosa* [=*P. brenda*] had been listed erroneously in the sample from station 1101, and that the species listed should have been *Conchoecia inermis* (Claus, 1891). Therefore, I herewith refer to *Conchoecia inermis* the specimens from sample 1101 that had been referred to *P. globosa* by Granata and Caporiacco (1949: 38) and to *Philomedes* species indeterminate by Kornicker (1982:5). Although *C. inermis* was not listed at station 1101 by Granata and Caporiacco (1949) on page 38, that station was reported to have the species on page 31. On page 31 station 1101 is listed as having been collected in the campaign of

1991; the year should have been 1901 according to Dr. Carpine.

Philomedidae Müller, 1906
Genus *Philomedes* Liljeborg, 1853

Discussion.—Two species of *Philomedes* have been reported from the Skagerrak: *P. brenda* (Baird, 1850) and *P. lilljeborgii* (Sars, 1865). A supplementary description of the latter is given herein, and a key is presented to species of *Philomedes* having a 7th limb with a terminal end similar to that of *P. lilljeborgii.*

Key to Adult Females of Certain Species of *Philomedes* (7th Limb with 5 or more Terminal Pegs 3–4 times Longer than Wide)

1\. Dorsal margin of mandibular basale with 3 bristles .... *P. curvata* Poulsen, 1962

– Dorsal margin of mandibular basale with 4–7 bristles 2

2\. 7th limb with 9–11 bristles 3

– 7th limb with more than 15 bristles 4

3\. Small process at inferior end of rostrum extending to outer edge of lamellar prolongation of selvage ... . *P. tetradens* Kornicker and Caraion, 1977

– Small process at inferior end of rostrum either lacking, or if present, not reaching outer edge of lamellar prolongation . . *P lilljeborgii* (Sars, 1865)

4\. 2nd endopodial joint of 2nd antenna with 3 bristles .... *P. orbicularis* Brady, 1907

– 2nd endopodial joint of 2nd antenna with 5 bristles .... *P. subantarctica* Kornicker, 1975

– 2nd endopodial joint of 2nd antenna with 2 bristles 5

5\. Carapace length greater than 3 mm and with diagonal bristle-bearing list on inner surface of caudal process; 7th limb with 10–11 pegs .... *P. multidentata* Chavtur, 1983

– Carapace length less than 3 mm and without diagonal bristle-bearing list on inner surface of caudal process; 7th limb with 5–7 pegs 6

6\. 4th joint of 1st antenna with 3 ventral bristles; 1st endopodial joint of 2nd antenna with 5 bristles .... *P. longidentata* Chavtur, 1983

– 4th joint of 1st antenna with 4 ventral bristles; 1st endopodial joint of 2nd antenna with 6 bristles .... *P. albatross* Kornicker, 1982

Philomedes lilljeborgii (Sars, 1865)
Figs. 1, 2a–d

Bradycinetus Lilljeborgii Sars, 1865:112.—Brady, 1868:468; 1872:59.—?Brady and Robertson, 1872:70.—Jones, Kirkby, Brady, 1874:9.

Philomedes Lilljeborgii.—Sars, 1869:356, 357; 1872:252, 280, 286; 1886:74, 89; 1887:220, 226; 1890:15.—Norman, 1891: 119, 121.—Müller, 1893:380; 1894:186, 209; 1897:2.—?Brady and Norman, 1896: 658–659, 661, pl. 5:figs. 4–6, pl. 52:figs. 3, 4.—?Gran, 1902:20, 66, 67, 80, 131, 132, 141–146, 151, 160, 161, 209, 210.—Ostenfeld, 1931:611.

Bradycinetus lilljeborgii.—Brady, 1871:293.

Bradycinetus lilljeborgi.—Brady, 1880:154.

Philomedes Lilljeborgi.—?Cleve, 1903:24.—Conseil Permanent International pour l'Exploration de la Mer, 1903:210, 286, 287, 306; 1904:25, 50–51, 61; 1906:97.—Ostenfeld and Wesenberg-Lund, 1909: 114.—?Apstein, 1911:169, pl. 23:fig. 4.

Philomedes Liljeborgii.—?O. Paulsen, 1909: 38–40; 1918:18, 20, 21.

Philomedes lilljeborgi.—?Steuer, 1910: 376.—Sars, 1922:14, 15, pl. 8.—Soot-Ryen, 1927:19.—Klie, 1929:3, 43; 1944: 2–4, fig. 4.—Müller, 1931:23 [excluding specimens from Kola Fjord].—Ostenfeld, 1931:641.—?Stephensen, 1938:3, 17.—Puri and Hulings, 1957:171.—Neale, 1965:269.—Puri, 1966:460.—Brattegard, 1967:302.—Carpine, 1970:64.—Hartmann, 1975:577.—Kornicker, 1975: 64, 271, 272.—Cohen and Kornicker, 1975:26.—Chavtur, 1983:11, 17, 39, 40.

Philomedes lilljeborgii.—Müller, 1912:XV, 26, 32, 428.—Kornicker, 1975:75–76; 1982:23; 1984:23.—Kornicker and Caraion, 1977:8–12, 15, 19.

Philomedes (Philomedes) Lilljeborgi.—Skogsberg, 1920:2, 349, 350, 354, 365, 366, 369, 375, 384–386, 389, 391, 402–411, 413, 414, 416, 422, figs.70–73.

Philomedes (Philomedes) lilljeborgi.—Elofson, 1941:233, 238–240, 369, 372, 375, 393, 394, 403, 405, 419, 420, 426, 451, 456, 467, 468, 472, 473, 486, 487, 488, 497, 523; 1943:3; 1969:11, 16–18, 139, 141, 143, 157, 165, 166, 176, 177, 181, 200, 203–205, 213, 215, 218, 219, 229–231, 241, 275.

Philomedes bonneti Kornicker and Caraion, 1977:3, 4, 9–15, figs. 6–10.—Kornicker, 1982:23 [key].

Not *Philomedes lilljeborgi.*—E. M. Poulsen, 1962:346, fig. 151.—Darby, 1965:25, 26, 53, pl. 10:figs. 1–11 [=*P. keslingi* Kornicker, 1984:23].

Holotype.—Lost (Skogsberg 1920:409).

Type locality.—Near Drobak, Christiania Fjord, 110–183 m.

Material.—2 vials in the Naturhistoriska Riksmuseet, Stockholm, Sweden. Vial 1: Approximately 130 juveniles and adult females and the following labels, "125," "contr. T. Skogsberg," "*Philomedes Lilljeborgii* (Sars), Koster Fjorden, Lerbotten, 100f, 5.8.1865," "5/8/1865, Koster Fjorden, 100f." Vial 2: Approximately 90 juveniles and adult females and the following labels, "129," "T. Skogsberg cont.," "*Philomedes Lilljeborgii* (Sars), Skagerak 330 f.l. Lindahl," a 4th small label having the same information as previous label except Skagerak spelled "Skagerrak." Skogsberg (1920: 410) referred to the sample in vial 1 as "Koster; 5. VIII. 1865; depth 180 m; clay; 130 specimens, mature females and larvae (coll. unknown); R. M. S. 125," and he referred to sample 129 in vial 2 as one of several samples collected by J. Lindahl without definite localities but at depths indicating they were taken in the Norwegian Depression; depth of the sample was given as 350 m. Skogsberg reported 211 females and juveniles in sample 129, fewer than in the vial I received.

Distribution.—Records of this species are well documented off the western coasts of Norway and Sweden and in the Skagerrak bordering Sweden at depths roughly between 50–914 m, but according to Elofson (1969:16) specimens are usually found at depths greater than 200 m. The species also has been reported southwest of Ireland, off Iceland, the Faeroe Islands, Beer Island, in the Barents Sea, and elsewhere in the North Sea; however, identifications from those areas are not well documented, and I have questioned some identifications in the synonymy. Confirmation is especially needed for Iceland, because the misidentification of specimens from near Iceland by Poulsen (1962:346) suggests that another species resembling *P. lilljeborgii* lives there. Kornicker and Caraion (1977:9) described *P. bonneti* collected off Mauritania at a depth of 1120 m. Except for being smaller, I cannot find a specific character to separate the species from *P. lilljeborgii* as defined herein, and therefore, have referred it to that species

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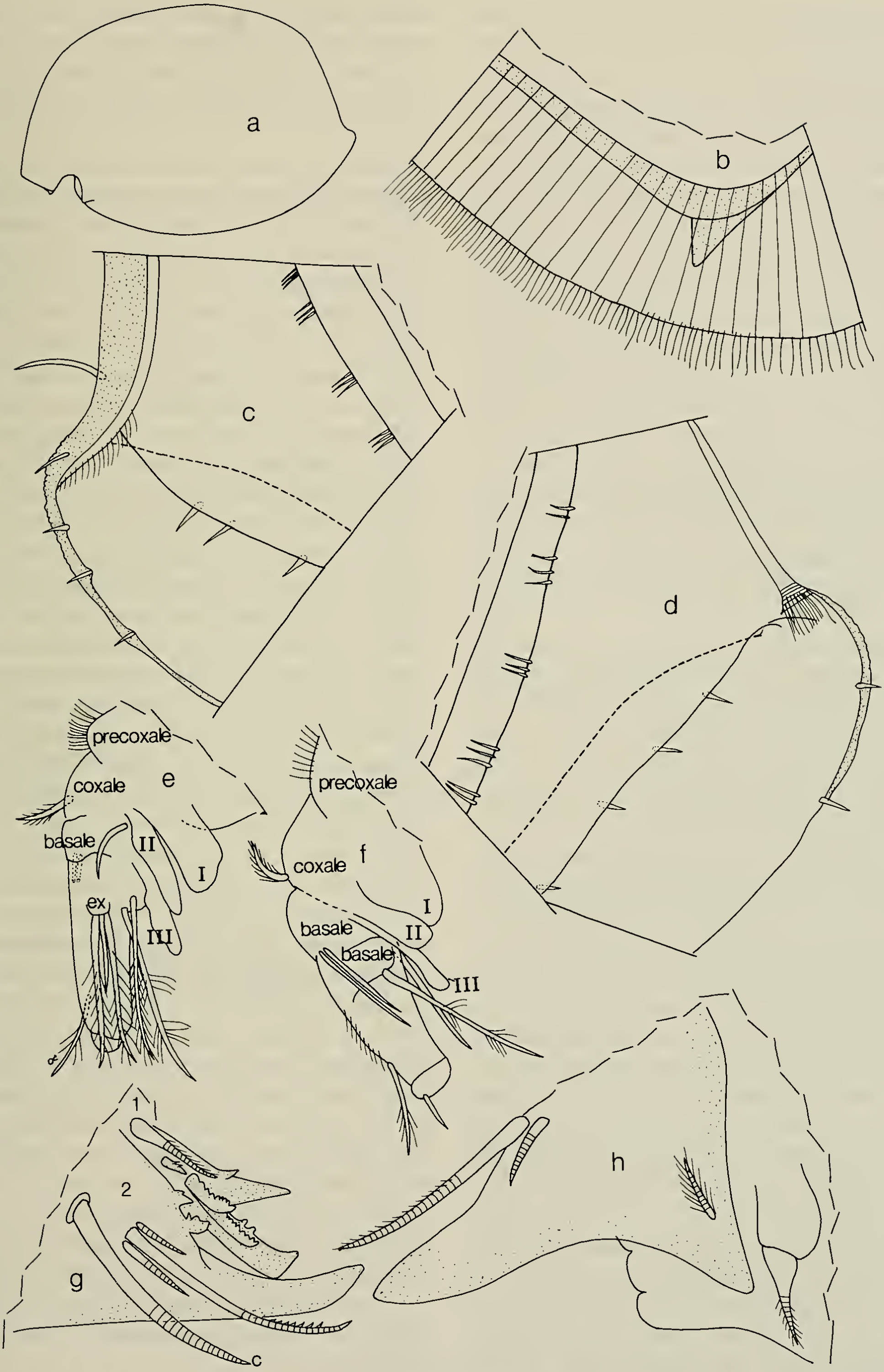
Fig. 1. *Philomedes lilljeborgii,* adult female from vial 1: a, Complete specimen, length 2.24 mm; b, Inferior tip of rostrum of right valve showing triangular process and lamellar prolongation of selvage, inside view; c, d, Tips of caudal processes of left and right valves, respectively, inside view; e, f, Lateral view of left maxilla and



medial view of right maxilla, respectively, not all bristles shown; g, 1st and 2nd exopodial joints of left 5th limb, posterior view; h, 2nd exopodial joint of right 5th limb, anterior view.

(see Discussion). This extends the range of *P. lilljeborgii* south to the continental slope of Mauritania.

Supplementary description of adult female (Figs. 1, 2a–d).—Carapace with slightly convex ventral and dorsal margins and fairly linear anterior and posterior margins (Fig. 1a); anterior edge of rostrum linear or very slightly concave; anterior and inferior corners of rostrum forming close to right angle; inferior corner of rostrum with small pointed process reaching about midwidth of lamellar prolongation of selvage (Fig. 1b); posteroventral corner of valve with small but distinct caudal process projecting posteriorly; minute process present ventral to incisur and just reaching or projecting past valve edge (Fig. 1a); outer edge of caudal process minutely crenulate when viewed at high magnification (×40 objective) (Fig. 1c, d).

Ornamentation: Carapace with widely scattered long and short slender bristles, some with broad base; about 10 bristles on outside of shell near edge along ventral and posterior margin of caudal process, additional bristles near outer edge of ventral and anterior margins of valve.

Infold (Fig. 1c, d): Rostral infold with about 17 spinous and divided bristles forming single row parallel to anterior edge of rostrum, and 4 shorter and more slender bare bristles along ventral edge of rostrum (bare bristle nearest to inner end of incisur shorter than others); 1 small bristle present on infold just posterior to inner end of incisur; anteroventral infold with 11–14 parallel striae and 16 short spinous bristles forming row (no striae between bristles and outer edge of valve); list with anterior end at base of posterior bristle (of anteroventral row), continuing posteriorly parallel to ventral margin, then bending dorsally away from valve edge (farthest from valve edge opposite caudal process); posteroventral and posterior list with slender bristles forming groups of 1–5. Narrow pocket present at caudal process with 4–5 small bristles along ventral edge; 1–3 small bristles on infold just anterior to pocket; 3 small bristles at outer edge of caudal process having bases just lateral to selvage (bristles not part of infold).

Selvage (Fig. 1b–d): Broad lamellar prolongation along rostrum and ventral margin of incisur appearing segmented (segments perpendicular to valve edge and with narrow striae), and with marginal fringe; selvage along anteroventral margin with long filaments with bases on lateral side of prolongation at about midwidth; prolongation along ventral and posteroventral margin with narrow striae (better developed in proximal half of prolongation) and marginal fringe; posterior half of prolongation of ventral selvage without lateral filaments and with proximal part defined by its distal edge at about midwidth of prolongation; prolongation along caudal process narrow and without marginal fringe; prolongation along posterior edge of valve dorsal to caudal process narrow and with marginal fringe; on right valve hairs forming tranverse rows just dorsal to caudal process (Fig. 1b–d); on left valve long hairs just dorsal to caudal process parallel valve edge (Fig. 1c).

Size: Sample 125, 2 specimens: 1st specimen, right valve in concavity slide and under cover slip, length 2.24 mm, height 1.51 mm; 2nd specimen, length 2.20 mm, height 1.50 mm. Skogsberg (1920:404) gave length of specimens he studied as 2.15–2.6 mm.

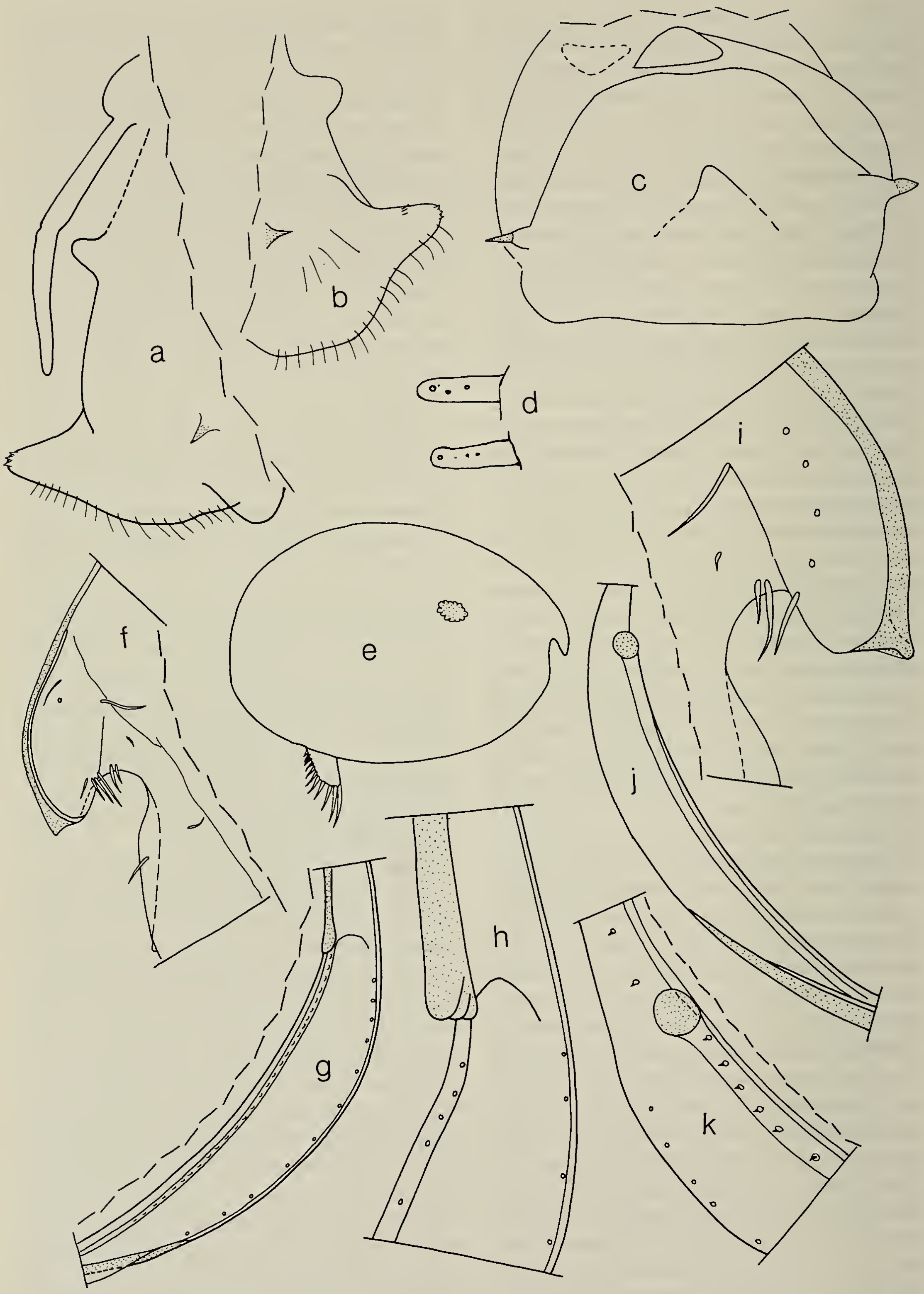
First antenna: Pilosity: 1st joint with medial spines forming rows near ventral margin and more widely scattered spines on medial surface; 2nd joint with medial spines forming rows near and on dorsal margin, a few longer medial spines proximally near ventral margin, lateral spines forming row parallel to distal margin in dorsal half of joint, and few lateral spines forming distal rows near ventral margin. Bristles of limb similar to those described by Skogsberg (1920:406).

Second antenna: Protopodite bare. Endopodite 2-jointed: 1st joint with 6 short bristles (5 proximal, 1 distal); 2nd joint of left limb of 1st specimen with 1 long ventral bristle (with wreaths of long spines) followed by 2 shorter ventral bristles (without long spines) and 1 recurved terminal filament; 2nd joint of right limb of same specimen with long ventral bristle (with wreaths of long spines) followed by 1 shorter bristle (without long spines) and recurved terminal filament. 2nd joint of left limb of 2nd specimen with 1 long ventral bristle (with wreaths of long spines) followed by 1 short bristle (without long spines), 1 longer bristle with long spines, and recurved terminal filament; right limb of 2nd specimen with 1 long bristle (with wreaths of long spines) followed by 1 short bristle (without long spines), 1 longer bristle with long spines, 1 short bristle without long spines, and recurved terminal filament. Exopodite: 1st joint with small straight medial bristle on distal margin; bristles of joints 2–5 short, without natatory hairs or ventral spines; bristles of joints 6–8 long, with natatory hairs; 9th joint with 7 bristles, all but shorter 1 or 2 bristles with natatory hairs; joints 3–8 with small basal spines (spines longer on distal joints); basal spine of 8th joint about half length of joint; lateral spine not observed on 9th joint; joints 3–8 with short spines forming rows.

Mandible: Bifurcate and spinous coxale endite with small ringed bristle near base; medial surface of coxale with spines forming rows. Basale: dorsal margin with 3 or 4 bristles (with few long spines near middle) distal to midlength and 2 terminal bristles (long bristle with 2 rings of long spines near middle; shorter bristle lateral, about half length of long bristle and about same length as dorsal margin of 1st endopodial joint); lateral side with 5 bristles near or on ventral margin; ventral margin with 3 distal bristles (both lateral and ventral bristles with wreaths of long spines); medial side with 6 proximal bristles (3 stout, pectinate, 3 slender with wreaths of long spines), and long spines forming rows. Exopodite about ¾ length of dorsal margin of 1st endopodial joint, hirsute distally, with 2 distal bristles (proximal longer and with wreaths of long spines; distal bare). 1st endopodial joint: ventral margin with 4 bristles, all with wreaths of long spines; medial surface with short spines forming rows. 2nd endopodial joint: ventral margin with 6 distal bristles forming 2 groups, each with 3 spinous bristles; dorsal margin with 11 or 12 bristles near middle forming 3 groups of 4 or 5, 1 (medial), and 6 bristles; medial surface with spines forming rows. End joint: with 3 claws with faint ventral proximal teeth, and 4 bristles.

Maxilla (Fig. 1e, f): Endite I broad, with 8 spinous and pectinate bristles; endite II slender, with about 6 spinous and pectinate bristles; endite III long, slender, with 1 proximal bare bristle and about 10 distal spinous and pectinate bristles. Precoxale with dorsal fringe of long hairs. Coxale with stout hirsute dorsal bristle. Basale with 4 distal bristles: 2 slender, dorsal, and 2 ventral (1 lateral, 1 medial). Exopodite with 3 bristles (1 short, bare, 2 long with wreaths of long hairs). 1st endopodial joint with dorsal spines, 1 alpha-bristle with wreaths of long spines, and 5 slender beta-bristles; bristles of end joint similar to those described by Skogsberg (1920:408).

Fifth limb (Fig. 1g, h): Epipodite with 55 bristles. 1st exopodial joint with 4 constituent teeth; distal tooth bifurcate with large pointed anterior proximal tooth having a smaller pointed tooth near its base (Fig. 1g); bristle proximal to small posterior tooth with short spines; anterior side near outer edge with short stout bristle on small lobe; usual 2 spinous anterior bristles not observed on specimen examined. 2nd exopodial joint with 2 small teeth (both with 1 or 2 marginal teeth) on inner curvature of the large flat triangular sclerotized tooth (Fig. 1g); group of 3 posterior bristles comprising stout pectinate middle bristle with 1 small bristle on each side; c-bristle stout, bare; distal outer corner or large flat tooth with small spinous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anterior bristle (Fig. 1h). 3rd exopodial joint with 3 bristles on inner lobe and 2 hirsute bristles on outer lobe. 4th and 5th joints fused, hirsute, with 5 spinous terminal bristles.

Sixth limb: Epipodite represented by 4 small hirsute bristles. Endite I small, with 2 medial and 1 terminal bristle; endite II narrower and about half length of endites III and IV, with 1 medial and 3 terminal bristles; endite III with 1 medial and 7 or 8 terminal bristles; endite IV with 1 medial and 8 terminal bristles. End joint with 29–30 hirsute and spinous bristles.

Seventh limb: With 9 or 10 bristles: proximal group with 4 or 5 bristles, 2 or 3 on each side, each with 5–6 bells; terminal group with 3 bristles on peg side, each with 4–5 bells, and 2 bristles on comb side, each with up to 6 bells; all bristles with distal marginal spines proximal to bells. Comb with about 13 teeth; each tooth comprising rounded central part with alar projection on each side; alar projection pointed at distal end; side opposite comb with 9 elongate rounded pegs (pegs arranged in ellipse without central peg, but appearing as 2 rows (each with 4–5 pegs) on appendage compressed under cover slip). (Skogsberg (1920: fig 72:14) illustrated limb with 11 pegs.)

Furca: Each lamella with 10 claws; claws decreasing in length along lamella; claws 1–6 with spines forming medial row near base, claws 7–10 without spines forming row; claw 1 of right lamella anterior to claw 1 of left lamella; claw 1 with teeth forming 2 rows and claws 2–6 with single row of stout teeth along slightly concave posterior margins; anterior margins of claws 1–6 convex and with few or no anterior spines; claws 7–10 with spines of similar size and abundance forming row along linear anterior and posterior margins (claws 7–10 could be considered secondary); hairs present on lamella following claw 10 and also between claws.

Bellonci organ (Fig. 2a): Elongate, cylindrical, with rounded tip.

Eyes: Lateral eyes cylindrical, minute, with few minute cells (ommatidia?) (Fig. 2d). Medial eye without pigment (Fig. 2a).

Upper lip (Fig. 2a–c): Tapering anteriorly and with minute glandular processes at tip.

Anterior of body (Fig. 2a): Rounded anterior process between medial eye and upper lip. Stout, lateral, pointed, spine-like process on each side of body proximal to upper lip (process not previously reported on the Philomedidae) (Fig. 2c).

Y-sclerite: Typical for genus.

Remarks.—A lateral spine-like process on each side of the body proximal to the upper lip has not been reported previously on members of the Philomedidae. However, such processes are visible on an SEM micrograph of *Tetragonodon ctenorynchus* (Brady, 1887) published by Kornicker and Caraion (1977: pl. 13b), suggesting that the processes might be common but were previously overlooked.

Variability.—Female: Skogsberg (1920: 406) gave the number of ventral bristles on the 2nd endopodial joint of the 2nd antenna as 3 or 4; one of the specimens studied herein has 2 ventral bristles on one limb and 3 on the other; thus expanding the variability of the number of ventral bristles to 2–4. Skogsberg (1920:408) gave the number of dorsal bristles on the mandibular basale as 6 or 7;

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Fig. 2. *Philomedes lilljeborgii,* adult female from vial 1: a, Anterior of body viewed from left side showing medial eye and Bellonci organ, rounded anterior process, and upper lip; b, Anterior of body viewed from right side showing anterior process and upper lip; c, Anterior of body viewed from front showing anterior process at top midwidth, and upper lip (angle near midwidth represents anterior tip of lip); d, Right and left lateral eyes. *Doloria sarsi,* adult female, holotype: e, Complete specimen showing right lateral eye as seen through shell and projecting furca, length 2.67 mm; f, Rostrum of right valve, inside view; g, Caudal process of right valve, inside view; h, Detail from g; i, Rostrum of left valve, inside view; j, Caudal process of left valve, inside view; k, Detail from j.

a specimen studied herein has 5 bristles on one mandible and 6 on the other; thus expanding the variability of the number of dorsal bristles to 5–7. Skogsberg (1920:408) gave the number of bristles on the 7th limb as 10 or 11. A specimen studied herein has 9 bristles on one limb and 10 on the other; thus expanding the variability of the number of bristles to 9–11. Skogsberg (1920:408) reported the basale of the maxilla to have 2 (rarely 3) anterior bristles. The specimen I examined has 2 bristles in that position.

Discussion.—Appendages of male *P. lilljeborgii* collected in the vicinity of either Norway or Sweden have not been described. However, the mandibular basale, maxilla, and 7th limbs of female and male *Philomedes* generally have the same number of bristles. According to Poulsen (1962:348, 349) the male from near Iceland that he referred to *P. lilljeborgii* has only three dorsal bristles on the mandibular basale, one anterior bristle on the basale of the maxilla, and 27–30 bristles on the 7th limb. These are outside the range of variability of these characters on female *P. lilljeborgii*; therefore, I here refer Poulsen's male to *Species Inquirenda.* Poulsen (1962:346) also referred a juvenile female to *P. lilljeborgii* but only gave its length; therefore, I here refer that specimen also to *Species Inquirenda.*

In a key to species of *Philomedes,* Chavtur (1983:38–40) separated *P. lilljeborgii* from other species by its having eight dorsal bristles on the mandibular basale. That number is outside the five to seven bristles that have been reported on specimens from Denmark and Sweden.

In their description of *P. bonneti* collected off Mauritania at a depth of 1120 m, Kornicker and Caraion (1977:15) listed for *P. bonneti* the following characters that separate *P. bonneti* from *P. lilljeborgii*: minute digitations along the posterior edge of the caudal process, five dorsal bristles on the mandibular basale, and nine bristles on the 7th limb. In the present study of *P. lilljeborgii,* minute digitations were observed (at high resolution, ×20 objective, ×15 eyepiece) along the posterior edge of the caudal process, and the variability of the number of dorsal bristles on the mandibular basale and on the 7th limb was found to include the number of bristles on those appendages of *P. bonneti.* That species, therefore, is here referred to *P. lilljeborgii.* The length of the single female measured by Kornicker and Caraion (1977:10) was 1.99 mm, smaller than females of *P. lilljeborgii* from Norway and Sweden (2.15–2.6 mm).

Cypridinidae Baird, 1850

Discussion.—The single specimen upon which the new species here described is based, is an adult female belonging to either the genus *Doloria* Skogsberg, 1920:223, or *Paradoloria* Hanai, 1974:119. Because the two genera can be separated only by morphological differences in adult males it is not possible with certainty to refer the new species to either genus. I have referred it to *Doloria* because it resembles in many characters the type species (*D. levis*) of *Doloria.*

Genus *Doloria* Skogsberg, 1920

Type species.—*Cypridina* (*Doloria*) *levis* Skogsberg, 1920:225.

Doloria sarsi, new species
Figs. 2e–k, 3

Etymology.—For G. O. Sars.

Holotype.—Adult female; unique specimen from vial R. M. S. 125, Naturhistoriska Rikmuseet, Stockholm, Sweden.

Type locality.—Koster Fiord, Lerbotton, Skagerrak, west coast of Sweden, depth 100 fm (182.9 m); collected 5 Aug 1865.

Distribution.—Known only from type locality.

Description of adult female (Figs. 2e–k, 3).—Carapace smooth, oval in lateral view with posteroventral caudal process not marked by abrupt change in curvature (Fig. 2e, g, j); incisur small, at valve midheight;

anterior edge and tip of rostrum unusual in having a lip folding inward (visible best in medial view at high resolution (with ×10 objective, 15× eyepiece; Fig. 2f, i).

Infold: Broad in area of rostrum, caudal process, and ventral to incisur, becoming narrower elsewhere (Fig. 2f, g, j). Bristles of rostral infold mostly missing on specimen but indicated by sockets on left valve (Fig. 2i); 2 unequal bristles at inner end of incisur (Fig. 2f, i); anteroventral infold with about 10 bifurcate bristles (several more indicated by sockets); broad list along anterior edge of caudal process with smooth posterior edge and minute inwardly oriented spine-like processes; list of caudal process of left valve terminating dorsally in round knob (Fig. 2j, k); list of caudal process of right valve terminating at ventral end of ridge along inner edge of posterodorsal infold (Fig. 2g, h); dorsal part of broad selvage of caudal process of right valve posterior to list with depression with convex dorsal margin (Fig. 2g, h). Infold of caudal process of right valve broader than that of left valve.

Selvage: Lamellar prolongation present along anterior and ventral margins of valves, absent along posterior margin; prolongation divided at inner end of incisur; prolongation along anteroventral margin with minute spines along edge, elsewhere edge smooth.

Locking device: When posterior edges of lateral outlines of drawings of left and right valves are superimposed, the rounded knob at dorsal end of list of caudal process of left valve (Fig. 2k) appears to lie within depression posterior to dorsal end of list of caudal process of right valve (Fig. 2h) suggesting a locking device possibly useful for aligning valves.

Size: Holotype, length 2.67 mm, height 1.87 mm.

First antenna (Fig. 3a, b): 1st joint bare. 2nd joint with small hairs forming rows along dorsal margin. 3rd joint short, with 2 bristles bearing short marginal spines (dorsal bristle proximal with base about ⅓ length of joint from proximal suture of joint, ventral bristle terminal). 4th joint elongate with 2 terminal bristles (1 ventral, 1 dorsal). Sensory bristle of 5th joint with 10 long stout proximal filaments (proximal 4 filaments with tips missing, remaining 6 filaments about ½ length of stem), 2 slender short distal filaments, and bifurcate tip. 6th joint with short medial bristle. 7th joint: a-bristle spinous, slightly longer than bristle of 6th joint; b-bristle about ⅔ length of sensory bristle of 5th joint, with 5 short marginal filaments, some pectinate; c-bristle ⅓ longer than sensory bristle, with 8 marginal filaments, and bifurcate tip. 8th joint: d- and e-bristles longer than b-bristle, bare with blunt tips; f-bristle same length as c-bristle, with 8 marginal filaments (some pectinate) and bifurcate tip; g-bristle longer than f-bristle, with 11 marginal filaments (some pectinate), and bifurcate tip.

Second antenna (Fig. 3c): Protopodite with small spinous medial bristle. Endopodite 3-jointed: 1st joint with 4 proximal bristles (3 short, 1 long) and 1 long distal bristle; 2nd joint elongate, bare; 3rd joint small, well defined from 2nd joint by suture, with long terminal filament. Exopodite: bristle of 2nd joint reaching just past 9th joint, with 19–23 slender ventral spines (spines longer distally), and no dorsal hairs or spines on left limb but some slender dorsal spines on right limb, tip of bristle with terminal papilla; bristles of joints 3–8 with natatory hairs, no spines; 9th joint with 4 bristles (3 long, 1 short), all with natatory hairs, no spines; joints 2–8 with basal spines; spine of 8th joint about ½ length of 9th joint; 9th joint with lateral spine longer than joint.

Mandible (Fig. 3d): Coxale endite tapering to point, spinous, with terminal spines not markedly stouter than others; small bristle near base of endite. Basale: ventral margin with 2 a-bristles, 1 small b-bristle, 2 c-bristles, and 2 d-bristles; dorsal margin with 1 midbristle (with short marginal spines) and 2 terminal bristles with short marginal spines. Exopodite hirsute, reach-


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ing past distal end of dorsal margin of 1st endopodial joint, with 2 distal bristles, both with short marginal spines, proximal bristle longer. 1st endopodial joint with few terminal spines on dorsal margin and 4 ventral bristles (2 long, 2 short on left limb, 1 long, 3 short on right limb (aberrant), all with marginal spines). 2nd endopodial joint: medial surface with few small distal spines; ventral margin with small spines and 3 slender bristles forming 2 groups of 1 and 2 bristles (medial and lateral bristle of distal pair about same diameter); dorsal margin with 6 long bristles followed by 1 short bristle (all with short marginal spines) and 14 cleaning-type bristles (6 with stout marginal spines, 8 with slender marginal spines) (dorsal bristles not shown on illustrated limb). End joint with 3 bare claws with hook-like tips (dorsal claw shorter than others) and 4 bristles (no bristles with broad proximal part).

Maxilla (Fig. 3e–h): Endite I broad with 8 spinous terminal bristles and claws; endite II narrow with 6 spinous terminal bristles and claws; endite III narrow with 1 slender proximal bristle (outline of bristle shown on Fig. 3e), 2 distal bristles on anterior edge, 1 short terminal claw, and 2 terminal bristles. Coxale with fringe of dorsal hairs and hirsute dorsal bristle. Basale with 4–6 bristles: 1 terminal (with long hairs) on ventral margin, 1 short bristle on distal edge near ventral margin, and 2–4 terminal bristles on dorsal margin. Exopodite with 3 bristles (1 proximal, 2 terminal). 1st endopodial joint with 2 alpha-bristles, 2 beta-bristles (longest pectinate), and dorsal hairs; cutting tooth weakly developed with slightly digitate edge. 2nd endopodial joint with 3 a-bristles, 2 small claw-like b-bristles, 2 or 3 short ringed b-bristles (3rd b-bristles could be interpreted to be 4th a-bristle), 2 stout ringed c-bristles, and 3 stout, curved, nonpectinate claw-like d-bristles (Fig. 3h).

Fifth limb (Fig. 3i–l): Tooth not observed on protopodite. Endite I with 7 spinous bristles; endite II with 2 spinous and 3 pectinate bristles; endite III with 3 bristles at inner corner (additional bristles obscure). 1st exopodial joint: main tooth with triangular peg (illustrated left limb probably aberrant in not having peg present on right limb) and 6 constituent teeth (secondary marginal teeth mostly bifurcate); spinous bristle proximal to peg. 2nd endopodial joint with spinous posterior c-bristle, spinous anterior d-bristle, 4 pectinate a-bristles, and total of 8 b- and b′-bristles; additional anterior bristles obscure on specimen. Inner lobe of 3rd exopodial joint undeveloped, with 2 bristles (1 with long hairs, other with short spines); outer lobe hirsute, with 2 bristles with long proximal hairs and short distal spines. 4th and 5th exopodial joints fused, hirsute, with 2 terminal bristles (outer with long proximal hairs and short distal spines, inner with long hairs). Epipodite incomplete, remaining part with 52 hirsute bristles.

Sixth limb (Fig. 3m): Epipodite with 2 or 3 bare bristles. Endite I with 2 short hirsute medial bristles and 2 long terminal bristles (1 with long proximal and short distal spines, other with long spines to tip); endite II with 2 short hirsute medial bristles and 2 long

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Fig. 3. *Doloria sarsi,* adult female, holotype: a, Left 1st antenna; b, Same, showing bristles of joints 7 and 8; c, Distal part of protopodite and endopodite of right 2nd antenna; d, Left mandible, dorsal bristles of 2nd endopodial joint not shown; e, Left maxilla, medial view, not all bristles shown; f, Right maxilla, lateral view, not all bristles shown; g, Same, endites I–III; h, Same, 3 stout d-bristles of end joint; i, Left 5th limb, posterior view; j, Same, endites I–III; k, Posterior view of right 5th limb showing peg and 2 proximal teeth of 1st exopodial joint; l, Same, exopodial joints 3–5 (joints 4 and 5 fused); m, Left 6th limb; n, Tip of 7th limb; o, Posterior of body showing genital ring (stippled), unextruded eggs (dashed circles), left lamella of furca, Y-sclerite and girdle; p, Anterior of body showing medial eye and Bellonci organ, rounded anterior process, lateral eye, and upper lip.

terminal bristles with long proximal and short distal spines; endite III with 1 medial bristle with long proximal and short distal spines, and 3 terminal bristles (1 or 2 with short spines, 1 or 2 with long proximal and short distal spines); endite IV with 3 or 4 bristles (2 with short marginal spines, 1 or 2 with long proximal and short distal spines). End joint with 14 bristles: 2 posterior bristles plumose; next 2 bristles with long proximal hairs and short distal spines; except for 2nd bristle from anterior end, which has only short spines, next 7 bristles along edge long, with long proximal and short distal spines; 3 short bristles on anterior half of joint with bases on lateral side of edge, with short marginal spines; lateral side of edge with long spines (spines absent between 2 posterior plumose bristles); medial surface of joint hirsute.

Seventh limb (Fig. 3n): Terminal segment with 10 bristles on comb side and 8 on jaw side; some bristles obscured on proximal segments, 10 observed on comb side, and 8 on peg side; total observed bristles 36 but more probably present. Comb comprising long central tooth with 4 slightly shorter teeth (with rounded tips and pointed alar projections near midlength) and 4 short teeth (with square tips) on each side; total number of comb teeth about 17. Jaw opposite comb resembling cupped palm with about 9 teeth along edge (lateral profile in Fig. 3n); muscles capable of actuating jaw illustrated in Fig. 3n.

Furca (Fig. 3o): Each lamella with 11 claws decreasing in width and length posteriorly along lamella; right lamella slightly anterior to left; all claws with teeth along posterior edge.

Bellonci organ (Fig. 3p): Short, cylindrical with rounded tip, with about 15 narrow rings near tip (not all rings shown in illustration).

Eyes: Lateral eyes well developed with about 20 ommatidia in field of dark pigment (Fig. 3p). Medial eye unpigmented (Fig. 3p).

Upper lip (Fig. 3p): In lateral view anteroventral margin of undivided part evenly rounded and bearing numerous small glandular openings; divided glandular part bearing small glandular openings; minute tusk bearing single glandular opening lateral to posterior end of divided part; posterior of lip evenly rounded, hirsute.

Genitalia (Fig. 3o): Comprising oval ring on each side of body anterior to furca.

Posterior of body (Fig. 3o): Evenly rounded.

Y-sclerite (Fig. 3o): Indistinct but seemingly typical for subfamily.

Eggs (Fig. 3o): Each side of body with cluster of 8 small unextruded eggs (16 total).

Comparisons.—Doloria sarsi resembles *D. levis* in that both species have the following combination of characters: dorsal bristle of the 3rd joint of the 1st antenna close to the 2nd joint, only three bristles on the ventral margin of the 2nd endopodial joint of the mandible, three claw-like nonpectinate d-bristles on the end joint of the maxilla, only two bristles on the fused 4th and 5th exopodial joints of the 5th limb, a toothed jaw opposite the comb of the 7th limb, and 11 claws on the furca. *Doloria sarsi* differs from *D. levis* in having two to four anterior bristles instead of only one on the basale of the maxilla. *Doloria levis* is known only from the vicinity of South Georgia and the continental subregion of Antarctica (Kornicker 1975:102). *Paradoloria acorensis* (Granata and Caporiacco, 1949:7) [the male of the species is unknown; thus, the species could belong in *Doloria*] is not well known; it is from the Azores (1482 m) and Bay of Biscay (1455 m) and differs from *D. sarsi* in having 12 instead of 11 furcal claws. Other species of *Doloria* and *Paradoloria* differ from *D. sarsi* in having more than two bristles on the fused 4th and 5th exopodial joints of the 5th limb, as well as in other characters. Poulsen (1962:147) stated that *Cypridina gracilis* Brady (1880: 156) (from the Azores, 1829 m) may possibly be included in *Paradoloria*. The large size of that species (length 5 mm) clearly distinguishes it from *D. sarsi* (length 2.67 mm).

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AMMOTHEA VERENAE AND *SERICOSURA VENTICOLA,* TWO NEW HYDROTHERMAL VENT-ASSOCIATED PYCNOGONIDS FROM THE NORTHEAST PACIFIC

C. Allan Child

Abstract.—Two new pycnogonid species, *Ammothea verenae* and *Sericosura venticola,* are described from hydrothermal vents on the Juan de Fuca Ridge, northeast Pacific. These first known vent-associated pycnogonids are compared with previously known species of the two genera; their distribution, possible reasons for the evolution of this distribution among these and similar genera, and observable characters in the species' morphologies in relation to hydrothermal vents are discussed.

Continuing investigations of hydrothermal vents on tectonic rifts in the deep oceans during the last decade since their discovery have revealed a wealth of fauna new to science. It is not surprising that these intensive investigations should discover pycnogonids among the often unique fauna associated with these vents. The two species described here are new and are also the first pycnogonids to be found in association with hydrothermal vents. Specimens of both genera to which the new species belong have been taken before at similar depths and in diverse localities, but none have been reported from or found associated with tectonic rifts. Bottom photographs supplied with some of the specimens reported here plainly show pycnogonids and other rift fauna in close association with vents. Well over half the specimens listed in the following "Materials Examined" sections are partly covered with layers of polymetallic sulfides spewed out of nearby vents. Clearly, the pycnogonids and other vent fauna must have developed adaptive strategies to permit their living and proliferating in these seemingly transient areas of wide temperature and chemical variation. How this has been accomplished is beyond the scope of speculation in this paper, although a few observations on adaptation are offered in the discussion section. It is sufficient to say in light of our present knowledge that they have adapted successfully with at least one of the new species found widespread along several hundred kilometers of the Juan de Fuca Ridge in vent temperatures at least as high as 85°C.

Family Ammotheidae

Genus *Ammothea* Leach, 1814

Ammothea verenae, new species

Fig. 1

Material examined.—ENDEAVOUR SEGMENT: vent at 47°57.1′N, 129°06.0′W, 2216 m, coll. DSRV *Alvin,* 2 Sep 1984, sta 1446-3-702, holotype male with eggs (USNM 233636), paratypes, 4 males with eggs, 1 male, 1 female (USNM 233637), paratypes, 5 males with eggs (NMC).—"TLC" Vent, 47°57.1′N, 129°06.3′W, 2250 m, coll. DSRV *Alvin,* 3 Sep 1984, sta A1446-719, paratype juvenile (USNM 233638).—Another vent near "TLC" Vent, same locality, 2199 m, coll. DSRV *Alvin,* 6 Sep 1984, sta A1451-706, paratypes, 1 male with eggs, 2 females, 1 juvenile (NMC).

Other material: EXPLORER RIDGE: Pogo Peaks Vent, 49°45.5′N, 130°16.2′W, 1853 m, coll. DSRV *Pisces IV,* 23 Jun 1984, sta P1492-714, 1 ♀, 1 juv (USNM), 1 ♀ ovig, 5 juv (NMC).—Magic Mountain, Gulati Gusher, 49°45′36″N, 130°16′07″W, 1818 m, coll. DSRV *Pisces IV,* 1 Jul 1984, sta P1494-703, 2 ♂, 4 ♀, 35 juv (UVBC).—Hottest vent (85°C), same locality, coll. DSRV *Pisces IV,* 1 Jul 1984, sta P1494-704, 1 ♂ (USNM).—Biomass sample, same locality, depth, and collector, 1 Jul 1984, sta P1494-718, 1 ♂, 9 ♀, 64 juv (USNM).—"Lunch Hour" Vent, same locality, collector, 1808 m, 2 Jul 1984, sta P1495-705, 1 ♂ with eggs, 1 ♂, 4 ♀, 28 juv (NMC).—Upper Magic Mountain, Crab Vent, 49°46′N, 130°18′W, 1780 m, coll. *Pisces IV,* 4 Jul 1984, sta P1494-701, 3 juv (USNM).—Same locality, collector, 1837 m, sta P1497-700, 4 Jul 1984, 3 ♂ with eggs, 1 ♂, 3 ♀, 8 juv (UVBC).—Busted Thruster Vent, 49°45.7′N, 130°16.1′W, 1823 m, coll. *Pisces IV,* 19 Aug 1984, sta P1505-717, 2 ♂ with eggs, 3 ♂, 4 ♀, 9 juv (UVBC), 2 ♂ with eggs, 1 ♀, 8 juv (USNM).

ENDEAVOUR SEGMENT: Juan de Fuca Ridge: vent at 47°57.0′N, 129°04.0′W, 2212 m, coll. DSRV *Alvin,* 24 Jul 1984, sta 1418, 1 ♀ (USNM).—Vent, associated with vestimentiferans, ca. 46°N, 130°W, ca. 2000 m, coll. DSRV *Alvin,* 25 Jul 1984, sta 1419, 1 ♀, 1 juv (USNM).

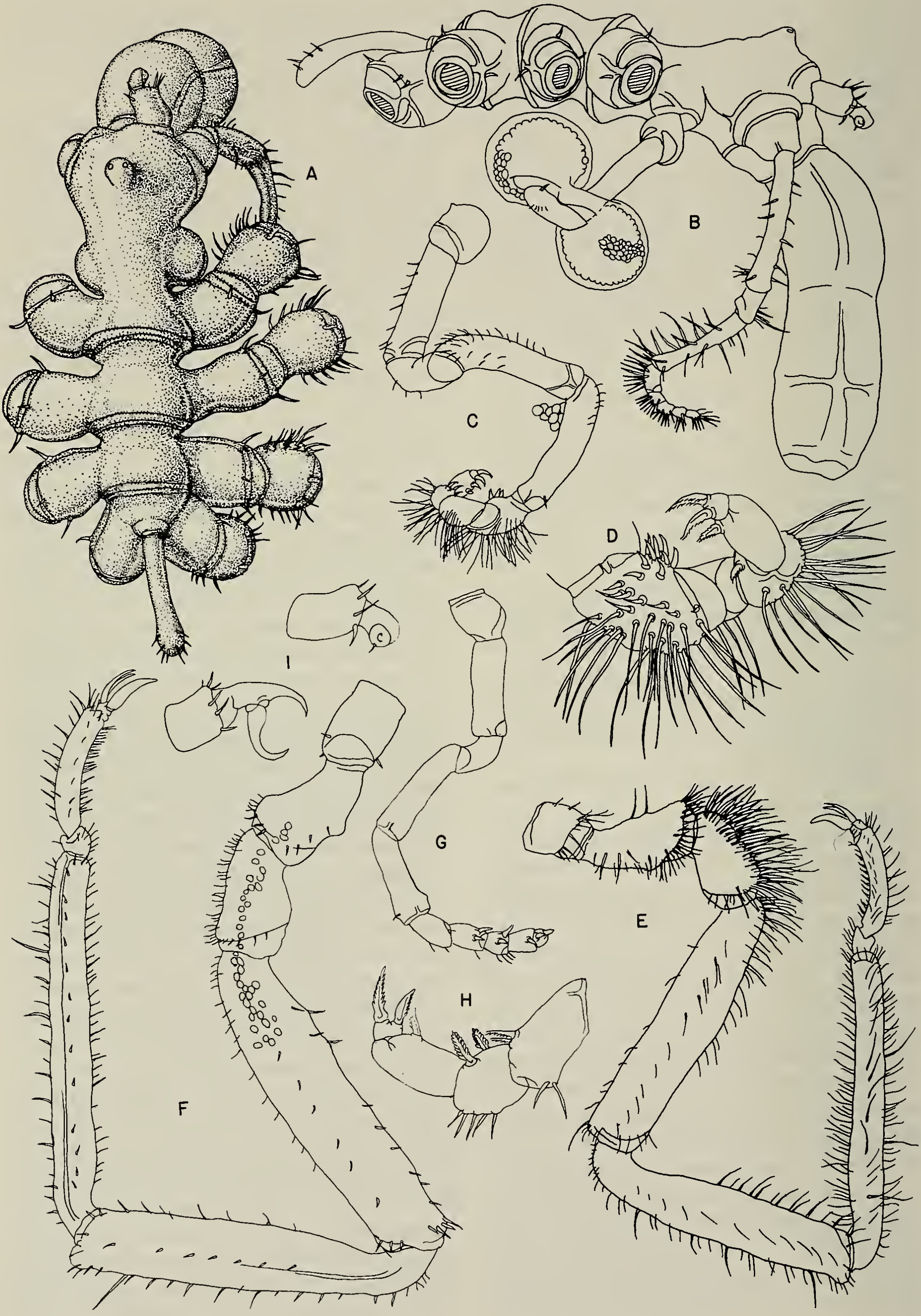
AXIAL SEAMOUNT: Devil Vent, near base of Hammond's Hell (60°C), 45°55.6′N, 130°01.8′W, 1570 m, coll. DSRV *Pisces IV,* 14 Jul 1986, sta P1720-710, 1 ♂ (USNM).—Hammond's Hell, same locality and depth, coll. *Pisces IV,* 19 Jul 1986, sta P1723-711, 1 ♀ ovig, 2 ♀ (USNM).—Inactive sulfide chimney near Embley's Inferno, same locality, depth, collector, sta P1725-712, 25 Jul 1986, 3 juv (NMC).—Demon Vent no. 1, same locality, depth, collector, sta P1728-709, 29 Jul 1986, 1 juv (USNM).—Not-So-Miserable Vent, near Holland's Hillock, same locality, depth, and collector, sta P1733-707, 3 Aug 1986, 2 ♂ with eggs, 1 ♂, 1 ♀, 4 juv (UVBC).—Miserable Vent, same locality, depth, and collector, sta P1733-708, 3 Aug 1986, 1 juv (USNM).—Vent, same locality, depth, and collector, sta P1733-713, 3 Aug 1986, 1 ♂ with eggs, 2 juv (USNM).

SOUTHERN JUAN DE FUCA RIDGE: vent 1, 44°39′15″N, 130°22′W, ca. 2225 m, coll. DSRV *Alvin,* 24 Oct 1984, sta A1463-7B-716, 2 ♀, 1 juv (USNM).

Description.—Male: size moderately large, leg span 43.4 mm. Integument smooth, without texture. Trunk moderately slender, posterior of each segment flared into expanded cowling, without tubercles. Neck greatly expanded anteriorly, glabrous. Ocular tubercle a low truncate cone, shorter than basal width, without eyes, lateral sensory papillae prominent. Ocular tubercle placed just anterior to midlength of expanded neck, over palp insertion. Oviger implantation posterior to neck expansion, at narrowest point, anterior to but almost touching first lateral processes. Lateral processes moderately crowded, separated by less than half their diameters, as long as 1.5 times their diameters, armed with single dorsodistal seta each and 1 or 2 laterodistal setae except at anterior and posterior extremities. Proboscis massive, as long as anterior 3 trunk segments, proximal half with distinct ventral bend, hint of tripartite segmentation lines present, mouth surface flat. Proboscis base a separate truncate cone segment about 0.15 as long as proboscis. Abdomen slender with slightly bulbous tip, as long as distal rim of first coxae on posterior legs, armed with several dorso- and laterodistal short setae.

Chelifore short, 2-segmented. Scape short, only twice as long as diameter, armed with few distal and lateral setae shorter than segment diameter. Chela vestigial, a short stump with hint of movable finger ventrally, armed with tiny ventral seta.

Palp 9-segmented, longer than proboscis, basal segment massive, 3 times wider than distal segments. Second segment longest, armed with few short setae increasing in numbers distally. Third segment as long as basal segment, slightly longer than fifth segment, armed with few dorsal setae, one longer than segment diameter. Fourth segment only 0.7 as long as second, armed with many ventral setae, most longer than seg-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ment diameter. Terminal 4 segments subequal in length, very setose ventrally, most setae longer than segment diameters.

Oviger segments 4 and 5 equal in length, slightly longer than second segment, each with many short proximal setae. Strigilis extremely setose; sixth segment with many long ectal setae and 8 plain short endal spines, seventh and eighth segments with corresponding ectal spines, fewer in number, ninth and tenth without setae. Terminal 4 segments with endal denticulate spines in the formula 1:1:1:2, each spine having many lateral serrations. Egg size less than half diameter of main oviger segments, carried in large ovoid clusters.

Legs moderately long, slender, extremely setose. First coxa with several lateral and ventral setae, some longer than segment diameter. Second coxa with fringe of many lateral and ventrodistal setae. Third coxa with ventral field of long closely spaced setae sufficient in numbers to hide ventral outline of segment. Femur armed with similar setae proximoventrally, decreasing in numbers distally, and line of shorter lateral and dorsal setae. Location of femoral cement gland pore not definitely established, but may be dorsodistal in fringe of setae or proximolaterally as pores along line of lateral setae. Second tibia longest segment, slightly longer than first tibia and femur which are subequal in length. Three major segments armed with lines of lateral, dorsal and ventral setae, some slightly longer than segment diameters. Propodus slender, moderately curved, without marked heel, sole with 11–13 narrow spines, flanked with short lateral setae fewer in numbers. Propodus shape and spination similar on all legs. Claw robust, well curved, about 0.4 as long as propodus, auxiliaries almost as long as main claw, slender, well curved. Sexual pores on second coxae of posterior 2 pairs of legs only.

Female paratype: slightly larger in all measurements except for oviger which is smaller than that of male. Strigilis with 2–5 ectal short setae, without fields of setae, terminal 4 segments with denticulate spines in formula 2:2:1:2. Sexual pores on all second coxae ventrally. Juvenile chela small, with slender very curved fingers overlapping at tips when closed, without teeth.

Measurements.—Holotype, in mm: trunk length (insertion of chelifore to tip 4th lateral processes) 5.6; trunk width (across 2nd lateral processes) 3.12; proboscis length 4.5; abdomen length 1.72; third leg, coxa 1 0.78; coxa 2 1.75; coxa 3 1.39; femur 4.3; tibia 1 4.32; tibia 2 4.68; tarsus 0.52; propodus 1.76; claw 0.65.

Distribution.—Known from the type locality, Endeavour Segment on Juan de Fuca Ridge in 2199–2250 m, and from Axial Seamount and Explorer Ridge in 1570–2225 m, all on or in close proximity to hydrothermal vents.

Etymology.—This species is named for Dr. Verena Tunnicliffe, University of Victoria, Victoria, British Columbia, Canada, who collected and contributed most of the specimens listed here.

Remarks.—This new species can be easily separated from most *Ammothea* species because it lacks the large dorsomedian trunk tubercles on the cowls of each segment posterior that are present in most species and most prominent in males. It can be further separated from most other known species by its total lack of specialized or differentiated sole spines and by having all propodal shape and armature alike. It lacks the large heel spines of most species and the dissimilarity of anterior leg propodi from those of

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Fig. 1. *Ammothea verenae,* male holotype: A, Trunk, dorsal view; B, Trunk, lateral view; C, Oviger; D, Oviger strigilis, enlarged; E, Third leg. Female paratype: F, Third leg with ova; G, Oviger; H, Oviger strigilis, enlarged; I, Chela of adult and of juvenile.

posterior legs. *Ammothea hilgendorfi* (Böhm) and *A. spicula* Nakamura and Child are the only northern species without dorsomedian trunk processes although both have major heel spines differing from those of the sole, and *A. australiensis* Flynn appears to be the only southern species with no trunk processes, but it also has major heel spines. Therefore, this new species is the only one known with uniform sole spines and no trunk processes.

The new species has other distinguishing characters such as the distinctive large bent proboscis, the extremely setose legs of the male, the giant palp first segment, and a lack of eyes on the very low ocular tubercle. The latter character is shared by only one other known species in this genus, *A. profunda* Losina-Losinsky. Most species of the genus are found in shallower depths or at least at depths where some light penetrates to justify the retention of eyes.

This species is apparently very common, at least in the restricted depths of the northeast Pacific where its hydrothermal vent habitats occur. It has been taken at vents, on sulfide chimneys, and adjacent to vents spewing sulfide particles such that over half the specimens listed above have some part to most of their anatomy encased in solidified polymetallic sulfide crusts. Photographs taken at some of the vent habitats show lava forms and other large clastic shapes covered with these sulfides and having pycnogonids, limpets, galatheid crabs, worms (Polynoidae), and unidentified fauna inhabiting most surfaces in good numbers. Unlike most of the sparse records showing lack of thermal tolerance for pycnogonids, these specimens apparently survive a wide range of temperatures. Recorded temperatures around some of the vents list differences of 4°–5° above ambient at corresponding depths, but one capture of this species was made at the "hottest vent" sampled on Explorer Ridge (85°C). Another specimen was taken at "Devil Vent" on Axial Seamount at 60°C. It is difficult to imagine how such delicate animals can survive these temperatures unless mixing among bottom currents is such that cooling takes place almost instantly after exposure to temperatures such as those above.

Genus *Sericosura* Fry and Hedgpeth, 1969

Sericosura venticola, new species

Fig. 2

Material examined.—ENDEAVOUR SEGMENT: vent, associated with vestimentiferans, 47°57.0′N, 129°04.0′W, 2208 m, coll. DSRV *Alvin* 25 Jul 1984, sta 1419, holotype male with eggs (USNM 233639).—Vent, 47°57.1′N, 129°06.0′W, 2216 m, coll. DSRV *Alvin,* 2 Sep 1984, sta A1446-3-702, paratype male with eggs (USNM 233640), paratype male with eggs (NMC).

Description.—Size moderately large, leg span 27.6 mm. Integument smooth, without papillae or other texture. Trunk slender, graceful, posterior of anterior 3 trunk segments flared into cowl, without tubercles. Neck gradually expanded anteriorly, armed with pair of short setae on both anterolateral tips. Ocular tubercle slightly taller than basal diameter, without eyes, with prominent lateral sensory papillae, rounded at apex, placed just anterior to midlength of neck. Oviger implantation massive, at narrowest point of neck, posterior to ocular tubercle, almost touching first lateral processes. Lateral processes almost touching, separated by less than half their diameters, swollen distally to constricted bases, only slightly longer than maximum diameters, armed with 1–3 laterodistal setae, none longer than half segment diameter. Proboscis massive, ovoid, without ventral bend, carried horizontally, without trace of segmentation lines, almost as long as trunk, mouth surface flat. Abdomen slender, curved ventrally, tip swollen, extending to distal rim of second coxae of fourth legs, armed with 5–6 distal short setae, with distinct basal segmentation line.

Chelifores short, 2-segmented. Scape twice

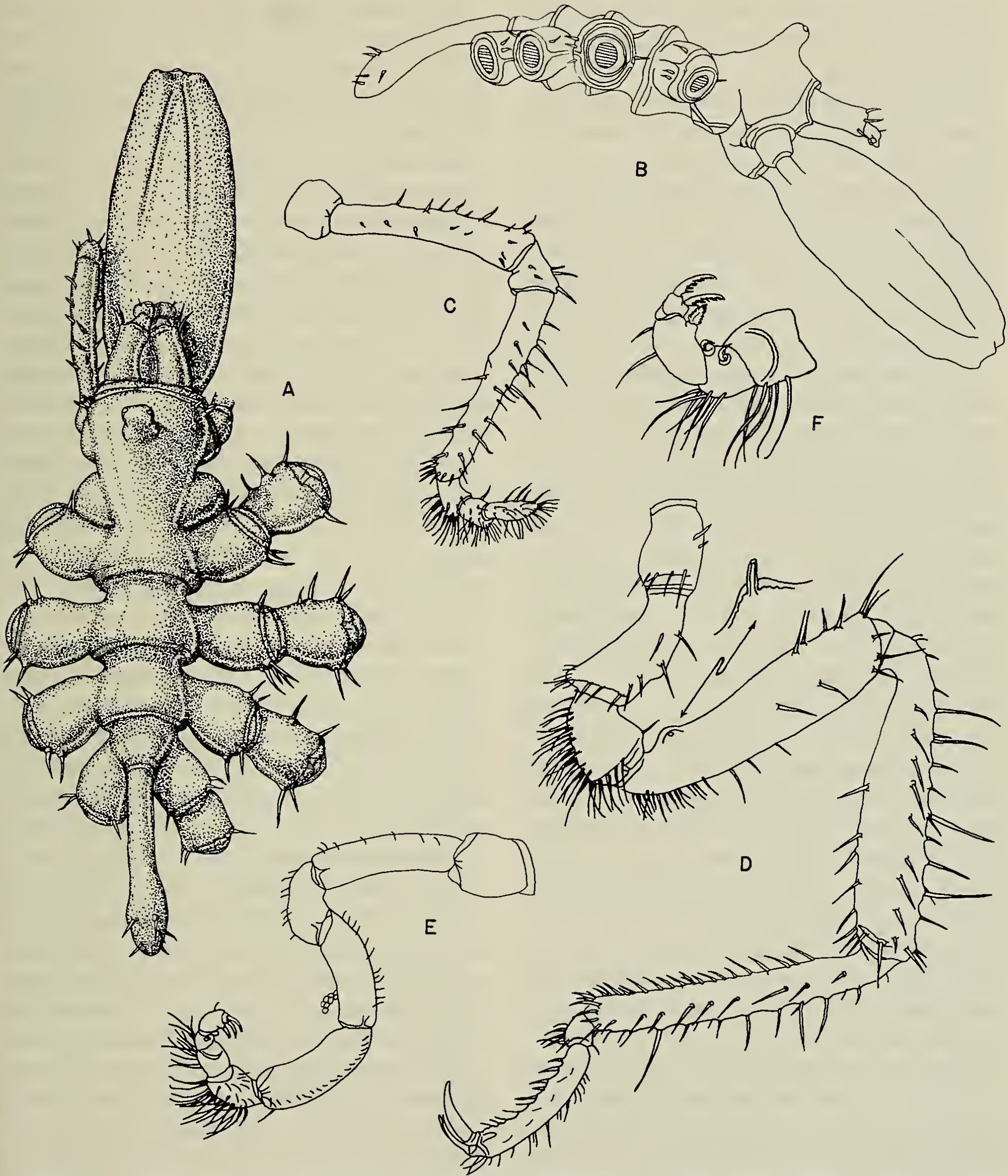

Fig. 2. *Sericosura venticola,* male holotype: A, Trunk, dorsal view; B, Trunk, lateral view; C, Palp; D, Third leg, with enlargement of cement gland; E, Oviger; F, Oviger strigilis, enlarged.

as long as diameter, slightly curved toward median line, armed distally with 3–4 short lateral setae. Chela tiny, vestigial, with only trace of movable finger, armed with single short distal seta.

Palp 7-segmented, heavily setose. Segments 2 and 4 subequal, armed with many dorsal and lateral setae, most shorter than segment diameter. Segments 5 and 6 subequal, with slight ventral swelling, armed with dense setae mostly longer than segments. Seventh segment cylindrical, as long as fifth and sixth combined, armed with dense setae of same length as those on more proximal segments.

Oviger second segment longest, length 3.5 times diameter, fourth and fifth segments slightly shorter, subequal, all armed with row of very short ectal setae. Strigilis heavily setose, ectal setae longer than segment diameters, with endal denticulate spines in formula 0:2:1:2, spines with many lateral serrations. Extremely tiny eggs carried cemented into hollow balls.

Legs moderately long, segments slender, very setose. First coxa armed with 1–2 anterior setae and fringe of latero- and ventrodistal setae. Second coxa with several dorsal and lateral setae and fringe of distal setae. Third coxa with dense field of ventral and distal setae, many as long as segment diameter. Femur with dense fringe of proximoventral short setae and several longer lateral and dorsodistal setae. Cement gland almost at proximal margin of femur, with low surface bulge and very short tube pointing anteriorly on each leg. Tube not visible from posterior surface. First tibia longest segment, femur and second tibia slightly shorter, equal in length. Tibiae armed with many lateral, dorsal and ventral setae, mostly in rows, few on dorsal surface longer than segment diameter. Tarsus short, armed with single dorsal and 5–6 ventral setae. Propodus moderately curved, without heel or larger heel spines, sole with 10–12 spines not longer than segment diameter. Propodus armed with short lateral and dorsal setae. Claw moderately curved, slightly over 0.3 length of propodus, auxiliary claws very slender, 0.7 as long as main claw. Sexual pores ventrodistal on second coxae of posterior 4 legs.

Female and juvenile characters unknown.

Measurements.—Holotype, in mm: Trunk length (chelifore insertion to tip 4th lateral processes) 3.58; trunk width (across 2nd lateral processes) 2.3; proboscis length 3.09; abdomen length 1.55; third leg, coxa 1 0.78; coxa 2 1.1; coxa 3 0.82; femur 2.58; tibia 1 2.74; tibia 2 2.58; tarsus 0.25; propodus 1.34; claw 0.48.

Distribution.—Known from the type locality only, the Endeavour Segment in 2208–2216 m.

Etymology.—The specific name refers to a vent dweller.

Remarks.—This new species is very similar to the other known species of the genus, *S. mitrata.* The differences are in a more slender and longer habitus of the entire animal in *S. venticola,* and its very different arrangement of appendage setae. The setae arrangement and number are dimorphic in both species, but the female of *S. mitrata* has a ventral fringe of long hair-like setae and many short setae on the tibiae. The male (Child 1982:19–20, fig. 6c), unlike *S. venticola,* has no such field of ventral setae and has fewer setae on any leg segment. In *S. venticola,* the female is unknown, but the male has a dense field of long setae on the ventral surface of the third coxae and the adjacent proximal surface of the femur. The other leg segments are quite setose and it is probably safe to predict that the legs of the female will have very different setation based on *S. mitrata.*

Other differences are found in the much shorter cement gland tube of *S. venticola,* its longer and more slender chelifores, a tarsus and propodus with many more sole spines and setae, its longer and more setose palp segments, and its lack of any of the very long lateral leg setae present on *S. mitrata.* The ovigers of both species are remarkably similar except that the strigilis of *S. venticola* has more setae. Although of little taxonomic value as a critical character, the leg span of the new species is more than twice that of *S. mitrata,* although the trunk lengths are more nearly alike.

There are only six known specimens, including the above three males, reported for this apparently rare genus. The other known species, *S. mitrata,* has been taken along the African side of the Antarctic coast in 219 m (Gordon 1944:54–57, as *Achelia mitra-*

ta), and on the Walvis Ridge in 2117–2154 m (Child 1982:19–21). There were no hydrothermally active localities mentioned at the Walvis Ridge collecting site, but their presence cannot be ruled out. The depth here almost coincides with the capture depths of the new species. Gordon described the blind *S. mitrata* from a single female specimen and remarked on the apparent anomaly of blindness versus the relatively shallow depth of capture. This could be related to net contamination from a previous deeper haul, but Fry and Hedgpeth (1969:112–113) comment on the same depth discrepancies of several other blind shallow Antarctic species, making them skeptical of such anomalies, particularly in cold Antarctic waters.

Discussion

The two new species, *Ammothea verenae* and *Sericosura venticola,* belong to previously known genera. The genus *Ammothea* Leach, 1814, contains about 23 species, none of which are known to be vent-specific, and most of which are found in the Antarctic, Subantarctic, or at least in the Southern Hemisphere. Of the 23 species, only four are found partly or exclusively in the Northern Hemisphere, all in the northern Pacific, suggesting that the genus had its origins and proliferation in Antarctic waters and has subsequently spread northward. All north Pacific species, *Ammothea hedgpethi* (Utinomi) (Japan), *A. hilgendorfi* (Böhm) (Pan-Pacific), *A. profunda* Losina-Losinsky (Kuril Islands), and *A. spicula* Nakamura and Child (Japan), have been collected in shallow depths (less than 200 m) except *A. profunda* which was taken in 1500 m. Fry and Hedgpeth (1969:94) suggest that this species "has spread into the Northern Hemisphere by way of the cold abyssal or hadal regions." This certainly might account for the spread of *Ammothea verenae,* at least to the northeast Pacific from elsewhere, but would not explain its spread along hydrothermal rifts and ridges, its only known habitat. This suggests a later adaptation to hydrothermal vent life after evolving first in northern Pacific areas. A cold abyssal distribution would also not explain the shallow and shore proliferation of *A. hilgendorfi,* principally around the rim of the northern Pacific, and presumably the presence of the two Japanese shallow-water species. *Ammothea hilgendorfi* must be a very long time resident of northern Pacific waters due to its extensive distribution from the Russian Arctic and China to the Society Islands and California.

There is one record of *A. hilgendorfi* from England, but a better north Atlantic counterpart to the Pacific species would be *Trygaeus communis* Dohrn. This genus probably split off from the parent *Ammothea* stock quite early, possibly from a species very much like *A. hilgendorfi, A. magniceps* Thomson, or *A. australiensis* Flynn, all of which are closely related and are superficially very much like *T. communis.* In becoming *Trygaeus,* the species discarded all trace of atrophied chelae while retaining the chelifore stump, and lost an oviger segment and a palp segment or two (the numbers vary among specimens). It shows a marked Tethyan distribution across the width of the Mediterranean.

Sericosura is another genus even more closely related to *Ammothea,* and it is probably not hydrothermal vent-specific. The second published record of *S. mitrata* (Child 1982:19–21, fig. 6) places it in much deeper water than the type (219 m versus 2100 m) and further north on the Walvis Ridge, a transverse oceanic ridge between continents said to be seismically inactive (Marvin 1973: 134) and distant from any locus of tectonic plate spreading.

The two new species of *Sericosura* and *Ammothea* described here appear superficially to be very similar when the ovigers, coxae setation, trunk habitus, and trunk–proboscis size are compared. In *Sericosura,* as in the genus *Trygaeus,* another genus has evolved with the secondary loss of appendage segments. *Sericosura* has seven palp segments while *Ammothea* has nine (sometimes eight), and the former genus has lost its eyes (unnecessary in deep water) in contrast to eyes being present in most of the *Ammothea* species, or at least those from shallow water. The terminal palp segment of *Sericosura* is elongate and it probably coalesced from two former segments while losing another from the original nine. The loss (or gain) of dorsomedian trunk tubercles, a common character present in most species of *Ammothea,* is the only other character differentiating *Sericosura* from *Ammothea,* but this is perhaps a secondary loss and is not unique among known *Ammothea* species. As noted above, dorsomedian trunk tubercles might have been a secondary gain in *Ammothea,* but they are taller or otherwise more marked in many juvenile specimens of the genus. The two species of *Sericosura* lack them.

There are many questions concerning the presence of pycnogonids at hydrothermal vents and the very few answers are almost entirely conjectural. This is due in large part to our lack of even rudimentary knowledge of life histories and habits of most pycnogonids. We know very little of food and habitat preference and there has been no study, to my knowledge, of egg size and fecundity as a function of the duration and number of larval stages. The details of these life habits are simply not available to us.

The extremely tiny egg size of both of these species would suggest shorter embryonic and protonymphon stages with an increased number of juvenile stages similar to those of decapod crustaceans (Van Dover et al. 1985:223). Egg size is seldom noted in pycnogonid reports, but among those species figured with eggs attached to the male ovigers, the egg size generally appears to be equal to at least half or as much as the full diameter of the oviger segments on which they are strung. This excludes some of the callipallenid genera and species and some of the *Nymphon* species which have what could be called giant eggs full of yolk. The eggs of *Ammothea verenae* are slightly larger than those of *Sericosura venticola,* in terms of the oviger segment size of each, but both egg sizes are sufficiently small to suggest a single pattern of abbreviated early development stages possibly related to hydrothermal vent-related habitats. The complete life history of so few pycnogonids is known with any certainty that it would be futile to speculate as to whether or not this abbreviated pattern with more juvenile stages is the exception to usual embryonic development or is the more normal course of events taken by the majority of pycnogonids.

Another question begging an answer in relation to hydrothermal vent-associated pycnogonids concerns the nature of food available to them. Pycnogonids are often found associated with sessile coelenterates from which they extract body juices with their suctorial proboscis. What sessile organisms are available in association with hydrothermal vents that are suitable for this suctorial form of extraction? The organisms most available appear to be vestimentiferans, palm worms, and vent-associated bacteria. There is nothing in hydrothermal vent-related literature, particularly in that of the Juan de Fuca Ridge, suggesting a prevalence of any form of sessile coelenterates at vents, but there is a form of mucus comprising a considerable portion of the total biomass (Tunnicliffe et al. 1985:459, 461) which, although low in organic content (less than 13% while containing 66.8% sulphur), could form a substantial part of the pycnogonid diet. Examination of the gut content of several specimens of *Ammothea verenae* was inconclusive, although what appeared to be small groups of bacteria were present. This evidence could be due to the ingestion of ubiquitous bacteria fortuitously, sulphur-oxidizing bacteria being present in almost all vent situations. No parts or recognizable tissues from worms were identified in the gut contents, although this does not rule out their ingestion. From the slight evidence available, no conclusive proof can therefore be discovered concerning the diet, or indeed, the life habits of these two vent-associated species.

Acknowledgments

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The specimens are deposited in the National Museum of Natural History, Smithsonian Institution, under the catalog numbers of the U.S. National Museum (USNM), the National Museum of Canada, Ottawa (NMC), and in the University of Victoria, Victoria, British Columbia (UVBC).

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NEW AND LITTLE KNOWN PYCNOGONIDA FROM ANTARCTIC AND SUBANTARCTIC WATERS

C. Allan Child

Abstract.—Five new species, *Ascorhynchus antipodus, A. cooki, Cilunculus spinicristus, Eurycyde antarctica,* and *Cheilopallene gigantea,* and one rare species, *Oropallene dimorpha* (Hoek), were sorted from various Antarctic collections taken from localities southwest of New Zealand, off the Antarctic Peninsula, and the Ross Sea. The new species are compared with known species of the genera and their distribution is given.

Many collections of Antarctic and Subantarctic pycnogonids have been deposited in the National Museum of Natural History both before and subsequent to Fry and Hedgpeth's (1969) partial treatment of the genera representing the last or most current monograph on the subject. Among the several thousand lots of pycnogonida sorted from bottom material, the five species described and figured here were found to be new to science. The five new species are *Ascorhynchus antipodus, A. cooki, Cilunculus spinicristus, Eurycyde antarctica,* and *Cheilopallene gigantea.* Another species, *Oropallene dimorpha* (Hoek), rarely recorded or figured in the literature, is refigured here with new capture records. So much effort has been expended in capturing and describing the pycnogonids and other taxa from Antarctic and Subantarctic waters that it might be thought remarkable that as any as five new species of Pycnogonida could be found to describe. To the contrary, the deeper waters around New Zealand, its Subantarctic islands, and those of Australia (Macquarie Island in particular), have had little collecting effort in comparison to the many expeditions that scoured the Ross Sea over the past 90 years. It is perhaps significant, then, that this report contains only one new species from the outer reaches of the Ross Sea, at the Cape Adare coast. It will be many years before it can be safely said that all is known of the Pycnogonida of the Ross Sea or of any other area of comparable size in the oceans of the world.

Family Ammotheidae Dohrn

Genus *Ascorhynchus* Sars, 1877

Ascorhynchus antipodus, new species

Fig. 1

Material examined.—Southwest Pacific Basin, E of the Antipodes Islands, 49°21′S, 172°16′W, 5340 m, coll. *Eltanin,* sta 25-366, 15 Nov 1966, holotype, female (USNM 233600).

Description.—Size moderately small, slender, leg span 20.4 mm. Integument closely papillose, imparting pebbled appearance. Trunk long, slender, posterior part of first three segments widely flaring, without median tubercles, narrowest diameter of trunk only half diameter of flared cowls. Lateral processes very short, only as long as their diameters, glabrous. Neck long, oviger implantation at half-length of neck, well anterior to first lateral processes. Neck armed with 2 conical anterolateral tubercles pointing obliquely above chelifore insertions. Ocular tubercle, sensory papillae and eyes entirely lacking. Proboscis slender, bipartite, without distal constriction, as long as first 2 trunk segments combined. Abdomen long, slender, glabrous, reaching almost to distal tip of second coxae of fourth legs.

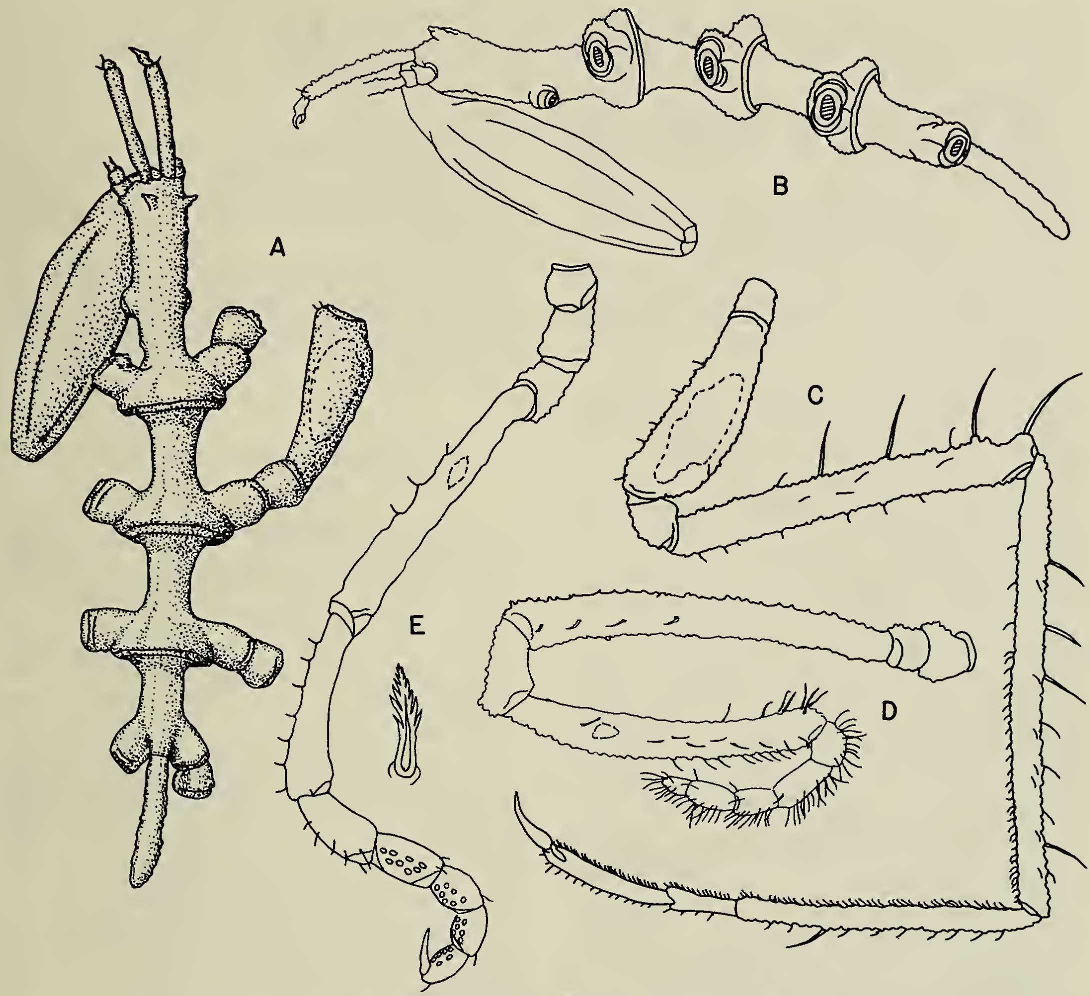

Fig. 1. *Ascorhynchus antipodus,* female holotype: A, Trunk, dorsal view; B, Trunk, lateral view; C, Third leg; D, Palp; E, Oviger, with enlargement of denticulate spine.

Chelifore scape of 1 segment cylindrical, slender, over 6 times longer than its diameter, armed with 2–3 short distal setae. Chela tiny, fingers fully formed, apparently functional, glabrous.

Palp segment 3 about 0.2 longer than segment 5, terminal 6 segments progressively more setose ventrally and laterally. Segment 6 equal in length to segments 8 and 9, segment 7 half again longer, segment 10 tiny, shorter and narrower than other terminal segments.

Oviger with few endal setae on major segments. Third segment longest, fourth only 0.6 as long, strigilis segments progressively shorter, armed with denticulate spines in 2 rows in distally progressing formula 8:7:6:6, with glabrous slightly curved terminal claw almost as long as terminal segment. Denticulate spines long, slender, with 5–6 denticles per side.

Legs moderately long, very slender, lightly spinose, with row of tiny setae on ventral tibiae and sole of tarsus and propodus. Second coxae long, almost 4 times length of first or third, swollen medially and distally with large number of ova. First tibiae longest of major segments with second tibiae shorter than femorae. Tarsus and propodus slender, tarsus half propodus length, both armed with very short setae. Claws moderately curved, all of equal length, 0.43 as long as propodus.

Male and juvenile characters unknown.

Measurements (in mm).—Trunk length (chelifore insertion to tip 4th lateral processes) 3.7; trunk width (across 2nd lateral processes) 1.24; proboscis length 2.2; abdomen length 0.91; third leg, coxa 1 0.3; coxa 2 1.18; coxa 3 0.31; femur 2.12; tibia 1 2.54; tibia 2 1.61; tarsus 0.4; propodus 0.78; claw 0.34.

Distribution.—Known only from the type locality, E of the Antipodes Islands, New Zealand, in 5340 m.

Etymology.—This species is named for the land nearest its place of capture, the Antipodes Islands.

Remarks.—This new species is sufficiently close to *Ascorhynchus bucerus* Turpaeva, from the northern Pacific, for them to form a geminate pair. The general habitus of the two is very similar and they were captured at approximately the same depth. The principal difference between them is that *A. bucerus* has 2-segmented scapes while this species has scapes of a single segment that are longer in relation to the trunk than those of *A. bucerus.* Palp segment 5 is subequal to segment 3 in *A. bucerus,* but segment 5 is 0.2 shorter than segment 3 in *A. antipodus.* Other differences are: *A. bucerus* has a palp terminal segment almost equal in length to the penultimate segment, the neck is longer in relation to other trunk segments, the oviger implant bulges are nearer the first lateral processes and in the posterior half of the neck, the abdomen is approximately equal in length to the fourth trunk segment, the tarsus is about 0.75 as long as the propodus, the femur is subequal in length to the second tibia, and in the oviger, segment 4 is shorter than segment 5. In *A. antipodus,* the palp terminal segment is only half as long as the penultimate segment, the neck is shorter, the oviger implant bulges are at the neck midpoint, the abdomen is longer than the posterior trunk segment, the tarsus is only half the length of the propodus, the femur is 0.2 longer than the second tibia, and oviger segment 4 is longer than segment 5.

The second coxae of this species, swollen with ova, are reminiscent of *A. ovicoxa* Stock, but the two species are otherwise quite dissimilar.

Placement and arrangement of the femoral cement gland aperture or apertures must await the capture of a male of this geminate new species.

Ascorhynchus cooki, new species
Fig. 2

Material examined.—Southwest Pacific, SW of Macquarie Island, 59°58′S, 155°31′E, 2985–2992 m, coll. *Eltanin,* sta 1964, 10 Feb 1967, holotype male (USNM 233601), 2 paratype females (USNM 233602).—N of Chatham Rise, New Zealand, 41°45′S, 178°05′W, 2610–2668 m, coll. *Eltanin,* sta 1711, 25 May 1966, 3 paratype females (USNM 233603).—SE of Cook Strait, New Zealand, 42°11′S, 175°11′E, 2612 m, coll. *Eltanin,* sta 25-371, 20 Nov 1966, paratype chelate juvenile (USNM 233604).

Description.—Size gigantic for genus, leg span 178 mm. Integument smooth, glabrous. Trunk slender, graceful, posterior of first 3 segments flaring into cowls having dorsomedian tubercles with rounded tips. Lateral processes twice as long as maximum diameters, without setae, with low dorsodistal tubercles rounded at tips. Neck long, oviger implantation directly ventral to ocular tubercle which is placed just posterior to median neck length. Ocular tubercle twice as long as diameter with anterior pair of eyes at median length, posterior pair of eyes more distal. Proboscis slender, tripartite, only as long as first trunk segment, mouth flat. Abdomen slender, extending only to distal rim of first coxae on fourth legs, glabrous, carried slightly ventral with distal half curved dorsally.

Chelifore scapes with 2 segments, armed

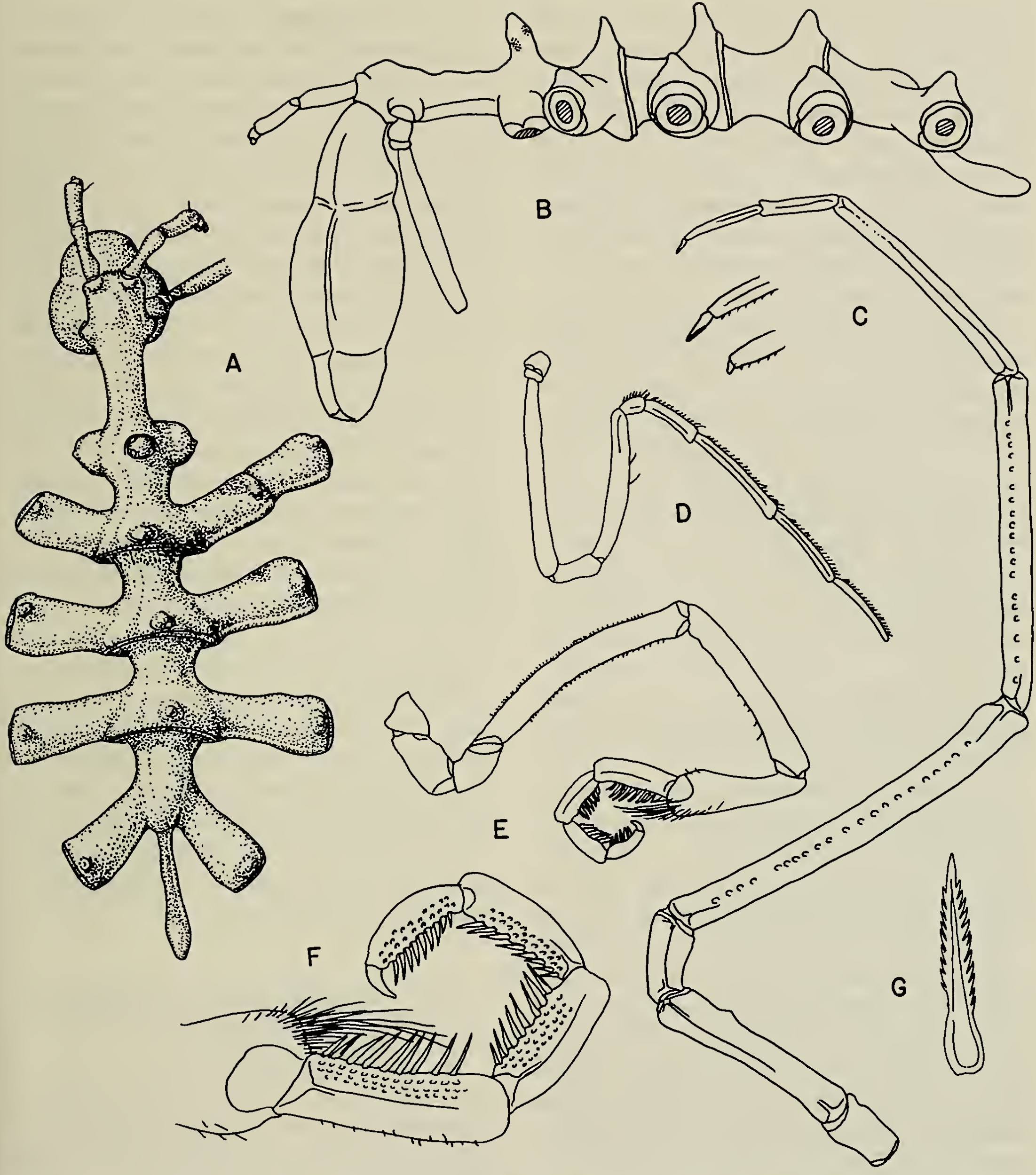

Fig. 2. *Ascorhynchus cooki,* male holotype: A, Trunk, dorsal view; B, Trunk, lateral view; C, Third leg, with enlargement of claws of first and third legs; D, Palp; E, Oviger; F, Oviger terminal segments, enlarged; G, Oviger denticulate spine, enlarged.

with 1–2 small distal setae. Scape segments subequal, slightly clubbed distally, short, each no longer than neck width. Chela tiny, vestigial, movable finger represented by tiny ventral bump, glabrous.

Palp third segment 3.5 times longer than fourth, terminal 5 segments very slender, numbered from shortest to longest; 6, 7, 10, 9, with 8 longest, all armed with ventral fringe of tiny setae.

Oviger segment 5 about 0.8 length of segment 4, both armed with tiny lateral setae.

Sixth segment clubbed distally, armed with distal fringe of short and long setae, some longer than segment diameter. Strigilis 4 segments increasingly shorter in length progressing distally, armed with 3–4 rows of denticulate spines, 1 row larger than lateral rows, larger row with formula 9:8:8:9, spines slender, with many lateral denticulations. Terminal claw well curved, short, only 0.35 length of terminal segment.

Legs long, slender, glabrous, femur longest segment with tibia 1 longer than tibia 2. Cement glands numbering 21–24 tiny pores on femur, 19–23 pores on entire length of tibia 1. Tarsus slender straight cylinder, subequal in length to slender slightly curved propodus, both armed with few tiny ventral setae. Claws of first pair of legs extremely tiny, only about 0.3 as long as other 6 claws, which only about 0.18 propodal length, none curved. Sex pores only on posterior 4 second coxae.

Female slightly larger, oviger without long setae and with fewer denticulate spines. Sexual pores on all second coxae.

Measurements (in mm).—Holotype: trunk length (chelifore insertion to tip 4th lateral processes) 25.5; trunk width (across 2nd lateral processes) 12.5; proboscis length 16; abdomen length 6; third leg, coxa 1 4.0; coxa 2 10.5; coxa 3 4.75; femur 20.5; tibia 1 22.0; tibia 2 12.5; tarsus 4.0; propodus 4.0; claw 0.75; claw of first legs 0.2.

Distribution.—Known from the type locality, the SW Pacific, SW of Macquarie Island, in 2985–2992 m, and from N of the Chatham Rise and off Cook Strait, New Zealand, in 2610–2668 m.

Etymology.—The new species is named for the great Pacific explorer, Captain James Cook.

Remarks.—This species is very close to *Ascorhynchus armatus* (Wilson), as will be seen in the following key of the five giant species known to this genus. Were it not for the very widely separated collecting localities for this new species (SW Pacific) and those of *A. armatus* (N. Atlantic), I would be more inclined to attribute the differences among the two species as possible variations within a single species. Male cement gland(s) have proved to be a stable character in most genera and form a good diagnostic element. The cement gland pores in *A. armatus* appear to be consistently greater in number (53–90) than those of *A. cooki* (40–47). With only a single male on which to count the pores, the number is within a narrow range and will probably form a wider range when more specimens of this deep-living giant become available. I believe the few differences, including trunk and lateral process tubercle dissimilarities, between the two species are sufficient to keep them as separate species until it can be established whether or not *A. armatus* inhabits the Pacific and if there are transitional specimens bridging the differences enumerated in the key.

The five giant species known to this genus all share the following characters; trunks with median dorsal tubercles, long abdomina, 2-segmented scapes, many cement gland pores on multiple leg segments, a tarsus almost as long or equal to the propodal length, and trunks at least 13 mm long or greater. Measurements will, of course, vary among specimens of any one species.

Key to the Giant Species of the Genus *Ascorhynchus*

1. Eyes present, however small; trunk length over 15 mm 2
– Eyes lacking; trunk length slightly over 13 mm .... *A. glaber* Hoek
2. Lateral processes smooth, without tubercles 3
– Lateral processes with tubercles of any size 4
3. Tarsus 0.8 propodal length; about 22 cement gland pores on femorae, first tibiae; propodal claws equal in length; scape first segment shorter than second .... *A. agassizi* Schimkewitsch

– Tarsus, propodus subequal; about 45–54 cement gland pores on femorae, first tibiae; first legs propodal claws shorter; scape first segment longer than second .. *A. japonicus* Ives

4. Lateral process tubercles tall, without setae; scape segments almost equal; ocular tubercle twice taller than basal diameter; chelifores almost glabrous, with few very short setae 5

– Lateral process tubercles tiny, processes with lateral setae; first scape segment only 0.5–0.6 length of segment 2; ocular tubercle no taller than base width; chelifores with some setae as long as segment diameters .. .. *A. pararmatus* Stock

5. Femorae with 21–24 cement gland pores, 19–23 on first tibiae; tarsus, propodus subequal in length; trunk, lateral process tubercles rounded at tips; third palp segment 3.5 length of fourth ....*A. cooki,* new species

– Femorae with 33–50 cement gland pores, 20–40 on first tibiae; tarsus 0.8 propodal length; trunk, lateral process tubercle tips pointed; third palp segment 4 times longer than fourth .... *A. armatus* (Wilson)

Genus *Cilunculus* Loman, 1908
Cilunculus spinicristus, new species
Fig. 3

Material examined.—N of Antipodes Islands, New Zealand, 49°40'S, 178°53'E, 476–540 m, coll. *Eltanin,* sta 27-1851, 3 Jan 1966, holotype male (damaged), USNM 233605.

Description.—Size moderately large, leg span slightly over 30 mm. Trunk robust, fully segmented, armed with 6–8 short spines on posterior rims of each raised segment. Lateral processes separated by slightly more than their diameters, as long as twice their diameters, armed with several short anterolateral, posterolateral, and dorsodistal spines. Anterolateral rim of first segment armed with 2 short spines per side. Neck broad, short, ovigers implanted at narrowest part. Neck flaring widely at anterior around chelifore insertion. Ocular tubercle implanted at midpoint of anterior neck broadening, over twice as tall as wide, with short truncate cone at tip, without eyes. Proboscis large, bulbous, without hint of distal or proximal segmentation lines, but with distinct longitudinal segmentation lines. Abdomen moderately long, slightly swollen distally, armed with 3 dorsodistal short setae, carried almost horizontally, slightly longer than distal rims of 4th leg second coxae.

Chelifore scape 1-segmented, broad, little longer than wide, with hint of segmentation line at proximal constriction, armed with few short distal setae. Chela vestigial, with distal cleft and knobs giving hint of fingers, unarmed.

Palp slender, first segment only slightly longer than wide, second segment longest, 0.25 longer than fourth, both armed with few lateral and dorsodistal setae. Third segment half length of fourth, armed with distal fringe of few short setae. Terminal segments each shorter than last, armed with ventral fringe of setae longer than segment diameters.

Oviger long, slender, armed with very few short setae. Second segment 0.75 as long as fourth, the longest. Fifth segment only slightly shorter than second. Strigilis 5 segments with few short setae, those of seventh and eighth segments longer than segment diameters. Denticulate spines only present on ninth and tenth segments; 1 on ninth, 2 on tenth, spines broad, with 7–8 lateral denticulations.

Legs moderately long, spinose. Coxae with few short lateral and dorsodistal spines, femur with many ventrally. Cement gland tube long, equal to segment diameter, placed just proximal to dorsodistal tip of femur, pointing distally, not elevated. First tibiae only slightly longer than femorae, second tibiae

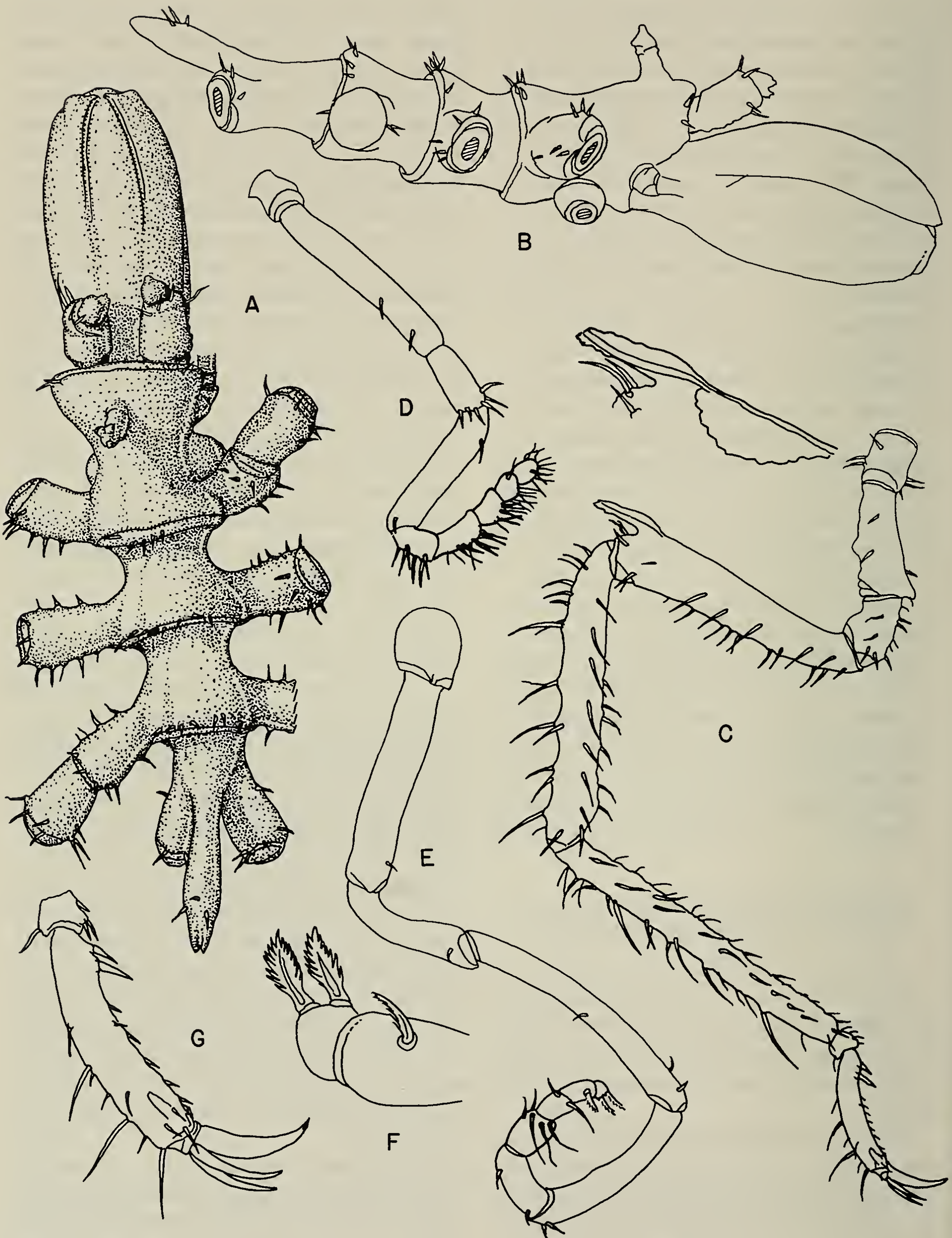

Fig. 3. *Cilunculus spinicrista,* male holotype: A, Trunk, dorsal view; B, Trunk, lateral view; C, Third leg, with cement gland and duct enlarged; D, Palp; E, Oviger; F, Oviger terminal segments, enlarged; G, Third leg terminal segments, enlarged.

longest, both armed with many lateral, dorsal, and ventral setae, few slightly longer than segment diameters. Tarsus very short, propodus over 5 times longer, well curved, armed with 2 heel spines and 6–7 very short sole spines, dorsally with several setae, 3 longer than propodal diameter. Claw robust, strongly curved only at tip, almost half propodal length. Auxiliary claws slender, moderately curved, 0.75 length of main claw. Sex pores on second coxae of posterior 2 pairs of legs.

Female and juvenile characters unknown.

Measurements (in mm).—Trunk length (chelifore insertion to tip 4th lateral processes) 3.98; trunk width (across 2nd lateral processes) 2.53; proboscis length 2.64; abdomen length 1.38; third leg, coxa 1 0.53; coxa 2 1.2; coxa 3 0.73; femur 2.8; tibia 1 2.88; tibia 2 3.49; tarsus 0.24; propodus 1.34; claw 0.58.

Distribution.—Known only from the type locality, N of the Antipodes Islands, New Zealand, in 476–540 m.

Etymology.—The new species name is a compound of the Latin *spina* and *crista,* referring to a spiny crest or ridge in reference to the spines on each of the median dorsal trunk ridges.

Remarks.—This new species differs from all other known *Cilunculus* species by the presence of the row of spines on the posterior rim of each trunk segment which lack any form of tubercles, the blind, moderately long, cylindrical ocular tubercle with a short blunt conical tip, the very broad, short chelifore scapes, the long, tenuous oviger, the very spiny legs, and the cement gland tube at the dorsodistal end of each femur, pointing distally instead of well elevated as in many species. The combination of these characters is not found in any other known species although the characters, taken separately, are not unique except perhaps the strong spines on the posterior trunk rims of the new species.

The genus is found worldwide in widely scattered localities with only a single species, *C. sewelli* Calman, known to have much breadth of distribution (E. Africa to New Zealand). Unfortunately, most species are known only from a type or type-lot, which is the case for many deep-water species and genera of pycnogonids. The majority of *Cilunculus* species are known from the Southern Hemisphere while several are known from Japan, the Caribbean, Bay of Biscay, and the English Channel. The southernmost records are for *C. cactoides* Fry and Hedgpeth, from the Ross Sea, Antarctica.

Cilunculus is a deeper water, more slender counterpart of the shallower genus *Ammothella,* and indeed, several of the species have been confused between these genera, while one or two have been described as species of other genera. As Fry and Hedgpeth (1969:124) declared, "At best, *Cilunculus* is an uneasy genus." Most writers including this one have thought it best to retain the genus as a separate entity while avoiding specific names that could become homonyms in a future generic or family revision.

Genus *Eurycyde* Schiödte, 1857

Eurycyde antarctica, new species

Fig. 4

Material examined.—E of Adare Peninsula, Ross Sea, Antarctica, 72°00′S, 172°28′E, 523–528 m, coll. *Eltanin,* sta 1997, 10 Jan 1968, holotype male, USNM 233606, paratype female, USNM 233607; NE of Cape Adare, Ross Sea, 71°17′S, 171°33′E, 659–714 m, coll. *Eltanin,* sta 1870, 14 Jan 1967, paratypes, 1 female, 1 juvenile, USNM 233608.

Description.—Size typical for genus, leg span slightly over 10 mm. Trunk robust, glabrous, completely segmented, each segment inserted anteriorly into swollen cowl of posterior of first 3 segments. Lateral processes moderately short, only 1.5 times as long as wide, separated by their diameters, armed with short, narrow, dorsodistal tubercles only half as tall as segment diameters, without setae or spines. Ocular tubercle

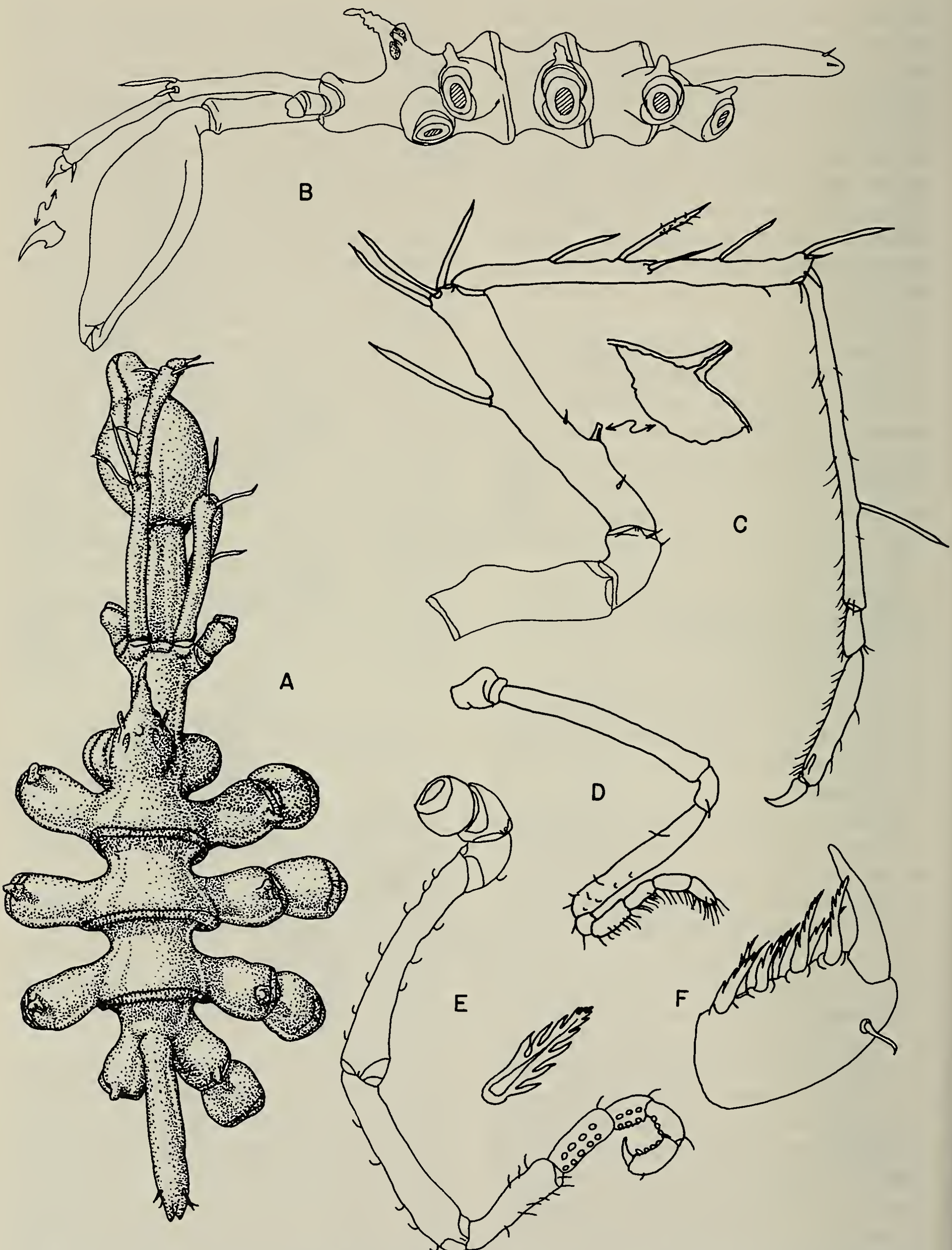

Fig. 4. *Eurycyde antarctica,* male holotype: A, Trunk, dorsal view; B, Trunk, lateral view; C, Third leg with cement gland tube enlarged; D, Palp; E, Oviger, with denticulate spine enlarged; F, Oviger terminal segment, enlarged.

with broad base tapering to slender anterior-pointing tip, glabrous, with lateral sensory papillae projecting as tiny slender tubercles, eyes darkly pigmented, of equal size, posterior pair placed distally to anterior more proximal pair. Oviger implantation directly ventral to ocular tubercle, at midpoint of first trunk segment. Proboscis of typical 2 segments, proximal segment cylindrical, half distal segment length. Second segment carried ventrally from narrow attachment to first segment, swollen at midlength, ovoid, with very narrow pointed mouth. Abdomen cylindrical, tapering distally, as long as midlength of second coxae of fourth legs, armed distally with 4 short setae, without long spines.

Chelifore scape 2-segmented, slender, long, extending to midlength of second proboscis segment, armed with 2–3 long broad spines on first segment which is 0.2 times longer than second segment. Second segment armed with 2–3 long spines similar to those of first segment. Chela tiny, with short, broad, curved immovable finger and tiny bud as movable finger, glabrous.

Palp 9-segmented, second segment longest, about 0.3 longer than fourth segment. Fifth segment shortest, not longer than wide. Terminal 5 segments subequal in length to fourth, terminal 4 with fields of ventral setae equal to or slightly longer than segments.

Oviger fairly long, major segments armed with few short, lateral, recurved setae. Fifth segment 0.85 as long as fourth, sixth half length of fifth. Strigilis 4 segments each shorter than last, armed with distal ectal seta each and 2 rows of endal denticulate spines in the formula (counting both rows), 9:6:5:7, with almost straight terminal claw lacking teeth. Denticulate spines narrow, with 5–6 denticles per side.

Legs slender, major segments each narrower than last distally, armed with few very long broad spines and several long pointed spines, with 1–2 pointed spines on tibiae having setules or "feathered." First coxae without tubercles of any description. Tibiae subequal in length, femorae slightly shorter. Cement gland a small swelling proximally, at 0.25 femur length, with short tube pointing obliquely anterior and distally. Tarsus 0.33 length of propodus. Propodus very slightly curved, without heel or heel spines, armed with many short sole spines. Claw broad, well curved, less than 0.3 propodal length, no auxiliaries.

Female slightly larger in most measurements. Legs with several more feathered sharp spines. Ova carried in very swollen second coxae, none found in femorae. Ocular tubercle with short blunt anterior tubercle half as tall as that of male. Neck shorter than male's, and lateral process tubercle shorter and broader based.

Measurements (in mm).—Trunk length (chelifore insertion to tip 4th lateral processes) 1.33; trunk width (across 2nd lateral processes) 0.86; proboscis length (second segment only) 0.84; abdomen length 0.55; third leg, coxa 1 0.23; coxa 2 0.56; coxa 3 0.25; femur 0.95; tibia 1 1.0; tibia 2 1.0; tarsus 0.14; propodus 0.43; claw 0.12.

Distribution.—Known only from its type locality, off Cape Adare and its Peninsula, Ross Sea, in 523–714 m.

Etymology.—This species is named for the Ocean in which it was collected.

Remarks.—Of the nine or ten recognized species of *Eurycyde,* this is the first known to have the following combination of characters; no ocular tubercle spines or setae, and no tubercles on the first coxae. It is also the first species of the genus to be found in Antarctic waters. Most known species are from tropical or at least tropical-temperate habitats. The only cold water species known was the first to be described; *E. hispida* (Krøyer), distributed from eastern Canada to the western Russian Arctic. This new species and *E. hispida* could be classified as the 'conservative' element of this genus because they both lack the long ocular tubercle spines and the spinose first coxae tubercles of many other species. The new species has very few long broad spines on any appendage, in contrast to the many spines on most species. The cement gland bulge and tube of the new species are smaller than those of most species where the male gland is known, and is close to those of *E. hispida.* This new species differs from any other, including *E. hispida,* in having much less spinose appendages and very different lateral process tubercles in a genus where most species have very slender pointed tubercles or none at all. All species of this genus are closely allied in characters such as oviger, palp, chelifore, and terminal leg segment lengths and shapes. No known *Eurycyde* species has the long pointed ocular tubercle without spines or setae present in this new species.

Family Callipallenidae Hilton
Genus *Cheilopallene* Stock, 1955
Cheilopallene gigantea, new species

Fig. 5

Material examined.—E of Antarctic (Palmer) Peninsula, Weddell Sea, Antarctica, off Larsen Ice Shelf, 66°28′S, 57°26′W, 581–610 m, coll. *Hero,* sta 3-28D, 17 Aug 1970, holotype male, USNM 233609.

Description.—Size extremely large for genus, leg span 57.6 mm. Trunk moderately robust, segments slightly inflated, glabrous. Lateral processes short, less than twice as long as diameters, separated by less than their diameters, armed with 2–3 dorsodistal small setae. Neck moderately long, tapering anteriorly toward greatly inflated anterior at chelifore and proboscis insertion, armed with 4 dorsodistal setae over chelifore insertion. Ocular tubercle low, only slightly taller than width at base, tip rounded, eyes large, lightly pigmented, sensory papillae tiny. Tubercle placed toward posterior of cephalic segment, just anterior to first lateral processes and slightly posterior to midpoint of oviger insertion bulges. Proboscis typical, fairly short, proximal half cylindrical, inflated distally, tapering to moderately large petal-like lips, each semirectangular, covered with closely packed pilose setae. Abdomen short, extending barely to tip of 4th lateral processes, armed with 4–5 short distal setae.

Chelifores massive, single segmented scapes very large in diameter. Chelae palm almost globular, fingers typical, shorter than palm, with uneven ridges and bumps as dentition. Scape armed with few short setae, chelae with many short setae on distal palm and fingers.

Oviger fully formed, of 10 segments with strigilis. Third segment slightly longer than first two combined in length. Third through sixth segments armed with rows of short ventral and dorsal setae. Fourth and fifth segments slightly curved, fifth slightly longer than fourth, armed with dorsodistal tubercle not quite as tall as segment diameter, armed with 5–6 short setae. Sixth segment with dorsal and ventral fringe of short setae increasing in numbers distally. Strigilis segments subequal in length, fully formed, armed with few short ectal setae, row of endal denticulate spines in formula 19:19: 18:16, and terminal claw slightly over half length of terminal segment, bearing 23–24 short closely spaced endal setae. Denticulate spines of 2 lengths; proximal forms shorter with 3 proximolateral serrations and many tiny crenulations distally, and distal spines, longer, with 3–4 lateral serrations grading into many fine crenulations distally. Egg size slightly greater than maximum diameter of widest segment.

Legs moderately setose with short setae, none as long as segment diameter, increasing in numbers on major distal segments. Tibia 2 longest segment, femur and tibia 1 subequal, second coxae slightly longer than first and third combined. Femur with 4 tiny slightly raised cement gland pores evenly spaced along length of segment. Tarsus short, about 0.22 length of propodus, armed with tuft of short ventral setae. Propodus slightly curved, without marked heel, with 4 large heel spines increasing in size distally from proximal smallest. Sole armed with many very short setae and short flanking setae.

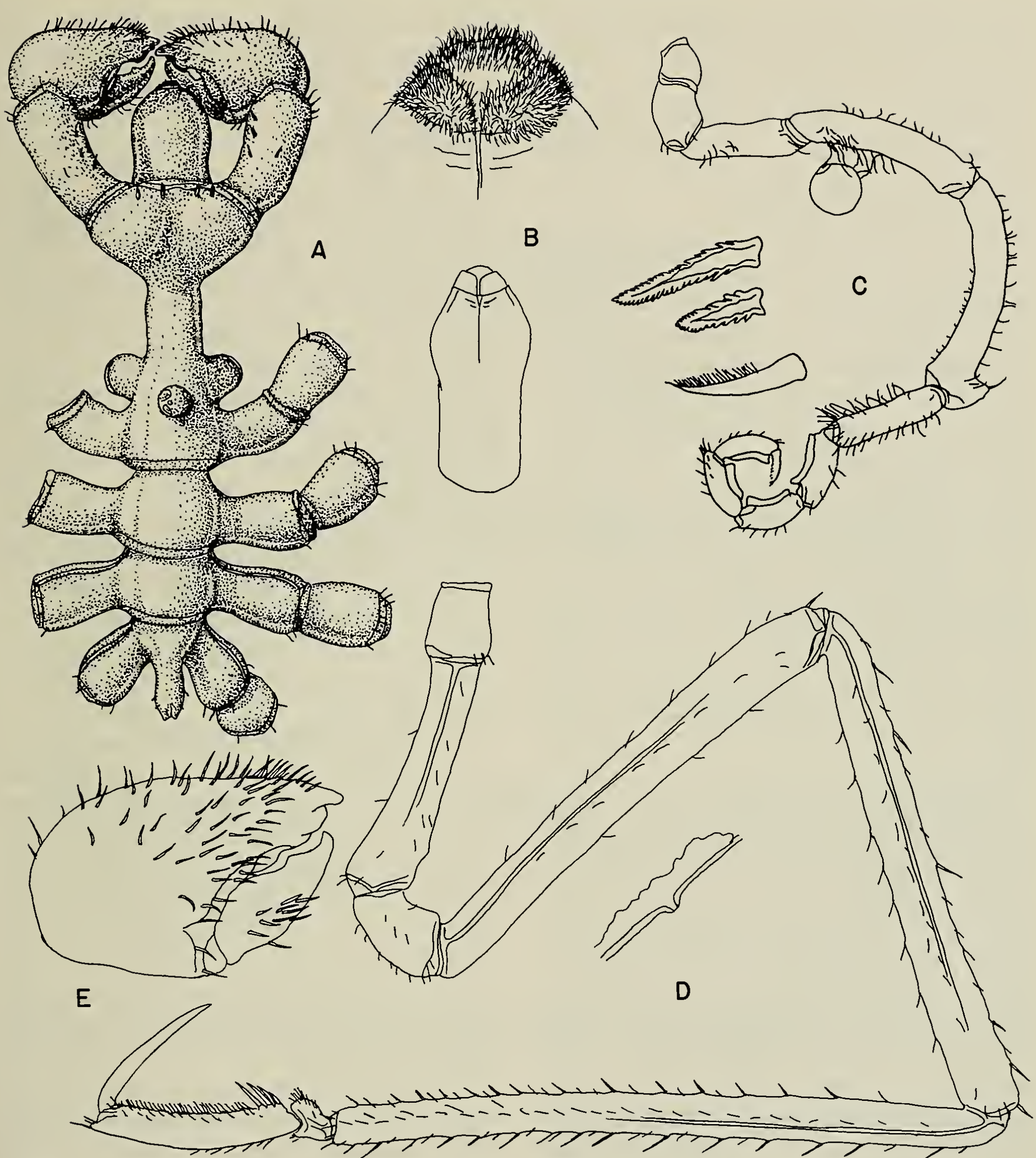

Fig. 5. *Cheilopallene gigantea,* male holotype: A, Trunk, dorsal view; B, Proboscis, ventral view, with lip setae removed (below), lips with setae (above); C, Oviger, with enlargements of distal and proximal denticulate spines and terminal claw; D, Third leg, with one cement gland pore enlarged; E, Chela.

Propodus tip slightly projecting. Claw long, slender, slightly curved, about 0.7 as long as propodus. Without auxiliary claws.

Measurements (in mm).—Trunk length (chelifore insertion to tip 4th lateral processes) 5.46; trunk width (across 2nd lateral processes) 3.08; proboscis length 1.62; abdomen length 0.58; third leg, coxa 1 1.02; coxa 2 2.62; coxa 3 1.22; femur 5.38; tibia 1 5.46; tibia 2 7.32; tarsus 0.48; propodus 2.15; claw 1.62.

Distribution.—Known only from the type locality, off the Larsen Ice Shelf on the east side of the Antarctic (Palmer) Peninsula, Antarctica, in 581–610 m.

Etymology.—This giant (Latin: *gigantea*) new species is named for its size which is at least four times larger than any other known species of the genus.

Remarks.—The enigmatic genus *Cheilopallene* now contains four known species, including this new species; *C. brevichela* Clark (Maldives), *C. clavigera* Stock (U.S. Virgin Islands), and *C. trappa* Clark (Snares Islands, New Zealand). Three of these four species have normal ten-segmented ovigers with a strigilis bearing denticulate spines, while the type of the genus, *C. clavigera* (Stock, 1955:230–233), has an elongate fifth oviger segment that is clubbed distally. A tiny sixth segment extends beyond this swollen tip and represents all that remains of the strigilis. A series of males of this species must be examined to discern whether or not this is the natural state of the oviger.

This abbreviated oviger appears also to be the natural form in many specimens of another genus erected to emphasize this character. Pushkin (1974:938–940) removed Hodgson's (1915) *Pallenopsis spicata* from that genus and placed it in his genus *Clavigeropallene,* because it bears seven oviger segments in the male (instead of the usual ten), with the sixth broadly clubbed, and lacks a strigilis. This oviger modification appears to be neither a localized distributional feature nor a monotypic malformation due to damage and subsequent regeneration in a number of specimens (Hodgson 1915, Calman 1915, Hodgson 1927, Gordon 1938). Instead, it is probably another apomorphic character in a group of genera that are undergoing rapid change and dissemination from areas of origin in the Southern Hemisphere. It appears that many and perhaps even the majority of genera (now numbering 24 or 25) in the family Callipallenidae had their origins in that hemisphere and have reached their present known distribution patterns through unknown means of transport. Without a planktonic larval stage or other means of active transport, many species are localized or endemic and their dissemination in the oceans of the world is probably quite slow. The distribution of most callipallenid genera is poorly known to fragmentary at best, as is true for most pycnogonids, but the majority of species in these genera have been taken in Southern Hemisphere localities or at least near the equator in Indo-Pacific localities. From this distributional evidence, Australia and South Africa are the two focal points of dissemination among the majority of genera in this family, with Antarctic polar seas containing a wealth of species with characters crossing many generic lines. This inevitably points toward a Gondwanaland land mass for the origins of the protofamily that lead to the many genera now extant, but without a valid geological record to support such an hypothesis, it must remain conjecture.

This species differs from the three others known, in addition to its very much larger size, by having much shorter lips covered by a thick coat of setae. In the other species, the lips are narrower, longer, glabrous, and described as 'petal-shaped'. The proboscis and its parts are very characteristic in almost all pycnogonids and have long served as one of the valid diagnostic features. The lips of this new species are not typical of others in the genus which have small glabrous triangular lips, but are more characteristic of other species in genera having lip fringes or heavily setose oral surfaces such as some of the *Parapallene, Pallenoides,* and *Pseudopallene* species. The lip characters are species-specific and do not always serve as diagnostic characters for the genera in this family.

The chelae of the four species are remarkably similar and all have the uneven endal finger surfaces. The movable finger appears to fit into a pseudosocket toward the tip of the immovable finger, but the use of such an arrangement for feeding or defense can only be conjectural.

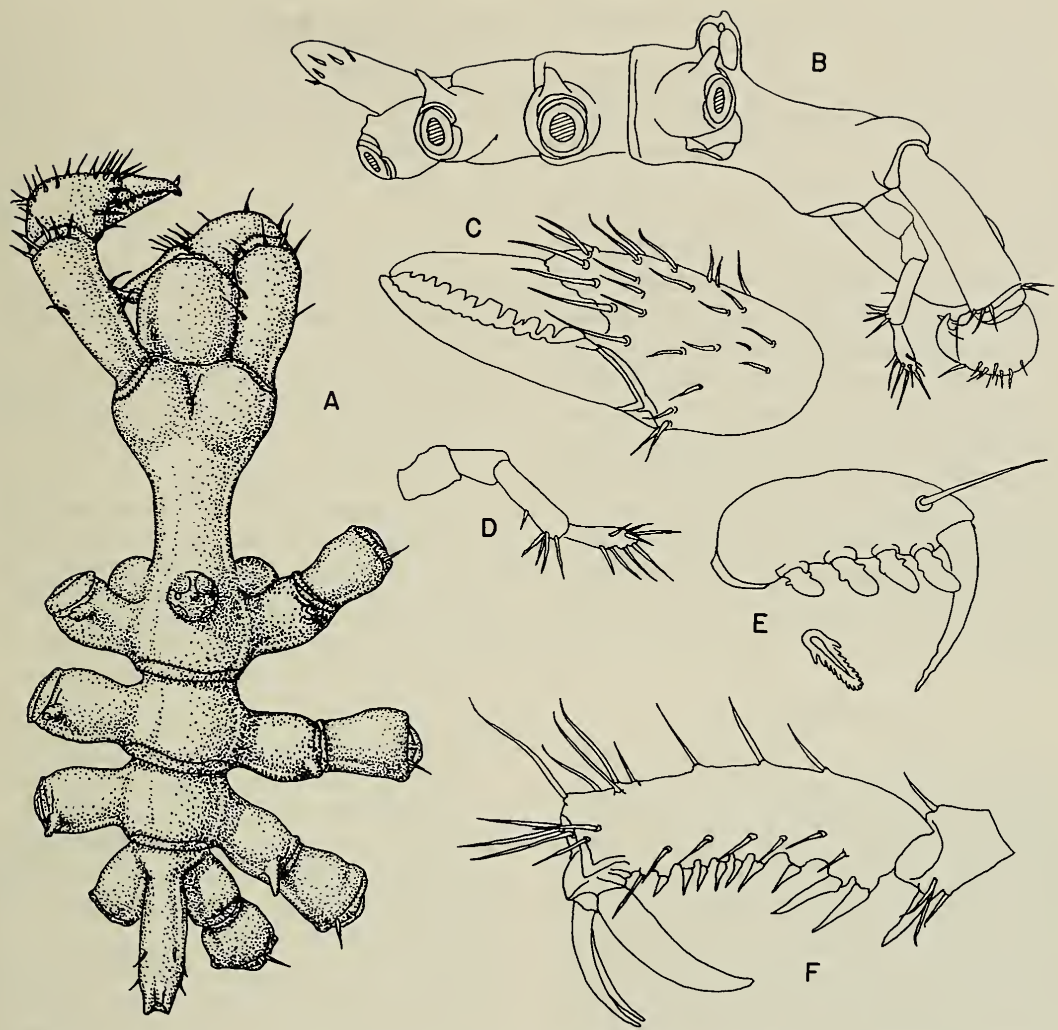

Fig. 6. *Oropallene dimorpha,* male: A, Trunk, dorsal view; B, Trunk, lateral view; C. Chela; D, Palp; E, Oviger terminal segment with distal spine enlarged; F, Third leg, terminal segments.

Genus *Oropallene* Schimkewitsch, 1930
Oropallene dimorpha (Hoek)
Fig. 6

Pallene dimorpha Hoek, 1898:290–293, pl. ii, figs. 1–6.

Oropallene dimorpha.—Schimkewitsch, 1930:245 [text], 291–292 [text].—Gordon, 1944:36.—Stock, 1954:29 [text].

Material examined.—NE of Macquarie Island, SW Pacific, 54°30′S, 158°59′E, 112–124 m, coll. *Eltanin,* sta 1974, 15 Feb 1967, 62 males with eggs, males, females, juveniles; same locality, 54°24′S, 159°01′E, 79–93 m, coll. *Eltanin,* sta 1417, 10 Feb 1965, 2 male juveniles.

Remarks.—These specimens constitute only the fourth and fifth capture records for this species, apparently not due to its rarity (62 specimens in one trawl sample above), but because of the scarcity of collections from the extremely inhospitable Kerguelen Islands (its type locality) and equally inhospitable Macquarie Island. Hoek (1898) described the species from 'few' specimens, while Gordon (1944) listed a female from Kerguelen and three juveniles from Macquarie which she attributed to this species.

To our knowledge, it is confined to the two areas in depths or 69–220 m.

The adult specimens have several marked differences from the type figured by Hoek. None of these specimens have the tall cone at the ocular tubercle apex, but instead have the tip rounded with a small papilla of varying size. Hoek's male specimen (Fig. 6) has a much smaller oviger terminal claw and more denticulate spines per strigilis segment. The type propodus is longer, has longer claws, and has a single large heel spine while these specimens have a shorter segment, shorter claws, and two heel spines. The second segment of the type palp is longer than the first while the reverse is the case with these specimens, but they are otherwise sufficiently like Hoek's figures and description to warrant classifying them as the same species.

Acknowledgments

I am grateful to the Smithsonian Oceanographic Sorting Center personnel who sorted and contributed the many thousand pycnogonid specimens to the National Museum, among which were the species described in this report. I am grateful to the invertebrate editor, Dr. T. E. Bowman, for making helpful suggestions for the improvement of this paper. The specimens are deposited in the National Museum of Natural History under U.S.N.M. catalog numbers.

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FOUR SPECIES OF SPHAERODORIDAE (ANNELIDA: POLYCHAETA) INCLUDING ONE NEW GENUS AND THREE NEW SPECIES FROM ALASKA

Jerry D. Kudenov

Abstract.—Four species of Sphaerodoridae (Polychaeta) including one new genus and three new species are described from Alaska. *Amacrodorum bipapillatum* is a new genus and species from the Aleutian Island of Akutan; *Sphaerodoropsis uzintunensis* and *S. katchemakensis* are both new species from Katchemak Bay, Homer; *Sphaerodoropsis sphaerulifer* (Moore, 1909) is also reported. *Amacrodorum* is partly characterized by the absence of macropapillae and the presence of two kinds of papillae. It is strongly isolated in the family, and superficially similar to *Levidorum* Hartman in that both taxa lack macropapillae. However, *Amacrodorum* differs from *Levidorum* in not having smooth body surfaces and in having head appendages; *Levidorum* was recently assigned to a separate family that may be more closely related to syllids (Perkins 1987). A key to described species of *Sphaerodoropsis* recorded from Alaska is presented.

A single, unusual sphaerodorid polychaete that could not be placed to a known genus led to a study of the family in Alaska. The specimen was obtained from a benthic survey in Akutan Straits, near the Aleutian Island of Akutan as part of an environmental impact study for the township of Akutan to obtain a permit from the Environmental Protection Agency for an offshore waste discharge site. Survey details and results are available in Jones & Stokes (1984a, b). Additional sphaerodorids were obtained from another impact study of a boat harbor expansion for the city of Homer by Dames and Moore (1984). Type materials are deposited in the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM).

Family Sphaerodoridae Malmgren
Amacrodorum, new genus

Type species.—*Amacrodorum bipapillatum* new species, by original designation.

Diagnosis.—Macro- and microtubercles absent; papillae present over all body surfaces of which both elliptical and hemispherical papillae present on dorsum. Anterior end truncate, with 1 median and 2 pairs of lateral antennae; all antennae short. Parapodia each with a single aciculum; setae simple; large recurved hooks absent.

Remarks.—*Amacrodorum* differs from all other described genera of sphaerodorids in lacking both macrotubercles and microtubercles, and in having two kinds of papillae. The hemispherical papillae appear not to have been described previously for the family. As such, *Amacrodorum* is highly isolated in the Sphaerodoridae. Fauchald (1974:270) made a similar observation for *Levidorum* Hartman, 1967, which totally lacks both macro- and microtubercles as well as papillae. In fact, Fauchald (1974:270), first suggested that one taxon each of amacropapillate (represented by *Levidorum*) and macropapillate species be recognized as separate families in a superfamily complex.

In light of this suggestion, Perkins (1987) both redescribed *Levidorum* and assigned it to the newly defined Levidoridae Perkins, 1987; *Levidorum* is the type genus by monotypy. However, Perkins states that *Levidorum* is more closely allied to syllids than to sphaerodorids, particularly since the two former groups both have a chitinous foregut and proventriculus. Perkins further suggests that both eye and setal morphologies of his newly described species further ally this family more closely to syllids than sphaerodorids. Palps may also be present in *Levidorum* which is a syllid trait not typically associated with sphaerodorids, although Perkins could not establish an homology between the palps of levodorids and syllids. Levodorids differ from both syllids and sphaerodorids in having perhaps two peristomial segments, each of which lacks cirri and antennae. However, it will be most informative histologically to confirm the presence of two peristomial segments before this particular trait can be critically accepted, especially since only one was noted by Fauchald (1974:270).

In any case, *Amacrodorum* differs strikingly from *Levidorum* in having papillae distributed over all general body surfaces, in having typical sphaerodorid prostomial antennae instead of "palps," in having one aciculum per parapodium rather than two–three, and in having setae entirely simple and not a mixture of either pseudocomposite and simple bristles. Given the removal of *Levidorum* by Perkins (1987), all other described sphaerodorid genera have dorsal macropapillae. A logical extension of Fauchald's suggestion would be to establish another family or subfamily for morphologically distinct sphaerodorids such as *Amacrodorum* (i.e. Amacrodoridae or Amacrodorinae). Clearly, this new sphaerodorid genus is strongly isolated within the family. While such an approach is probably justifiable, it is clearly parsimonius to retain *Amacrodorum* in the Sphaerodoridae for the present time.

Etymology.—*Amacrodorum* derives from Latin, *A,* meaning without, *macro,* meaning large, and *dorum,* meaning dorsal surface, referring to the absence of dorsal macrotubercles. Gender: Feminine.

Amacrodorum bipapillatum, new species
Figs. 1, 2A

Material examined.—ALASKA: Akutan Island, Akutan Harbor, just north and east of Akun Strait, sta 11-3, sample 23, 54°09′72″N, 165°42′83″W, 59 m, poorly sorted silty sand, 18 Sep 1983, coll. Harvey Van Veldhuizen; Holotype USNM 102784.

Description.—A small species, measuring 2.1 mm long, 0.45 mm wide without parapodia, 0.5 mm wide with for 16 setigers. Body short, grub-like, widest anteriorly; translucent, lacking pigmentation; white yolky eggs visible through body wall.

Prostomium truncate anteriorly; median antenna stout, digitiform, distally blunt (Fig. 1A, B). All lateral antennae digitiform, distally blunt, having similar lengths, longer than median antenna. Superior laterals each with 2 proximal papillar spurs (Fig. 1B); inferior lateral antennae lacking proximal spurs. Eyes numbering 1 pair (Fig. 1A). Peristomial cirri shorter than median antenna, distally inflated, blunt (Fig. 1A, B). Proboscis short, muscular, extending to setiger 2. Six papillae encircled by prostomial antennae; papillae otherwise present on peristomium.

Parapodia uniramous, stout, as long as wide (Fig. 1C, D); acicular lobe truncate, with presetal lobes digitiform, distally round, projecting well beyond acicular lobe; postsetal lobes absent (Fig. 1C–E). Ventral cirri conical, distally blunt, projecting beyond acicular lobe (Fig. 1D, E). Parapodial papillae numbering only 1, present on anterior parapodial surfaces; all other parapodial surfaces lacking papillae (Fig. 1C, D).

Dorsal macrotubercles, microtubercles absent. Dorsum otherwise with hemispherical and elliptical papillae (Fig. 1F, G) ar-

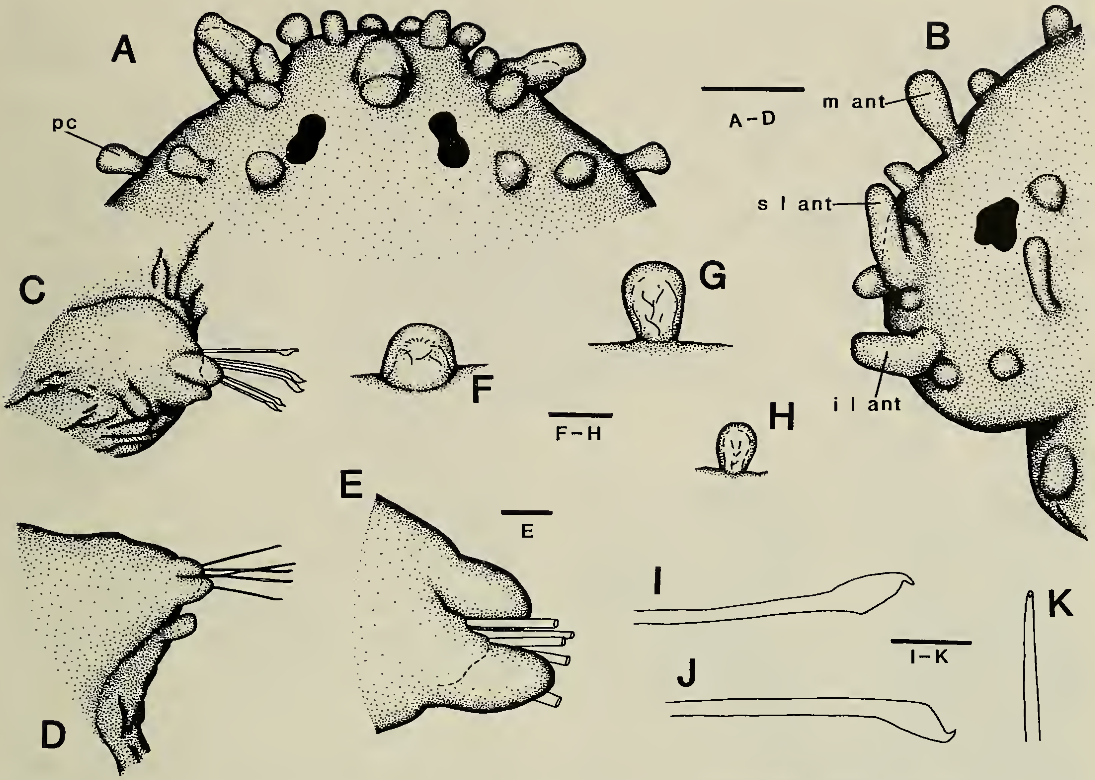

Fig. 1. *Amacrodorum bipapillatum,* holotype (USNM 102784): A, Anterior segments, dorsal view; B, Anterior segments, left lateral view; C, Left setiger 14, oblique anterolateral view; D, Left setiger 13, dorsal view; E, Left setiger 12, detail of distal parapodium, anterior parapodial papilla not shown, dorsal view; F, Hemispherical papillae, lateral view; G, Ellipsoidal papilla, lateral view; H, Ventral papilla, lateral view; I, Superior simple seta, lateral view; J, Inferior simple setae, lateral view; K, Simple seta, dorsal view. m ant, median antenna; s l ant, superior median antenna; i l ant, inferior median antenna. Scales: A–D = 0.05 mm; E, J–K = 0.01 mm; F–H = 0.02 mm.

ranged in complex pattern of 13 rows (Fig. 2A). Ventral papillae resembling dorsal papillae, arranged in zig-zag pattern of 7 alternating rows of elliptical and hemispherical papillae (Fig. 1H).

Simple falcigers present in all setigers, typically numbering 4–5 per fascicle, having sharp, distally recurved tips, and blade-shaped subdistal regions having smooth dorsal cutting edges (Fig. 1I–K); subdistal spurs on concave cutting surfaces absent.

Remarks.—*Amacrodorum bipapillatum* differs from all other described sphaerodorids in having two kinds of papillae present on dorsal and ventral surfaces. The setae of *A. bipapillatum* superficially resemble those of *Sphaerodorum recurvatum* Fauchald, 1974, *S. vietnamense* Fauchald, 1974, and other members of this genus in having distally recurved tips. However, the above species of *Sphaerodorum* also possess a small subdistal spur on concave cutting surfaces which is absent in *A. bipapillatum.* These *Sphaerodorum* species also tend to have long, tapering recurved distal tips and not short, stout tips.

Etymology.—The epithet, *bipapillatum* refers to the presence of two different kinds of body papillae. It is considered a noun in apposition.

Type locality.—Akutan Harbor, Akutan Island, Alaska.

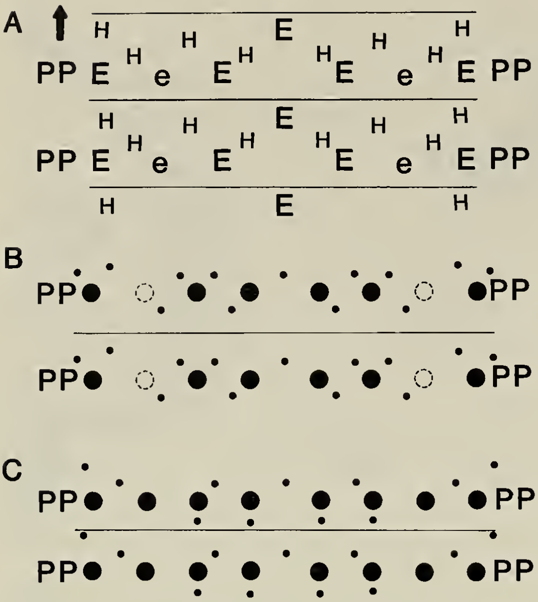

Fig. 2. *Amacrodorum bipapillatum,* holotype (USNM 102784): A, Distribution pattern of dorsal body papillae from setigers 6–7. B, *Sphaerodoropsis uzintunensis,* holotype (USNM 102810): Same, setigers 8–9. C, *Sphaerodoropsis katchemakensis,* holotype (USNM 102782): Same, setigers 6–7. Relative sizes of papillae reflected in different sized letters. H = hemispherical papillae; E = large elliptical papillae; e = small elliptical papillae. Large black dots refer to macropapillae; small dots to papillae. Arrow points anteriorly. A–C, schematic, not to scale.

Sphaerodoropsis Hartman and Fauchald, 1971

Sphaerodoropsis uzintunensis, new species

Figs. 2B, 3

Material examined.—ALASKA: Katchemak Bay, Homer Spit Boat Harbor, sta 210-1, 59°36′18.4″N, 151°24′41.8″W, 10 m, silt-clay, 28 Feb 1984, coll. Dave Erikson, 1 paratype, USNM 102808.—Sta 215-2 59°36′19.1″N, 151°24′39.0″W, 15 m, silt-clay, 28 Feb 1984, coll. Dennis Lees, 1 paratype, USNM 102809.—Sta 310-1, 59°36′11.7″N, 151°24′35.7″W, 3 m, slightly silty fine sand with shrimp wastes, 29 Feb 1984, coll. Dennis Lees, holotype having 18 setigers, USNM 102810, 1 paratype, USNM 102811.—Sta 315-1, 59°36′14.8″N, 151°24′34.5″W, 15 m, silt-clay, 29 Feb 1984, coll. Bill Blaylock, 3 paratypes, including worm of 16 setigers as illustrated, USNM 102812.—Sta. 315-4, same, 1 paratype, USNM 102813.

Description.—A small species, measuring 2.2 mm long, 0.7 mm wide without parapodia, 0.75 mm wide with parapodia, for up to 20 setigers. Holotype 16 mm long, 0.7 mm wide without parapodia, 0.75 mm wide with parapodia, for 18 setigers. Body short, grub-like, widest medially; macrotubercles of holotype with traces of gray coloration, otherwise lacking pigmentation, and light yellow in alcohol.

Prostomium reduced, truncate anteriorly; median antenna stout, digitiform, distally blunt (Fig. 3A, B). All lateral antennae digitiform, distally blunt, longer than median antenna; inferior lateral antennae slightly longer than superior lateral antennae. All lateral antennae each with 4 proximal papillar spurs (Fig. 3A, B). Eyes numbering 1 pair (Fig. 3A–C). Peristomium reduced; peristomial cirri about as long as median antenna, digitiform, distally blunt (Fig. 3A–D). Proboscis long, muscular, extending over setigers 3–7. Seven papillae tightly encircled by prostomial antennae; papillae otherwise present on peristomium (Fig. 3C).

Parapodia uniramous, stout, about 2× longer than high at base (Fig. 3E, F); acicular lobe triangular and distally pointed; 1 presetal lobe, distally blunt, subdistally inflated, projecting well beyond acicular lobe (Fig. 3E, F); 1 distal postsetal lobe inserted just behind superior dorsal edge level with acicular lobe (Fig. 3E, F). Ventral cirrus conical to trapezoidal, distally blunt, approaching but not projecting beyond acicular lobe (Fig. 3E, F). Parapodial papillae numbering 3, including 1 on anterior surfaces, and 1 each on proximal dorsal superior (not shown) and ventral inferior edges (Fig. 3E, F); absent from posterior parapodial surfaces.

Dorsal macrotubercles sessile (Fig. 3G), arranged in 6–8 longitudinal rows (Fig. 3D), each macrotubercle spherical, with 13–15 longitudinal rows of long, papillae arranged in complex nonrandom pattern (Fig. 2B).

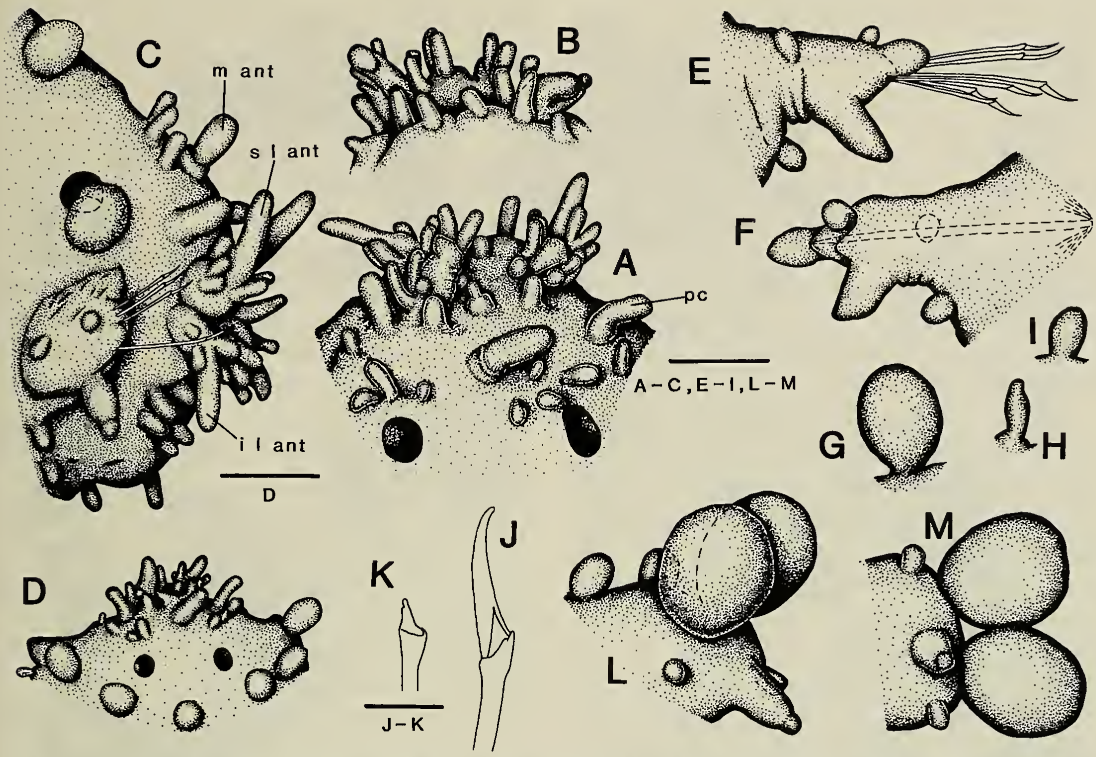

Fig. 3. *Sphaerodoropsis uzintunensis,* paratype (USNM 102812): A, Head region, dorsal view; B, Head region, ventral view; C, Anterior segments, lateral view; D, Anterior segments, dorsal view; E, Left setiger 7, anteroventral view, dorsal superior papilla omitted; F, Same, posterior view, setae and dorsal superior papilla omitted; G, Macrotubercle, lateral view; H, Dorsal papilla, lateral view; I, Ventral papilla, lateral view; J, Composite falciger, lateral view; K, Detail, shaft tip of composite falciger, ventrolateral view; L, Pygidium, lateral view; M, Same, ventral view. m ant, median antenna; s l ant, superior median antenna; i l ant, inferior median antenna. Scales: A–C, E–I, L–M = 0.05 mm; D, J–K = 0.01 mm.

Ventrum with 9 alternating rows of small, elliptical papillae (Fig. 3I) forming zig-zag pattern.

Composite falcigers numbering 4–6 per fascicle; blades long, smooth, distally recurved, unidentate (Fig. 3E, J), decreasing in length within a fascicle; shafts long; shaft tips slightly inflated, with dorsal superior distal surfaces smooth; dorsal superior branch long, spike-shaped, subdistally notched, ventral inferior branch truncate, forming socket for blade (Fig. 3K).

Pygidium terminal; paired anal cirri huge, larger than dorsal macrotubercles, spherical, with large, conspicuous unpaired midventral cirrus flanked by pair of smaller, digitiform papillae (Fig. 3L, M).

Remarks.—*Sphaerodoropsis uzintunensis,* new species, is related to both *S. sphaerulifer* (Moore, 1909), and *S. benguellarum* (Day, 1963) in having similar numbers of sessile macrotubercles and a single presetal parapodial lobe. *Sphaerodoropsis uzintunensis* has a single postsetal lobe, which is absent from the other two species. *S. uzintunensis* further differs from *S. sphaerulifer* in having proximal papillar spurs on prostomial antennae and in having small dorsal papillae distributed between adjacent rows of macrotubercles. This species is also superficially similar to *Sphaerodoropsis minuta* (Webster and Benedict, 1887) from which it differs in having six to eight dorsal macrotubercles rather than the usual 10–12 macrotubercles; only one instead of two, postsetal parapodial lobes; one parapodial papilla each on anterior parapodial surfaces and proximal ventral inferior parapodial

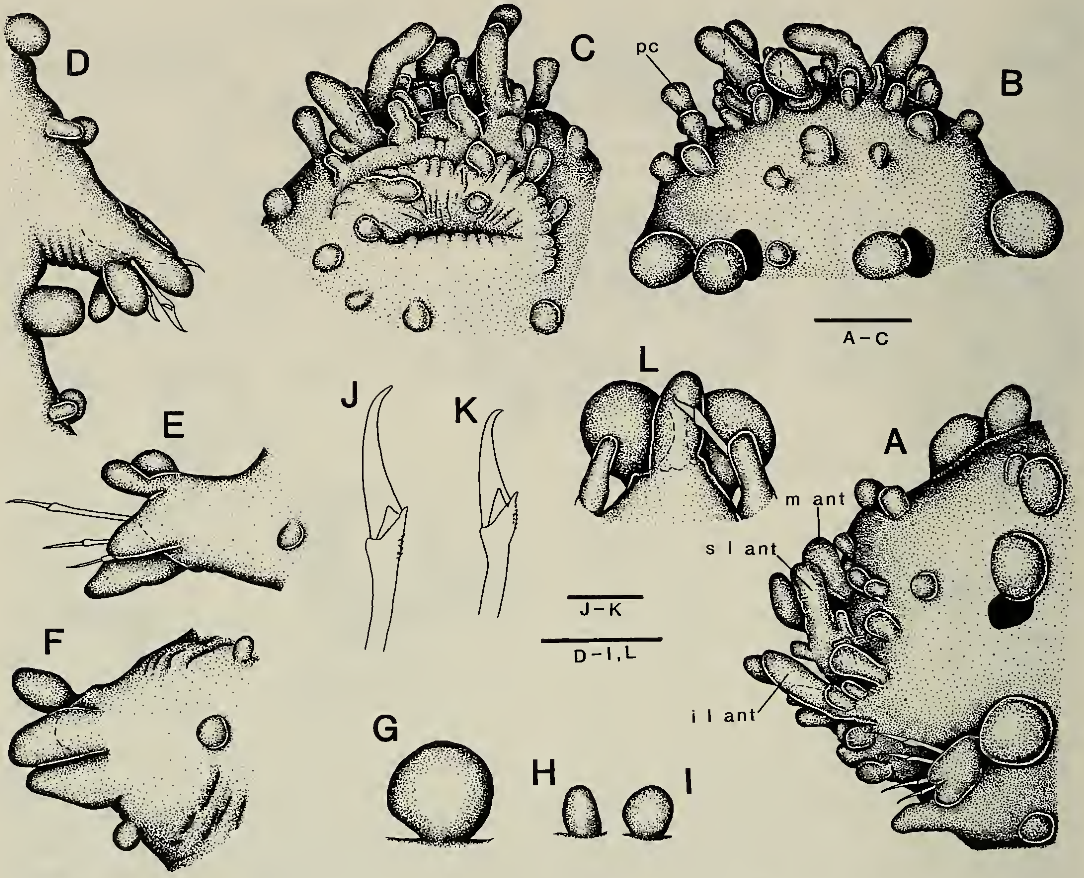

Fig. 4. *Sphaerodoropsis katchemakensis,* holotype (USNM 102782): A, Head region, lateral view; B, Same, dorsal view; C, Same, ventral view; D, Right setiger 6, dorsal view; E, Right setiger 6, anterior view; F, Left setiger 6, posterior view; G, Macropapilla, lateral view; H–I, Papillae, lateral view; J–K, Composite falcigers, lateral view; L, Pygidium, ventral view. m ant, median antenna; s l ant, superior median antenna; i l ant, inferior median antenna. Scales: A–C, D–I, L = 0.05 mm; J–K = 0.01 mm.

edges rather than one each on both anterior and posterior parapodial surfaces; and smooth and not minutely serrated composite falcigers.

Etymology.—The epithet derives from the Tanainan Indian place name for the Homer Spit where this species was discovered.

Type locality.—Homer Boat Harbor, Homer, Alaska.

Sphaerodoropsis katchemakensis,
new species
Fig. 2C, 4

Material examined.—ALASKA: Katchemak Bay, Homer Spit Boat Harbor, sta 200-4, 59°36′18.0″N, 151°24′44.5″W, 5 m, coarse to fine sand between boulders and cobble, 28 Feb 1984, coll. Dave Erikson, 2 paratypes, USNM 102783.—Sta 210-1, 59°36′18.4″N, 151°24′41.8″W, 10 m, silt-clay, 28 Feb 1984, coll. Dennis Lees, holotype, USNM 102782.

Description.—A small species; holotype measuring 1.2 mm long, 0.6 mm wide without parapodia, 0.65 mm wide with parapodia, for 14 setigers. Body short, truncate anteriorly and posteriorly, widest posteriorly; lacking pigmentation; light brown to white in alcohol.

Prostomium truncate anteriorly; median antenna short, strongly inflated, distally blunt (Fig. 4A, B). All lateral antennae digitiform, distally blunt, much longer than median antenna; superior lateral antennae longest. Superior lateral antennae each with 3 proximal papillar spurs; inferior laterals each with 2 (Fig. 4A–C). Eyes well developed, numbering 1 pair (Fig. 4A). Peristomial cirri distally inflated, blunt, about as long as median antenna. Proboscis short, muscular, extending over setigers 3–6. Three papillae including 1 median unpaired and 2 ventral papillae encircled by prostomial antennae (Fig. 4A, C); papillae present on peristomium (Fig. 4A, B).

Parapodia uniramous, short, stout, about as long as wide (Fig. 4D–F); acicular lobe rounded to triangular; presetal lobes numbering 1 per parapodium, digitiform, distally blunt, projecting well beyond acicular lobe (Fig. 4D–F); postsetal lobes digitiform to distally inflated, numbering 1–2, variably distributed, with setigers 2–4 each with 2 and all others each with 1. Ventral cirrus bluntly conical, extending beyond acicular lobe (Fig. 4D). Parapodial papillae numbering 3, including 1 on anterior surfaces, and 1 each on proximal dorsal superior and ventral inferior edges (Fig. 4D–F); absent from posterior parapodial surfaces. One interramal papilla present between adjacent parapodia (Fig. 4D).

Dorsal macrotubercles spherical, sessile, variable sized (Fig. 4G), arrayed in 8–9 longitudinal rows, accompanied by around 10 smaller papillae (Fig. 4H) arranged in complex non-random pattern (Fig. 2C). Ventrum with 11 alternating rows of papillae (Fig. 4I) forming zig-zag pattern.

Composite falcigers generally numbering 4–5 per fascicle; blades moderately long, smooth, distally recurved, unidentate (Fig. 4J, K), decreasing in length both within a fascicle and posteriorly along body; shafts moderately long to short; shaft tips distally serrated along dorsal superior edges (Fig. 4J, K), with dorsal superior branch long, spike-shaped, sometimes subdistally notched, ventral inferior branch truncate, forming socket for blade (Fig. 4J, K).

Pygidium terminal, paired anal cirri spherical, with unpaired midventral digitiform cirrus (Fig. 4L).

Remarks.—*Sphaerodoropsis katchemakensis* is closely related to *S. uzintunensis.* It is probable that these two represent sibling species. For example, both species have identical distributions of parapodial papillae; a single presetal and generally a single postsetal lobe, although *S. katchemackensis* has two postsetal lobes in anteriormost parapodia; overlapping numbers of dorsal longitudinal rows of macrotubercles; complex and nonrandom distributions of dorsal papillae; triangular shaped acicular lobes; similar distribution patterns of ventral papillae; and similar numbers of setae, all with smooth cutting margins.

Sphaerodoropsis katchemakensis differs from *S. uzintunensis* in having 2 proximal spurs on each inferior lateral and three spurs on each superior lateral prostomial antennae, instead of four on each. In all, three papillae are encompassed by the antennae of *S. katchemakensis,* instead of seven as in *S. uzintunensis.* Rows of dorsal papillae number ten rows in *S. katchemakensis,* and 13–15 in *S. uzintunensis.* Parapodia are as long as wide in *S. katchemakensis,* and twice the width in *S. uzintunensis.* Ventral cirri of *S. katchemakensis* extend beyond the acicular lobes of parapodia, and do not in *S. uzintunensis.* Lastly, distal regions of setal shafts are conspicuously serrated in *S. kachemakensis* and smooth in *S. uzintunensis.*

Specimens of *S. katchemakensis* were initially identified as *Sphaerodoropsis minuta* (Webster and Benedict, 1887) based on the presence of two parapodial postsetal lobes in anteriormost parapodia, and the numbers of dorsal macrotubercles (Webster and Benedict 1887, Pettibone 1963, Hartman 1968, Banse and Hobson 1974). However, detailed examinations revealed that usually only one postsetal lobe is present instead of two; the ventral cirrus projects well beyond the acicular lobe, and approaches but does not surpass the tip of the presetal lobe, rather than not extending beyond the acicular lobe; acicular lobes are shorter, and do not project to or beyond the postsetal lobes; the total number of parapodial papillae number three instead of two; the posterior parapodial surfaces lack papillae whereas one is present in *S. minuta*; the number of dorsal macrotubercles number eight to nine, not 10–12 to 14; and the blades of composite falcigers are smooth and not serrated. These differences are both consistent in the present materials and differ significantly from *S. minuta.*

Etymology.—The epithet, *katchemakensis,* derives from the name of Katchemak Bay, Alaska, where this species was discovered.

Type locality.—Homer Boat Harbor, Homer, Alaska.

Sphaerodoropsis sphaerulifer (Moore, 1909)

Sphaerodorum sphaerulifer Moore, 1909: 336.—Uschakov, 1955:222.

Sphaerodoridium sphaerulifer.—Lützen, 1961:415.—Banse and Hobson, 1968: 18.—Hartman, 1968:605.

Sphaerodoropsis sphaerulifer.—Fauchald, 1974:277.—Banse and Hobson, 1974:76.

Material examined.—ALASKA: Katchemak Bay, Homer Spit Boat Harbor, sta 215-1, 59°36′19.1″N, 151°24′39.0″W, 15 m, silt-clay, 28 Feb 1984, coll. Dennis Lees, 1 specimen, USNM 102800.—Sta 215-2, same, 1 specimen, USNM 102801.

Remarks.—These two specimens are tentatively referred to *S. sphaerulifer* on the basis of Banse and Hobson (1974), and pending receipt of additional material. A more precise determination is not possible since their prostomia are either distorted (USNM 102800) or fully retracted (USNM 102801). In any case, these specimens agree generally with previous descriptions, and differ in some important ways from those provided by Moore (1909), Hartman (1968), and Fauchald (1974). For example, Fauchald (1974), who embellished Moore's (1909) original contribution, describes the presence of small papillae between the macropapillae, distally truncate parapodial lobes, and short falcate blades on compound setae. Specimens from Alaska differ in totally lacking papillae between dorsal macropapillae, in having triangular acicular lobes, and in having notably long falcate blades. As such, Alaskan specimens appear to agree more closely with descriptions provided by Uschakov (1955), Lützen (1961), and Banse and Hobson (1974). Additional materials from southcentral Alaska are needed before this apparent discrepancy involving the type species for the genus can be resolved.

Distribution.—Newly reported from Alaska; previously recorded from British Columbia, Washington, California, Sea of Japan, Sea of Okhotsk.

Key to Species of *Sphaerodoropsis* Recorded from Alaska

In all, eight described species of sphaerodorids have been recorded from Alaskan waters in published accounts as follows:

Amacrodorum bipapillatum: this study, Akutan Island.

Sphaerodoridium claparedii (Greeff), Beaufort Sea; (Bilyard and Carey 1980).

Sphaerodoropsis biserialis (Berkeley and Berkeley), southeast and southcentral Alaska, ?Aleutian Islands to Japan; (Lützen 1961, Hartman 1968, Imajima 1969) *S. minuta* (Webster and Benedict), Beaufort and Chukchi Seas, southcentral and southeast Alaska; (Hartman 1968, Bilyard and Carey 1970, Kudenov, unpublished data).

S. katchemakensis: this study, Katchemak Bay, Homer, Alaska.

S. sphaerulifer (Moore), southcentral Alaska; this study.

S. uzintunensis: this study, Katchemak Bay, Homer, Alaska.

Sphaerodorum papullifer Moore, southeast Alaska, (Kudenov, unpublished).

The following key is based on published records of *Sphaerodoropsis* species from Alaskan waters, and partly follows Banse and Hobson (1974:76).

1. Dorsum with 4 dorsal longitudinal rows of macrotubercles . . . *S. biserialis*
– Dorsum with 6–14 dorsal longitudinal rows of macrotubercles 2
2. Blades of composite setae minutely serrated 3
– Blades of composite setae smooth, not minutely serrated 4
3. Dorsum with 7–8 dorsal longitudinal rows of macrotubercles; dorsum without papillae; parapodia without postsetal lobes . . . . *S. sphaerulifer*
– Dorsum with 10–14, normally 10–12 dorsal longitudinal rows of macrotubercles; dorsum with papillae; parapodia with 2 postsetal lobes . . . . *S. minuta*
4. Dorsum with 8–9 dorsal longitudinal rows of macrotubercles; superior and inferior lateral antennae each with 3 and 2 proximal spurs; ventral cirri project beyond acicular parapodial lobes . . . . *S. katchemakensis*
– Dorsum with 6–8 dorsal longitudinal rows of macrotubercles; superior and inferior lateral antennae each with 4 proximal spurs; ventral cirri do not project beyond acicular lobes . . . . *S. uzintunensis*

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FIVE NEW SPECIES OF SPHAERODORIDAE (ANNELIDA: POLYCHAETA) FROM THE GULF OF MEXICO

Jerry D. Kudenov

Abstract.—Five new species of Sphaerodoridae (Annelida: Polychaeta) are described from the Gulf of Mexico, including *Clavodorum mexicanum, Ephesiella bipapillata, Sphaerephesia fauchaldi, Sphaerodoridium lutzeni,* and *Sphaerodoropsis vittori.*

This study is based on two small collections of sphaerodorids from the Gulf of Mexico. One collection derives from Dr. Henry Kritzler, while the other was taken as part of the Bureau of Land Management's Outer Continental Shelf Baseline Environmental Survey along the coasts of Mississippi, Alabama, and Florida (MAFLA), southwest Florida (SOWFLA), the Louisiana Offshore Oil Port Study (LOOP), and the Mississippi Sound Study (MS). All MAFLA samples were collected by Dames and Moore, and SOWFLA samples by Woodward-Clyde Environmental Consultants. Details of the MAFLA survey are given by Dames and Moore (1979). In all, five new species of sphaerodorids are described from the northern Gulf of Mexico, including *Clavodorum mexicanum, Ephesiella bipapillata, Sphaerephesia fauchaldi, Sphaerodoridium lutzeni* and *Sphaerodoropsis vittori.*

These materials were generously made available by Joan M. Uebelacker and Paul G. Johnson, Barry Vittor and Associates, Mobile, Alabama, and most were originally treated by Kudenov (1984). All materials, including types, are deposited in the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM).

Clavodorum Hartman and Fauchald, 1971

Clavodorum mexicanum, new species

Fig. 1

Material examined.—FLORIDA, GULF OF MEXICO: MAFLA sta 2209H, 27°52′30.5″N, 83°33′59.0″W, clayey-sandy-silt, 34 m Feb 1978; holotype, USNM 102786.—SOFLA sta 8C, 26°16.72′N, 83°12.81′W, fine sand, 48 m, Nov 1980; 1 paratype, USNM 102787.—ALABAMA, GULF OF MEXICO: MS sta 477-8, 30°01.89′N, 88°27.63′W, sand, 23.8 m, 31 Mar 1981; 1 paratype, USNM 102788.

Description.—Body short, grub-like, widest anteriorly; brown to white in alcohol. Length of holotype 2.1 mm; width to 0.6 mm without parapodia, 1 mm with parapodia; complete, having 21 setigers.

Prostomium truncate; median antenna long, gradually tapering, extending posteriorly to setiger 1 (Fig. 1A). Superior lateral antennae cylindrical, distally blunt, lacking proximal spurs. Inferior lateral antennae similar to superior ones, shorter, lacking proximal spurs. One pair of eyes present at level of peristomial cirri, latter papilliform. Proboscis short, muscular, extending posteriorly to setiger 6.

Parapodia uniramous, up to 4× longer than wide; acicular lobes conical, with pre-

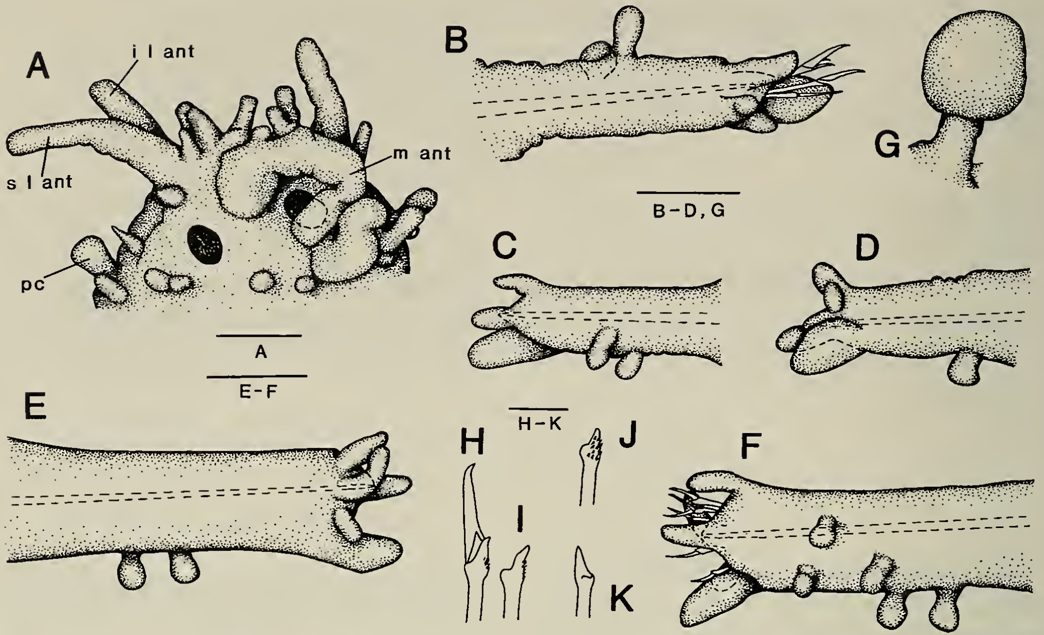

Fig. 1. *Clavodorum mexicanum*, new species (A–D, G–K: paratype, USNM 102787; E–F: holotype, USNM 102786): A, Anterior end, dorsal view [specimen illustrated missing right superior lateral antenna]; B, Parapodium, right setiger 9, dorsal view; C, Same, right setiger 14, anterior view; D, Same, left setiger 7, posterior view; E, Same, right setiger 8, posterior view; F, Same, anterior view; G, Macrotubercle; H, Composite falciger, lateral view; I, Same, shaft tip, lateral view; J, Same, ventrolateral view; K, Same, dorsolateral view; m ant, median antenna; s l ant, superior median antenna; i l ant, inferior median antenna. Scales: A, B–D, E–F, G = 0.05 mm; H–K = 0.1 mm.

setal lobe and 1–2 postsetal lobes, latter depending on body size, absent from last 3–4 setigers; all digitiform (Fig. 1B–F). Parapodia maximally developed around setiger 12, decreasing gradually in size posteriorly; last reduced abruptly. Ventral cirri thickly digitiform, inserted terminally on parapodia, extending beyond acicular lobes. Parapodial papillae numbering 3–6, depending on body size; with 16-setiger specimen (USNM 102787) having 1 papilla each on anterior parapodial surfaces, ventral inferior and dorsal superior distal edges (Fig. 1B–D); 21-setiger specimen (USNM 102786) having 3 papillae on anterior parapodial surfaces, 2 on ventral inferior edges, 1 on dorsal superior distal edge (Fig. 1E, F). Papillae absent from dorsal superior edges and posterior surfaces (Fig. 1B, D, E).

Dorsal macrotubercles stalked (Fig. 1G), arranged in 6 longitudinal rows, each macrotubercle having slender column and spherical head. Ventral papillae arranged in zig-zag pattern of 10 alternating rows, each papilla ellipsoidal.

Composite falcigers numbering up to 6 per fascicle; blades smooth, unidentate (Fig. 1H), decreasing slightly in length inferiorly within a fascicle (Fig. 1F); shaft tips inflated, with dorsal superior branch long, conical and spinulose (Fig. 1H–J), ventral inferior branch medially notched, forming socket for blade (Fig. 1K).

Remarks.—*Clavodorum mexicanum* is most closely allied to *C. atlanticum* Hartman and Fauchald, 1971, from deep water near the Bermuda Islands, in having six rows of dorsal macrotubercles and in lacking elongate parapodia posteriorly. *Clavodorum mexicanum* differs from its congener in lacking accessory papillae on superior lateral antennae, in lacking postsetal lobes in the last three to four setigers, in having eyes, in having two postsetal lobes instead of one, and in having ten ventral rows of papillae. *Clavodorum mexicanum* is also closely related to *C. longipes* Fauchald, 1974, in lacking postsetal parapodial lobes, that are absent from the last two to three parapodia in *C. mexicanum,* and the last eight to nine parapodia in *C. longipes.* Both *C. mexicanum* and *C. atlanticum* differ from *C. longipes* in lacking elongate parapodia in far posterior setigers. *Clavodorum mexicanum* was cited as *Clavodorum* sp. A by Kudenov (1984:36–39).

Size range.—Length 1.4–2.8 mm; width 0.3–0.5 mm without parapodia, 0.5–0.8 mm with parapodia; 16–21 setigers.

Etymology.—The epithet refers to the Gulf of Mexico from which this species was collected.

Distribution.—Northeast Gulf of Mexico, offshore of Alabama, Florida, fine sand to sandy-clayey-silt, 23.8–48 m.

Ephesiella Chamberlin, 1919, sensu Hartman and Fauchald, 1971

Ephesiella bipapillata, new species

Fig. 2

Material examined.—LOUISIANA, GULF OF MEXICO: LOOP sta 481-8, 28°56′06″N, 90°01′30″W, 33.6 m, 11 Nov 1979; holotype, USNM 102789.—Sta 482-2, 28°54′48″N, 89°59′05″W, 33.6 m, 16 Apr 1980; 1 paratype, USNM 102790.

Description.—Body elongate, widest medially; white or pink (due to prior staining in rose bengal) in alcohol. Length of holotype 3.5 mm; width to 0.5 mm without parapodia, 0.6 mm with parapodia; complete, having 57 setigers.

Prostomium truncate; median antenna short, digitiform; 2 pairs of lateral antennae equally long, cirriform (Fig. 2A). One pair of eyes present at level of peristomial cirri (Fig. 2A), latter digitiform, short. Single papilla present near base of each lateral antenna; median papilla inserted anterior to median antenna (Fig. 2A).

Parapodia uniramous, short, 2× longer than wide; acicular lobes conical; pre- and postsetal lobes absent (Fig. 2B–D). Parapodial papillae numbering 9, including 4 on anterior surfaces (Fig. 2B); 3 on posterior surfaces, including 1 inserted on upper part of acicular lobe (Fig. 2C), 2 on dorsal superior edges (Fig. 2B–D). Latter including 1 near base of parapodium, and 1 inserted distally near tip of acicular lobe being large, erect. Ventral cirrus digitiform, basally inflated, not projecting beyond parapodial lobes (Fig. 2B–D).

Dorsal macrotubercles sessile, arranged in 2 longitudinal rows, each macrotubercle spherical with terminal papilla (Fig. 2E). Dorsal microtubercles arranged in 2 longitudinal rows, each microtubercle digitiform (Fig. 2F). Papillae distributed over dorsum in 22 longitudinal rows, including 3 each between rows of macro- and microtubercles, 16 between rows of microtubercles. Ventrum with 4 longitudinal rows of small elliptical papillae.

Single, stout recurved hook present in parapodia of setiger 1 (Fig. 2G). Composite falcigers numbering up to 5 per fascicle, present in all parapodia from setiger 2; blades smooth, unidentate, decreasing in length inferiorly within a fascicle (Fig. 2H–J); shaft tips inflated, obliquely truncate, with dorsal superior branch longest, pointed, ventral inferior branch forming socket for blade (Fig. 2H).

Remarks.—*Ephesiella bipapillata* is most closely allied to *Ephesiella mixta* Hartman and Fauchald, 1971, from abyssal depths in the northwest Atlantic, in having recurved hooks in setiger 1, two pairs of long lateral antennae, ventral cirri not projecting beyond parapodial lobes, and erect dorsal superior papillae on all parapodia. *Ephesiella bipapillata* differs from its congener in having only one instead of two simple hooks per fascicle, in having two dorsal superior distal papillae instead of one, and in having 26 total rows of dorsal and ventral papillae instead of a sparse, and an apparently random pattern.

Size range.—Length 2–3.5 mm; width

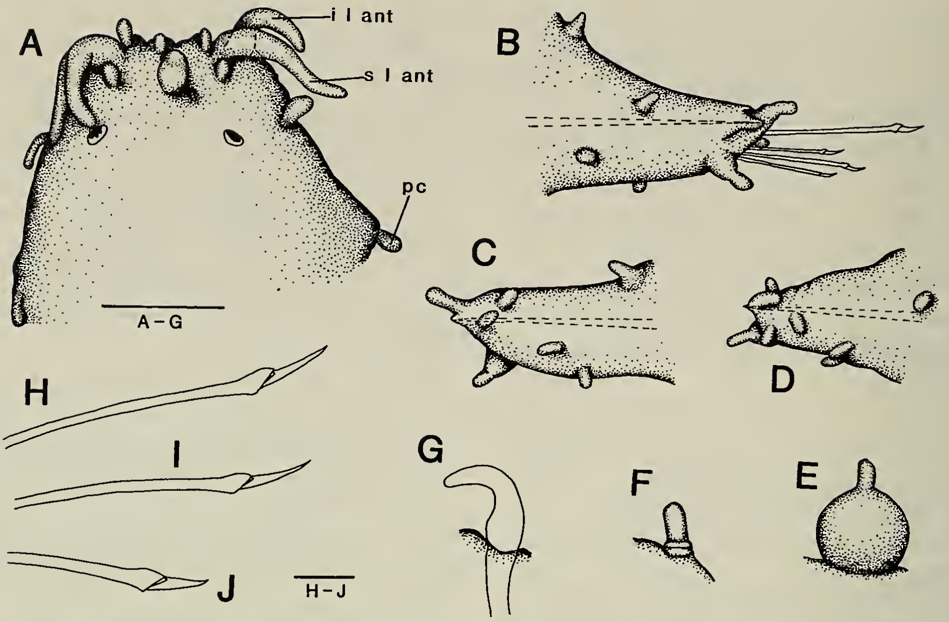

Fig. 2. *Ephesiella bipapillata,* new species (holotype, USNM 102789): A, Anterior end, dorsal view; B, Parapodium, right setiger 14, posterior view; C, Same, anterior view; D, Same, right setiger 17, oblique dorsolateral view of anterior surface exposing ventral cirrus; E, Macrotubercle; F, Microtubercle; G, Recurved simple hook, setiger 1; H–J, Composite falcigers from the same fascicle; H, Superior seta; I, Intermediate seta; J, Inferior seta; m ant, median antenna; s l ant, superior median antenna; i l ant, inferior median antenna. Scales: A–G = 0.05 mm; H–I = 0.01 mm.

without parapodia 0.2–0.5 mm, 0.3–0.6 mm wide with parapodia; 33–57 setigers.

Etymology.—The epithet derives from the presence of two dorsal superior distal parapodial papillae.

Distribution.—Northcentral Gulf of Mexico, 33.6 m.

Sphaerephesia Fauchald, 1972
Sphaerephesia fauchaldi, new species
Fig. 3

Material examined.—FLORIDA: GULF OF MEXICO: SOFLA sta 16B, 25°45.7′N, 83°11.07′W, fine sand, 54 m, Apr 1981; holotype, USNM 102785.

Description.—Body short, grub-like, widest anteriorly; translucent to white in alcohol. Length of holotype 2.2 mm; width 0.6 mm without parapodia, 0.8 mm wide with parapodia; complete, having 16 setigers. Holotype ovigerous.

Prostomium truncate anteriorly; median antenna large, stout, distally blunt (Fig. 3A, B). Superior lateral antennae short, slender; medial and inferior pairs each 2× longer, cylindrical, inflated basally, all lacking proximal papillar spurs (Fig. 3A, B). Eyes absent. Peristomial cirri digitiform, distally blunt, about as long as medial, inferior antennae (Fig. 3A, B). Proboscis short, muscular, extending posteriorly to setiger 4. Eight papillae encircled by prostomial antennae (not illustrated); papillae otherwise present on peristomium.

Parapodia uniramous, up to 2× longer than wide; acicular lobes rounded, with presetal lobe large, conical, projecting beyond acicular lobe; postsetal lobes absent (Fig. 3C, D). Ventral cirri digitiform, inserted on distal ⅓ of parapodial lobes, extending beyond acicular lobes (Fig. 3C, D). Parapodial papillae number 8, including 4 on anterior parapodial surfaces; 2 on posterior surfaces; 2 on superior dorsal edges including one inserted distally; ventral inferior edges lacking papillae (Fig. 3C, D).

Dorsal macrotubercles sessile, arranged

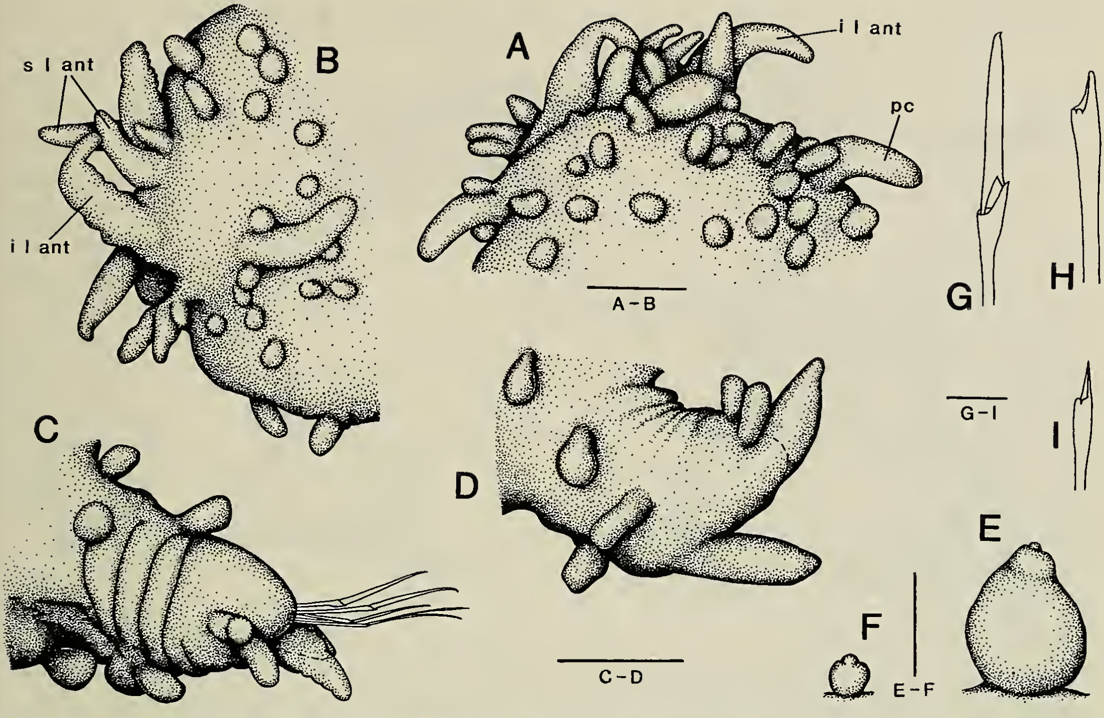

Fig. 3. *Sphaerephesia fauchaldi,* new species (holotype, USNM 102785): A, Anterior end, dorsal view; B, Anterior end, left lateral view; C, Parapodium, left setiger 9, dorsal view; D, Same, left setiger 12, oblique anterolateral view; E, Macrotubercle; F, Microtubercle; G, Composite falciger, lateral view; H, Same, shaft tip, lateral ventral view; I, Same, ventrolateral view; m ant, median antenna; s l ant, superior median antenna; i l ant, inferior median antenna. Scales: A–B, C–D, E–F = 0.05 mm; G–I = 0.01 mm.

in 4 longitudinal rows, each macrotubercle spherical with stout terminal papilla (Fig. 3E). Dorsum otherwise with approximately 12 irregular rows of microtubercles (Fig. 3F), each having small spherical heads. Ventral papillae appearing to be arranged in 12 irregular longitudinal rows.

Composite falcigers numbering 5–7 per fascicles anteriorly, increasing up to 16 posteriorly; blades long, smooth, with falcate unidentate tips (Fig. 3G); shaft tips not inflated, with dorsal superior branch entire, spike-shaped and ventral inferior branch medially notched, forming socket for blade (Fig. 3H, I).

Remarks.—*Sphaerephesia fauchaldi* is most closely allied to *Sphaerephesia chilensis* Fauchald, 1974, from intertidal and shallow subtidal depths of central and southern Chile, in having eight papillae encircled by three pairs of similarly shaped prostomial antennae (which could not be illustrated), and similar composite falcigers. *Sphaerephesia fauchaldi* differs from its congener in having five instead of one to two parapodial papillae, and in having 12 rows of sessile dorsal microtubercles.

These two species are zoogeographically and probably also evolutionarily related. *Sphaerephesia chilensis* is known from the southeastern Pacific (Chile), while *Sphaerephesia fauchaldi* is newly reported from the northeastern Gulf of Mexico. It is probable that these species may have diverged from a more widely distributed ancestral stock present in these regions prior to the Miocene closure of the Panama Isthmus. *Sphaerephesia fauchaldi* was cited as *Sphaerephesia* sp. A by Kudenov (1984:36–3).

Etymology.—The epithet is named after Kristian Fauchald in honor of his contributions to our understanding of this family.

Distribution.—East Gulf of Mexico, offshore of Florida, fine sand, 54 m.

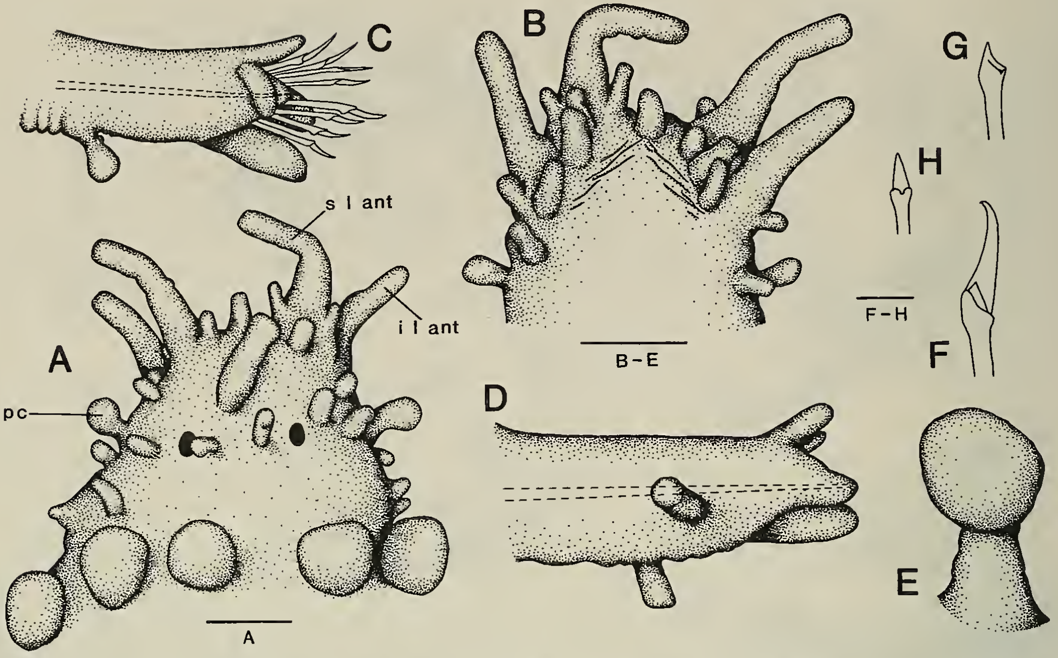

Fig. 4. *Sphaerodoridium lutzeni,* new species (A–G: holotype, USNM 102803; H, paratype, USNM 102807): A, Anterior end, dorsal view; B, Anterior end, ventral view; C, Parapodium, right setiger 8, posterior view; D, Same, left setiger 5, anterior view; E, Macrotubercle; F, Composite falciger, lateral view; G, Same, shaft tip, lateroventral view; H, Same, ventral view; m ant, median antenna; s l ant, superior median antenna; i l ant, inferior median antenna. Scales: A, B–E = 0.05 mm; F–H = 0.01 mm.

Sphaerodoridium Lützen, 1961, restricted sensu Fauchald, 1974

Sphaerodoridium lutzeni, new species
Fig. 4

Material examined.—FLORIDA, GULF OF MEXICO: MAFLA sta 2209C, 27°52′30.5″N, 83°33′59.0″W, clayey-sandy-silt, 34 m, Aug 1977; 1 paratype, USNM 102802.—Sta 2209G, 27°52′30.5″N, 83°33′59.0″W, clayey-sandy-silt, 34 m, Aug 1977; holotype, USNM 102803.—Sta 2210C, 27°57′28.8″N, 83°42′29.2″W, silty-very fine sand, 37 m, Jul 1976; 1 paratype, USNM 102804.—?Sta 2422F, 29°30′N, 84°27′W, medium fine sand, 24 m, Jul 1976; 1 specimen, USNM 102805.—Sta 2423C, 29°37′00.8″N, 84°17′00.2″W, silty fine sand, 19 m, Nov 1977; 2 paratypes, USNM 102806.—Sta 2536G, 29°30′0.16″N, 86°24′59.0″W, clayey silt, 189 m, Jul 1976; 2 paratypes, USNM 102807.

Description.—Body grub-like; transparent body wall with white macrotubercles in alcohol. Length of holotype 2 mm; width 0.3 mm without parapodia, 0.4 mm wide with parapodia; complete, having 16 setigers.

Anterior end bluntly rounded; median antenna short, digitiform; superior lateral antennae long, digitiform, each with 2 proximal papillae (Fig. 4A); inferior lateral antennae similar to median in shape, size, each with single proximal papilla (Fig. 4B). One pair of eyes present at level of peristomial cirri (Fig. 4A). Peristomial cirri digitiform, shorter than median antenna (Fig. 4A, B). Proboscis large, extending posteriorly to setiger 5. Papillae present on prostomium, peristomium.

Parapodia uniramous, up to 4× longer than wide; acicular lobes conical, with presetal lobes large, digitiform, projecting beyond acicular lobe; postsetal lobes absent

(Fig. 4C, D). Parapodial papillae numbering 4, including 1 on anterior surfaces (Fig. 4D); 1 on ventral inferior edges (Fig. 4C, D); and 2 on dorsal superior distal edges, superiormost of these largest (Fig. 4C, D). Ventral cirri large, thick, digitiform, inserted distally on parapodial lobes, equalling length of presetal lobes, extending beyond acicular lobes (Fig. 4C, D).

Dorsal macrotubercles stalked, arranged in up to 6 longitudinal rows, each macrotubercle having stout column and spherical head (Fig. 4E). Ventral papillae arranged in zig-zag pattern of 6 alternating rows. Papillae otherwise absent from dorsal and lateral surfaces.

Composite falcigers numbering up to 10 per fascicle; blades smooth, recurved, unidentate (Fig. 4F), decreasing only slightly inferiorly within a fascicle; shaft tips inflated, with dorsal superior branch long, conical, and ventral inferior branch medially notched, forming socket for blade (Fig. 4G, H).

Remarks.—*Sphaerodoridium lutzeni* differs from the only other described species, *Sphaerodoridium caparedii* (Greeff 1866) in having inferior lateral prostomial antennae each with a single proximal papilla, in lacking ventral transverse rows of papillae, in lacking papillae on dorsal and lateral surfaces, in having a regular zig-zag pattern of six alternating rows of ventral papillae, and in having four instead of two parapodial papillae. It is highly probable that the specimen of *Sphaerodoridium* (*Ephesiella*) *claparedii* sensu Day (1973:36) is referrable to *Sphaerodoridium lutzeni* since it lacks dorsal papillae. *Sphaerodoridium lutzeni* was cited as *Sphaerodoridium* sp. A by Kudenov (1984:36–11).

Size range.—Length 0.9–2.5 mm; width 0.2–0.5 mm without parapodia, 0.3–0.8 mm with parapodia; 8–16 setigers.

Etymology.—The epithet is named after Professor Jörgen Lützen, who first proposed the genus *Sphaerodoridium.*

Distribution.—Northeast Gulf of Mexico, offshore of Florida, silty, very fine sand to clayey silt, 19–189 m.

Sphaerodoropsis Hartman and Fauchald, 1971

Sphaerodoropsis vittori, new species

Fig. 5

Material examined.—ALABAMA, OFF MOBILE BAY, GULF OF MEXICO: MALFA sta 19C, 29°36′10.9″N, 87°23′30.9″W, 75 m, 30 May 1974; 1 specimen, USNM 102791.—Sta 2644I, 29°36.2′N, 87°23.5′W, medium sand, 75 m, Jun 1975; 1 specimen, USNM 102795.—Sta 2645I, 29°35′00.5″N, 87°20′02.2″W, coarse sand, 106 m, Nov 1977; 1 paratype, USNM 102796.—FLORIDA, GULF OF MEXICO: MALFA sta 2528F, 29°54′58.6″N, 86°04′58.5″W, 37 m, coarse sand, Sep 1977; 1 paratype, USNM 102792.—Sta 2533C, 29°42′59.9″N, 85°15′28.6″W, coarse sand, 67 m, Jul 1976; 1 specimen, USNM 102794.—Sta 2528G, same; 1 paratype, USNM 102793.—Sta 2746D, 27°03.5′N, 84°13.7′W, silty, very fine sand, 121 m, Feb 1978; holotype, USNM 102797.—Sta SOFLA 4C, 26°45.81′N, 83°32.12′W, medium sand, 56 m, Mar 1981; 1 paratype, USNM 102798.—Sta 5A, 26°45.7′N, 84°00.13′W, coarse sand, 91 m, May 1981; 1 paratype, USNM 102799.

Description.—Body grub-like, widest anteriorly; light brown to white in alcohol. Length of holotype 3.5 mm (3.8 mm with proboscis everted); width 1 mm without parapodia, 1.2 mm wide with parapodia; complete, having 32 setigers.

Anterior end truncate; median antenna short, digitiform; 2 pairs cirriform lateral antennae, with superior lateral antennae shorter than inferior lateral antennae (Fig. 5A [angle of illustration distorts this relationship]). Eyes absent. Peristomial cirri digitiform, longer, larger than median antenna. Proboscis large, muscular, extending posteriorly to setiger 8 (everted in holotype). Prostomium, peristomium studded with

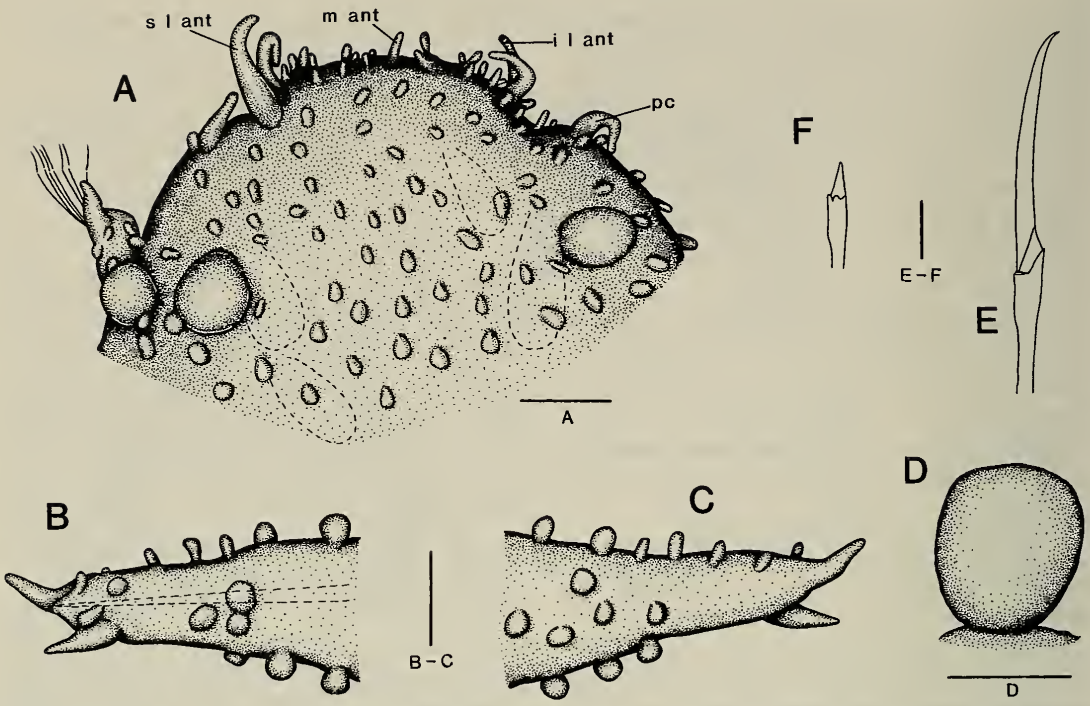

Fig. 5. *Sphaerodoropsis vittori,* new species (holotype, USNM 102797): A, Anterior end, oblique dorsal view from posterior perspective [angle of illustration incorrectly suggesting lateral prostomial antennae of equal lengths]; B, Parapodium, left setiger 13, posterior view; C, Same, anterior view; D, Macrotubercle; E, Composite falciger, lateral view; F, Same, shaft tip, ventrolateral view; m ant, median antenna; s l ant, superior median antenna; i l ant, inferior median antenna. Scales: A, B–C, D = 0.05 mm; E–F = 0.01 mm.

small papillae, including cluster of 3 near base of inferior lateral antennae (Fig. 5A).

Parapodia uniramous, short, up to 3× longer than wide; acicular lobes conical; presetal lobes long, digitiform; postsetal lobes absent (Fig. 5B, C). Parapodial papillae stout, numbering 20, including postsetal superior papilla inserted on acicular lobe (Fig. 5B); 6 on anterior surfaces (Fig. 5C); 5 on posterior surfaces (Fig. 5B); 5 on dorsal superior edges (Fig. 5C); 3 on ventral inferior edges (Fig. 5C). Ventral cirri subulate, projecting beyond acicular lobes.

Dorsal macrotubercles sessile (Fig. 5D), arranged in 4 longitudinal rows, each macrotubercle spherical. Dorsum and ventrum densely covered by short randomly arranged papillae.

Composite falcigers numbering up to 10 per fascicle; blades long, smooth, distally recurved, unidentate (Fig. 5E), decreasing in length ventrally within a fascicle; shafts long; shaft tips inflated, with dorsal superior branch long, spike-shaped, distally entire or sometimes bifid, and ventral inferior branch medially notched, forming socket for blade (Fig. 5F).

Remarks. —*Sphaerodoropsis vittori* is most closely allied to *Sphaerodoropsis triplicata* Fauchald, 1974, from a depth of 675–715 m offshore of Durban, South Africa, in having four rows of dorsal macrotubercles, two pairs of lateral prostomial antennae, a presetal parapodial lobe, dorsal superior parapodial papillae, and ventral cirri projecting well beyond acicular lobes. *Sphaerodoropsis vittori* differs from its congener in having only one superior parapodial papilla instead of two large ones, in having up to 13 additional stout parapodial papillae rather than smooth and wrinkled parapodia, and a cluster of three prostomial papillae near the base of each inferior lateral antenna. *Sphaerodoropsis vittori* is also related to *Sphaerodoropsis philippi* Fauvel, 1911, in having numerous parapodial papillae. However, *Sphaerodoropsis vittori* differs from *S. philippi* in having 20 stout papillae per parapodium instead of up to 10–11 slender ones. *Sphaerodoropsis philippi* further lacks both dorsal superior distal parapodial papillae, and ventral cirri that project beyond acicular lobes. *Sphaerodoropsis vittori* was cited as *Sphaerodoropsis* sp. A by Kudenov (1984:36–5).

Size range.—Length 0.7–7.5 mm; width 0.2–0.5 without parapodia, 0.3–0.8 mm with parapodia; 12–32 setigers.

Etymology.—The epithet takes its name from Barry M. Vittor, in recognition of his efforts to characterize the polychaete fauna of the northeastern Gulf of Mexico.

Distribution.—Northeast and east Gulf of Mexico, offshore of Florida, silty, very fine sand to coarse sand, 37–121 m.

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NEW AND PREVIOUSLY KNOWN TAXA OF ISIDID OCTOCORALS (COELENTERATA: GORGONACEA), PARTLY FROM ANTARCTIC WATERS

Frederick M. Bayer and Jeffrey Stefani

Abstract.—The classification and taxonomic characters of the gorgonacean family Isididae are discussed, and a revised key to world genera is presented. The Austral genus *Primnoisis* Studer [and Wright] and its type species *P. antarctica* (Studer) are discussed on the basis of material taken by HMS *Challenger* and by R/V *Hero,* and a new species, *P. mimas,* is described from South Georgia. The genus *Echinisis* Thomson and Rennet and its type species *E. spicata* (Hickson) are discussed on the basis of material taken by USARP, and three new species, *E. eltanin, E. vema,* and *E. persephone* are described. The genus *Sclerisis* Studer is discussed and its type species, *S. pulchella* Studer, is redescribed on the basis of a specimen obtained by USARP. *Ceratoisis ramosa* Hickson is redescribed and the species reassigned to the genus *Chathamisis* Grant. A new genus, *Stenisis,* is established for the Caribbean *Primnoisis humilis* Deichmann, and the species is redescribed on the basis of recently collected specimens. A new genus and species, *Australisis sarmentosa,* are established for abundant sub-Antarctic material obtained by USARP. Five new finds of *Ceratoisis microspiculata* Molander are reported from Antarctic localities, variation among the specimens described, and the species assigned to a new genus *Tenuisis.* The genus *Chelidonisis* Studer, heretofore known only from eastern Atlantic localities, is reported from the Gulf of Mexico and the Philippine Islands. A new subspecies, *C. aurantiaca mexicana,* and a new species, *C. philippinensis,* are described.

In the course of describing a collection of isidid octocorals from New Caledonia (Bayer and Stefani, 1987), it was necessary to examine a wide range of specimens, both identified and unidentified, belonging to that family. Among these were detected six undescribed species that were not pertinent to the New Caledonian fauna and consequently were omitted from that paper. In addition, two incorrect generic allocations were discovered which require new genus-level taxa, and two records of *Chelidonisis* from the collections of the National Museum of Natural History, Smithsonian Institution, that substantially widen the range of that genus are recorded as a new subspecies and a new species respectively. These species are the subject of the present paper.

Abbreviations

BM(NH) = British Museum (Natural History)
USARP = United States Antarctic Research Program
USNM = National Museum of Natural History, Smithsonian Institution

Classification

The currently accepted subdivision of the family Isididae into subfamilies was proposed by Kükenthal (1915, 1919, 1924) and modified by Grant (1976). Although that system is open to some criticism, it is not the purpose of this paper to revise the subfamilies. Grant's characterization of subfamilies and allocation of genera, here reduced to key form, is as follows:

1 (4). Polyps retractile.
2 (3). Sclerites of polyps are thorny spindles. Muricellisidinae (*Muricellisis*).
3 (2). Sclerites of polyps are small rods with tubercles. Isidinae (*Isis, Chelidonisis*).
4 (1). Polyps non-rectractile.
5 (6). Sclerites of polyps include needles, spindles or rods. Keratoisidinae (*Keratoisis, Lepidisis, Acanella, Isidella*).
6 (5). Sclerites of polyps are exclusively scales.
7 (8). Polyps with operculum. Peltastisidinae (*Peltastisis, Chathamisis, Minuisis*).
8 (7). Polyps without operculum.
9(10). Scales of polyps cycloid, with smooth margin, irregularly arranged. Circinisidinae (*Circinisis*).
10 (9). Scales of polyps crescentic, with dentate or serrate margin, transversely placed. Mopseinae (*Mopsea, Primnoisis*).

Taxonomic Characters

Classification and identification of isidid octocorals has traditionally been based upon (1) retractability of the polyps, (2) growth form of the colonies, (3) details of the articulated axial skeleton, (4) shape and size of the calcareous sclerites, and (5) arrangement of sclerites on the individual polyps. To this character array Grant (1976) has added (6) the presence or absence of sclerites specially differentiated as opercular scales protecting the oral region of the polyps.

1. Retractility.—The distinction between retractility (line 1 in the key plan above) and non-retractility (line 4) directly involves the anatomical concepts of anthocodia and anthostele (Bourne 1900) and is often blurred, both here and elsewhere in the Gorgonacea. In the case of the sole genus, *Muricellisis* of the Muricellisidinae, the polyps consist of a distal part (anthocodia) armed with sclerites that form a crown and points, which is completely retractile within a proximal, calicular part (anthostele) stiffened by sclerites, which projects above the general coenenchymal surface. The tentacles fold inward over the mouth and are enclosed within the crown and points, just as is the case in *Paramuricea.*

In the case of *Isis,* the polyps are nearly or quite devoid of sclerites and have no proximal calicular part filled with sclerites; they are completely retractile within a thick, common coenenchyme. Consequently, the polyps of *Isis,* although completely retractile, are not composed of anthocodia and anthostele.

In the case of *Keratoisis* and other genera attributed to Keratoisidinae, the polyps usually are armed with numerous sclerites that fill the body wall and extend into the tentacles. The polyps are proportionally very tall and the spiculation of the distal part is continuous with that of the proximal part. As there is no division into anthocodia and anthostele, the polyps cannot withdraw the entire distal part within the proximal body wall, but can only fold the tentacles over the mouth. Because of their height and the thinness of the common coenenchyme, retraction is impossible.

The polyps of *Chelidonisis,* which have been considered retractile because they form conspicuous hemispherical or bluntly conical calyces (Kükenthal 1919:599, 631; 1924: 414, 445), demonstrate an intermediate condition. The spiculation of the body wall is continuous with that of the tentacles, which merely fold inward over the mouth; the projecting "calyx" is actually the sclerite-filled body wall of the polyp. The polyps are not retractile in the same way that those of either *Muricellisis* or *Isis* are retractile, and in this sense they differ from the polyps of *Keratoisis* only in relative height and in form of the sclerites.

Terminology: The term "calyx," equivalent to Kükenthal's "Polypenkelch," is correct for the anthostele of *Muricellisis* but is not appropriate for the different structure formed by the polyps of *Chelidonisis, Mopsea, Acanthoisis* and other isidids, primnoids and ellisellids that are unable to withdraw the distal part of the polyp into a specialized proximal part (Bayer et al. 1983: 6). The term "verruca" was used by Verrill, Deichmann and others not only for this kind of structure, but for the true "calyx" as well. Verseveldt (1940:5) employed "verruca" for the wart-like anthostele when the anthocodia is retracted. As it is useful to distinguish between an anthostelar calyx and the "calyx" of polyps that are incapable of retraction, and Bayer et al. (1983) recommended no term for the latter, it might now be appropriate to restrict the term "calyx" to the former condition and revive "verruca" for the latter. The adjectival form "verrucal" should be used in preference to Deichmann's "verrucinal" (probably falsely analogous to "calicinal").

2. *Growth form.* —The manner of branching and colonial form developed in the subfamily Mopseinae (+Peltastisidinae and Circinisidinae Grant) are (1) filiform, unbranched, (2) planar, dichotomous or pinnate, and (3) branched in all directions, bushy or bottle-brush shaped. These colonial types were the main characteristics distinguishing genera until *Echinisis* was established by Thomson and Rennet (1931) for bottle-brush colonies with strongly spinose polyp-sclerites. Subsequently, Grant (1976) employed the development of a distinctly differentiated operculum of 8 plates to establish the genera *Chathamisis* and *Minuisis* for species not otherwise different from *Primnoisis.*

The shape of isidid colonies ranges from simple, unbranched whips to densely branched, bushy or arborescent forms, comparable to the range of form present in other families. Recurrent patterns of branching are pinnate, dichotomous, and bottle-brush forms that correspond exactly with the growth forms of primnoid colonies.

3. *Axial skeleton.* —Although the overall aspect of isidid colonies depends upon the diverse form of the supporting axis, the articulated nature of the axis is consistent. Branching may take place from the horny nodes or from the calcareous internodes. The internodes may be long or short, hollow or solid, longitudinally grooved or not, smooth or sculptured with granules, thorns or spines.

4. *Sclerites.* —The distinction between spindles (or rods or needles) and scales is by no means sharp, as spindles can be more or less flattened depending, at least in part, upon the space in which they occur. The larger sclerites of the polyps of all Keratoisidinae are cylindrical rods or tapered spindles, but the small sclerites may be thin scales even though their thickness is not limited by space. In *Tenuisis exilis* described below, the sclerites of the polyp body are elongated and tapered, but are flat and scale-like even though they seem not to be limited by space. They are, in fact, scales, not spindles, thus excluding *Tenuisis* from Keratoisidinae.

5. The arrangement and number of sclerites in the body of the polyp influences its mobility. The polyps of *Isis* are essentially devoid of sclerites, hence can withdraw completely into the thick common coenenchyme that invests the supporting axis. Long sclerites placed longitudinally, as in *Keratoisis,* preclude any appreciable shortening of the body during contraction, whereas smaller sclerites transversely placed, as in *Mopsea,* permit the body to be shortened to a greater or lesser extent. Added protection is gained by turning the oral end of the polyp inward toward the axis during contraction, a motion possible if the sclerites along the adaxial side of the body are smaller or fewer than those along the abaxial side.

6. Operculum.—The differentiation of the distal body scales and the proximal tentacle scales as protective structures for the contracted polyp is so inconsistent that its use as a character at the subfamily level is suspect. Among species of *Mopsea* alone, there are species with (1) a well-differentiated operculum of eight triangular scales (*Mopsea plumacea* Briggs), (2) a series of triangular to crescentic scales transversely arranged along the base of the tentacles (*Mopsea whiteleggei*), and (3) narrow scales set en chevron on the base of the tentacles (*Mopsea encrinula*). In Grant's system, *Mopsea whiteleggei* and *M. encrinula* fall in the Mopseinae, but *Mopsea plumacea* would fall in the Peltastisidinae.

In *Echinisis spicata,* the scales of the two distalmost circles of body sclerites project spine-like around the bases of the tentacles. Within these marginal scales eight acutely triangular scales of the tentacle bases fold inward over the infolded tentacles, which bear smaller triangular scales decreasing in size distad along the tentacle backs, followed by transversely set crescentic scales. If the eight triangular scales are treated as an "operculum," as Grant (1976) did, *E. spicata* should fit without difficulty in the subfamily Peltastisidinae, as the polyp sclerites are exclusively scales, even though they have deeply incised margins.

In the three new species here ascribed to *Echinisis,* the distalmost circle of body scales (i.e., "marginals") can fold inward over the bases of the tentacles in complete contraction, forming an apparent operculum, but these scales are poorly differentiated from those on the base of the tentacles making it difficult to distinguish "opercular" scales from those following.

From this it can only be concluded that the degree of differentiation of the sclerites to form an "operculum" is variable, ranging from narrow scales set en chevron on the bases of the tentacles, through a series of imbricating crescentic scales transversely arranged, to a single large triangular or triradiate scale on the base of each tentacle, followed distally by smaller scales. In speciose genera such as *Mopsea,* all of these conditions and intergrades occur. It therefore appears that this character is more important at the species level than at the generic level. However, until more material is available for evaluation, the genera *Chathamisis* Grant and *Minuisis* Grant are maintained as distinct from *Primnoisis* Wright and Studer.

Family Isididae Lamouroux, 1812, sensu lato

The continuing increase in collections and discovery of new species obscures some of the taxonomic boundaries that have become accepted over the past century, making the allocation of species to genera, and of genera to subfamilies, increasingly problematical. Material both old and new now at our disposal requires the establishment of four new genera of Isididae in addition to the revalidation of two others suggested in a separate paper (Bayer and Stefani 1987), bringing to 20 the number of genera in this family. As the relationship of the various genera is unclear and the boundaries of the subfamilies are blurred, no attempt is made here to propose a "natural" arrangement. Accordingly, we offer the following artificial key for the differentiation of the genera of Isididae here recognized.

1(2). Polyps unarmed or with only a few tiny rods in tentacles, contractile within thick coenenchyme. Sclerites of coenenchyme are small clubs in surface layer, with capstans and tuberculate spindles in the deeper layers, sometimes developing as double heads or coarse pebbles .... *Isis* Linnaeus, 1758

2(1). Polyps armed with numerous sclerites, conspicuously projecting above the thin coenenchyme.

3(4). Sclerites of polyps organized as crown and points in anthocodiae fully retractile within prominent calycular anthosteles. Sclerites are thorny spindles .... *Muricellisis* Kükenthal, 1915

4(2). Sclerites of polyps not organized as crown and points, polyps not divided into anthocodial and anthostelar portions; tentacles fold inward at summit of prominent verrucae, but upper part of polyp does not retract into lower.

5(6). Coenenchymal sclerites are 6-radiates ....*Chelidonisis* Studer, 1890

6(5). Coenenchymal sclerites if present never 6-radiate.

7(8). Sclerites of polyps are cycloid scales with smooth margins ....*Circinisis* Grant, 1976

8(22). Sclerites of polyps are transversely arranged plates.

9(16). Eight large scales at bases of tentacles are differentiated as a distinct operculum.

10(11). Colonies unbranched, filiform ....*Peltastisis* Nutting, 1910

11(10). Colonies branched.

12(13). Opercular scales triangular .. .. *Minuisis* Grant, 1976

13(12). Opercular scales triradiate.

14(15). Polyp sclerites of distalmost 1–3 whorls below tentacles furnished with a strong projecting spike .... *Echinisis* Thomson and Rennet, 1931

15(14). Polyp sclerites of distalmost 1–3 whorls without projecting spike .. *Chathamisis* Grant, 1976

16(9). No well-differentiated operculum of eight scales; bases of tentacles covered by several transverse, oblique, or converging scales.

17(21). Polyps tall, clavate, often recurved toward axis.

18(19). Colonies bushy, often bottlebrush shaped .... *Primnoisis* Studer [and Wright], 1887

19(20). Colonies pinnate, dichotomous, or openly irregular; internodes of axis longitudinally fluted, often but not always with small spines or denticles on the ribs ....*Mopsea* Lamouroux, 1816

20(18). Colonies planar, distantly pinnate; internodes of axis not fluted, covered with low, blunt prickles ....*Stenisis,* n. gen.

21(17). Polyps short, not recurved toward axis .... *Acanthoisis* Studer [and Wright], 1887

22(7). Sclerites of polyps are not transversely set plates but spindles, rods, or slender flat scales arranged longitudinally or obliquely.

23(26). Colonies unbranched.

24(25). Colonies tall, polyps all around; internodes of axis usually hollow, sometimes longitudinally fluted, surface smooth ...*Lepidisis* Verrill, 1883

25(26). Colonies small, polyps biserial; internodes of axis solid, not longitudinally fluted, covered with low, sharp prickles ....*Caribisis,* n. gen.

26(29). Colonies branched from the nodes.

27(28). Branches arranged in whorls, growth form bushy ....*Acanella* Gray, 1870

28(27). Branches not in whorls, growth form approximately planar .. .. *Isidella* Gray, 1857

29(23). Colonies branched from the internodes.

30(31). Sclerites of polyps are minute

flat scales never projecting between the tentacle bases .... *Tenuisis,* n. gen.

31(30). Sclerites of polyps are spindles or rods.

32(33). Polyps filled with slender, sharp spindles arranged conspicuously en chevron; no strong spindles projecting spine-like between bases of tentacles; colonies abundantly bushy; axis with numerous horny nodes throughout, internodes not longitudinally ribbed or fluted, covered with small sharp prickles most conspicuous on distal internodes .... *Australisis,* n. gen.

33(32). Polyps with strong, longitudinally or obliquely arranged spindles not en chevron.

34(35). Colonies pinnate or bottle-brush shaped, of small or moderate size, main axis with few nodes joining long internodes expanded as runway for commensal polychaete worm. Spike-like sclerites around oral end of polyp, if present, aligned on the bases of tentacles, between the mesenterial insertions ..... *Sclerisis* Studer, 1878

35(34). Colonies not bottle-brush shaped, large and robust, axis with numerous nodes throughout, joining internodes not expanded as runway for commensal worms. Oral end of polyps with strong spindles or needles projecting spine-like between bases of tentacles .. .. *Keratoisis* Wright, 1869

Primnoisis Studer [and Wright], 1887

Primnoisis Studer [and Wright], 1887:46.—Wright and Studer, 1889:34.—Kükenthal, 1912:339; 1919:611; 1924:432.—Gravier, 1913:456.—Deichmann, 1936: 250.—Bayer, 1956:F222; 1981:942.—Grant, 1976:10, 35.
Ceratoisis (part).—Hickson, 1907:7.

Type species.—*Isis antarctica* Studer, 1879; by monotypy.

Diagnosis.—Isidids branched from the internodes, in several planes or on all sides in the form of a bottle-brush; polyps cylindrical or clavate, standing straight or inclined from the axis, sometimes recurved toward the axis, scattered on all sides of the branches; sclerites in the form of serrated scales or plates, sometimes narrow and fusiform, transversely placed in the polyps; bases of tentacles armed with converging scales.

Remarks.—As originally constituted, *Primnoisis* contained a single species, *Isis antarctica* Studer; the original specimen taken northwest of Kerguelen by the *Gazelle* was a denuded axis of bottle-brush growth form. The characters of the polyps and their spiculation remained unknown until the *Challenger* Expedition obtained living specimens of strikingly similar habitus in 310 fathoms off Prince Edward Island. Because of its distinctive growth-form (now known to be shared by several species of *Primnoisis* and *Echinisis*), Studer in collaboration with E. P. Wright identified the *Challenger* material with that from Kerguelen taken by the *Gazelle* cruise, briefly described the polyps and spiculation, and established the genus *Primnoisis* (Studer [and Wright], 1887:45). However, the bare axis of the type specimen of *Isis antarctica* could belong to any of several species in at least two genera, so the generic characters of *Primnoisis* are based upon the *Challenger* specimen so identified and described in detail in the *Challenger* report, not upon the type of *Isis antarctica,* its nominal type species.

Comparison of our drawing (Fig. 3a) with Wright and Studer's illustration of the same material (1889:pl. 8, fig. 2a) immediately reveals a discrepancy in the shape of the polyps. Although we at first suspected that either the *Challenger* specimens are a composite of more than one species, or the illustrations of the polyps of *P. rigida* (1889: pl. 8, fig. 3a) and *antarctica* (pl. 8, fig. 2a) were transposed, we are informed by Mr. Simon J. Moore (British Museum [Nat. Hist.]) that neither is the case. His examination of all the *Challenger* specimens labeled as *P. antarctica* shows them to be homogeneous and in agreement with our drawing. His comparison of *antarctica* with *P. rigida* shows that the polyps of the latter are distinctly recurved, in conformity with pl. 8, fig. 3a, whereas the polyps of *antarctica* are bent inward little, if at all. Consequently, the discrepancy probably can be attributed to inaccuracy of drawing introduced by the commercial lithographer who prepared the plates for the *Challenger* report.

Three new species also of profusely bushy, if not strictly bottle-brush, growth form were added to *Primnoisis* by Wright and Studer (1889:34–40). This dense branching has been accepted as a generic character distinguishing *Primnoisis* from *Mopsea,* in which branching is "always" planar (either pinnate or dichotomous), and on the basis of it several more species have been added to the genus over the years. These include *Ceratoisis spicata* Hickson and *Primnoisis armata* Kükenthal (both now included in *Echinisis* on the strength of spicular characters of the polyps), *P. formosa* Gravier and *P. fragilis* Kükenthal.

Primnoisis delicatula Hickson, *Ceratoisis ramosa* Hickson (transferred to *Primnoisis* by Kükenthal 1919), and *Primnoisis humilis* Deichmann, although abundantly branched, depart from the "characteristic" growth form of *Primnoisis* and differ in other characters as well, hence cannot justifiably be retained in *Primnoisis.*

The branchlets of *P. ramosa* have a very strong tendency to remain in one plane, and the polyps have a kind of operculum formed by a single large triradiate scale resting upon one or more crescentic scales at the base of each tentacle. These scales, particularly mentioned by Hickson (1904:224), consist of a crescentic or bifurcate base and strong apical spike. Owing to the stylization of the drawing, the disposition of the opercular scales is not clearly shown in Hickson's figure of the polyps (pl. 8, fig. 12); each octant ordinarily includes only one large triradiate scale, the base of which rests upon one or two crescentic "circum-opercular" scales. Considering these features, *Ceratoisis ramosa* Hickson, 1904, falls in Grant's genus *Chathamisis* rather than in *Primnoisis.*

Primnoisis humilis Deichmann (1936: 251) was described only from the fragmentary type specimen from off the Dry Tortugas and has never been illustrated. Three finds taken by the University of Miami Deep-sea Expeditions consist of several specimens in good condition, which provide additional morphological information as well as distributional data, are now placed on record. These specimens show that the species has consistently planar colonies branched in an openly pinnate or "lateral" manner, *Mopsea*-like polyps with transverse sclerites, and ungrooved internodes covered with low prickles, characters incompatible with *Mopsea, Primnoisis,* and all other genera of Isididae. *Primnoisis humilis* Deichmann is therefore assigned to a new genus *Stenisis,* described below.

Kükenthal (1924) recognized eight valid and four doubtful species in the genus *Primnoisis* Studer and Wright, 1887. Two of the species he considered valid, *P. spicata* (Hickson) and *P. armata* Kükenthal, are at present assigned to a genus of their own, *Echinisis* Thomson and Rennet, 1931. Of the species considered doubtful by Kükenthal, *P. pulchella* (Studer) is the type species of the distinct genus *Sclerisis* Studer, 1879; *P. ramosa* (Hickson, 1905), originally described in *Ceratoisis* [sic], can be reassigned to the genus *Chathamisis* Grant as demonstrated in this paper; *P. ramosa* Thomson and Ritchie, 1906 (not Hickson, 1905) was based upon denuded axis and is insufficiently characterized for subsequent recognition; *P. formosa* Gravier, 1913, is possibly a valid species but is not clearly differentiated from certain of those species recognized as valid by Kükenthal. Subsequent to Kükenthal's summary in 1924, Deichmann (1936:251) described *Primnoisis humilis,* a new species taken off Florida by the U.S. Coast Survey steamer *Blake,* the first record of the genus in the northern hemisphere. Study of material more extensive than that available to Deichmann now demonstrates that *P. humilis* cannot be retained in *Primnoisis* as now constituted, so a new genus is proposed for it in these pages.

The nominal species attributable to *Primnoisis* are as follows:

1. *Primnoisis antarctica* (Studer), from Prince Edward Island.
2. *Primnoisis sparsa* Wright and Studer, from Prince Edward Island.
3. *Primnoisis ambigua* Wright and Studer, from Kerguelen Island.
4. *Primnoisis rigida* Wright and Studer, from off Rio de la Plata.
5. *Primnoisis fragilis* Kükenthal, from Gauss Station, Antarctic.
6. *Primnoisis mimas* n. sp., from off South Georgia.

As the polyps of *Primnoisis* do not materially differ in spiculation from those of *Mopsea,* these genera are distinguished chiefly by colonial form. On the basis of this criterion, *P. delicatula* Hickson is more appropriately assigned to the genus *Mopsea* and appears to be close to *M. gracilis* Gravier, although not branched strictly in one plane.

Primnoisis fragilis Kükenthal (1912:342) has the bottle-brush form of *P. antarctica* and polyps not much different in size. The marginal scales were depicted as roughly triangular with their apices projecting as points around the distal end of the polyp. The transverse body scales as originally illustrated (Kükenthal 1912:342; 1924:436, fig. 206) are unusually large, but this large size may be more apparent than real, because it is notoriously difficult to discern the shape and edges of all the scales covering the polyps.

As the shape and armature of the polyps and the general form of the sclerites in the subfamily Mopseinae Gray (+ Peltastisidinae and Circinisidinae Grant) are so uniform, generic distinctions are with few exceptions based mainly on colonial form and pattern of branching. Unbranched, filiform or flagelliform colonies comprise *Peltastisis* and *Circinisis,* planar colonies branched either pinnately or dichotomously have been assigned to *Mopsea* and *Acanthoisis* (with the recent addition of *Circinisis*), and colonies abundantly branched in all direction comprise the genera *Primnoisis* and *Echinisis.* The recently established genera *Chathamisis* and *Minuisis* (Grant, 1976) have essentially *Primnoisis* growth form but were distinguished on the basis of opercular development.

Primnoisis antarctica (Studer, 1879)
Figs. 1a, 2, 3a, b, 4

?*Isis antarctica* Studer, 1879:661, pl. 5, fig. 32.

Primnoisis antarctica.—Wright and Studer, 1889:35, pl. 8, figs. 2, 2a, 2b; pl. 9, fig. 6.

Material examined.—Branchlet from one colony from off Marion Island, Prince Edward Islands: 46°41′00″S, 38°10′00″E, 310 fathoms; HMS *Challenger* sta 145A, 27 Dec 1873, BM(NH) 1889.7.5.24.

Antarctic Peninsula, Palmer Archipelago, Graham Land: 64°49.4′S to 64°49.5′S, 62°51.9′W, 120–148 m, *Hero* cruise 721, sta 730, 27 Dec 1971. Three nearly complete

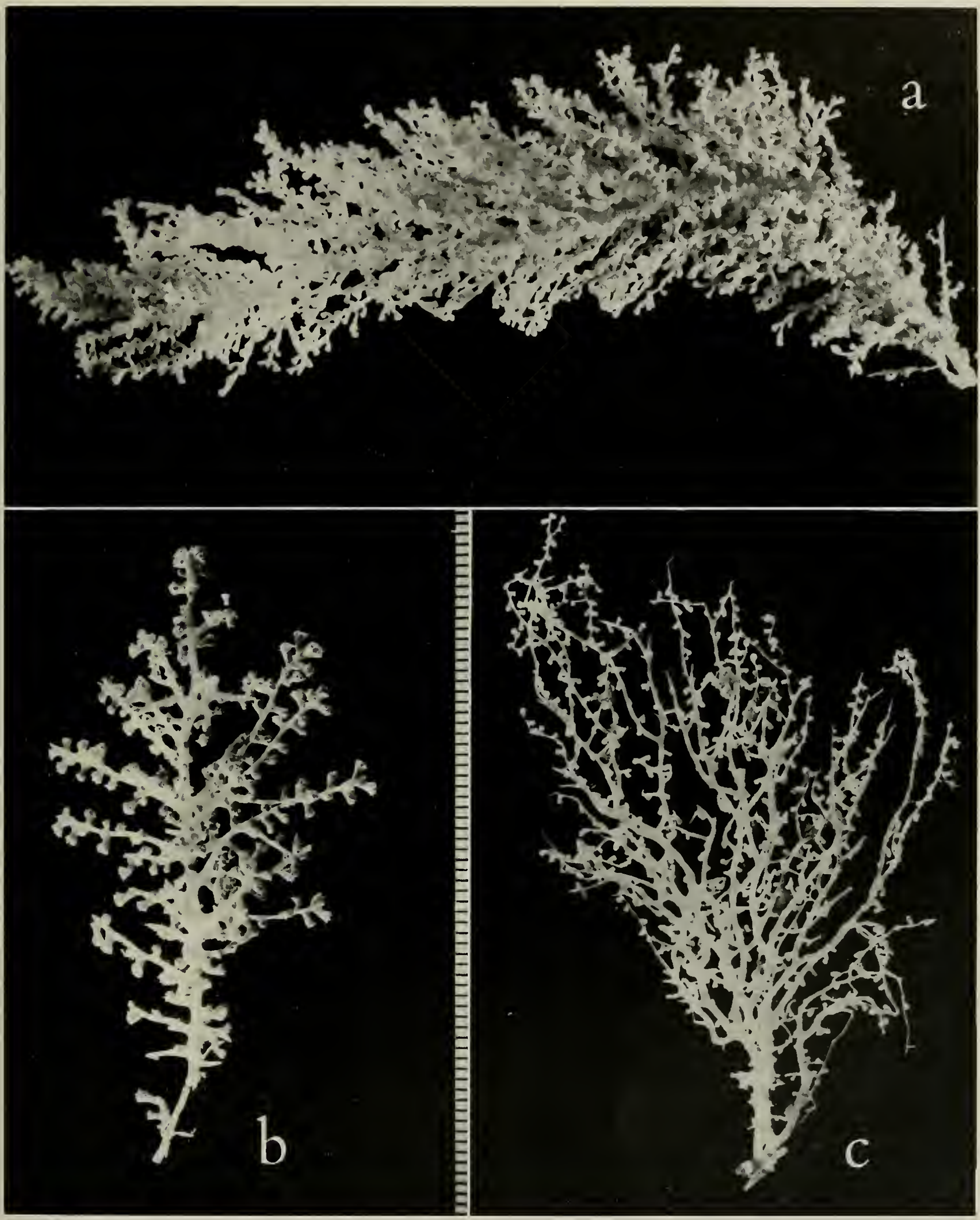


Fig. 1. a, *Primnoisis antarctica* (Studer), USNM 78355; b, *Echinisis spicata* (Hickson), USNM 75222; c, *Chathamisis ramosa* (Hickson), USNM 43071. Vertical scale divided in mm applies to all three specimens.

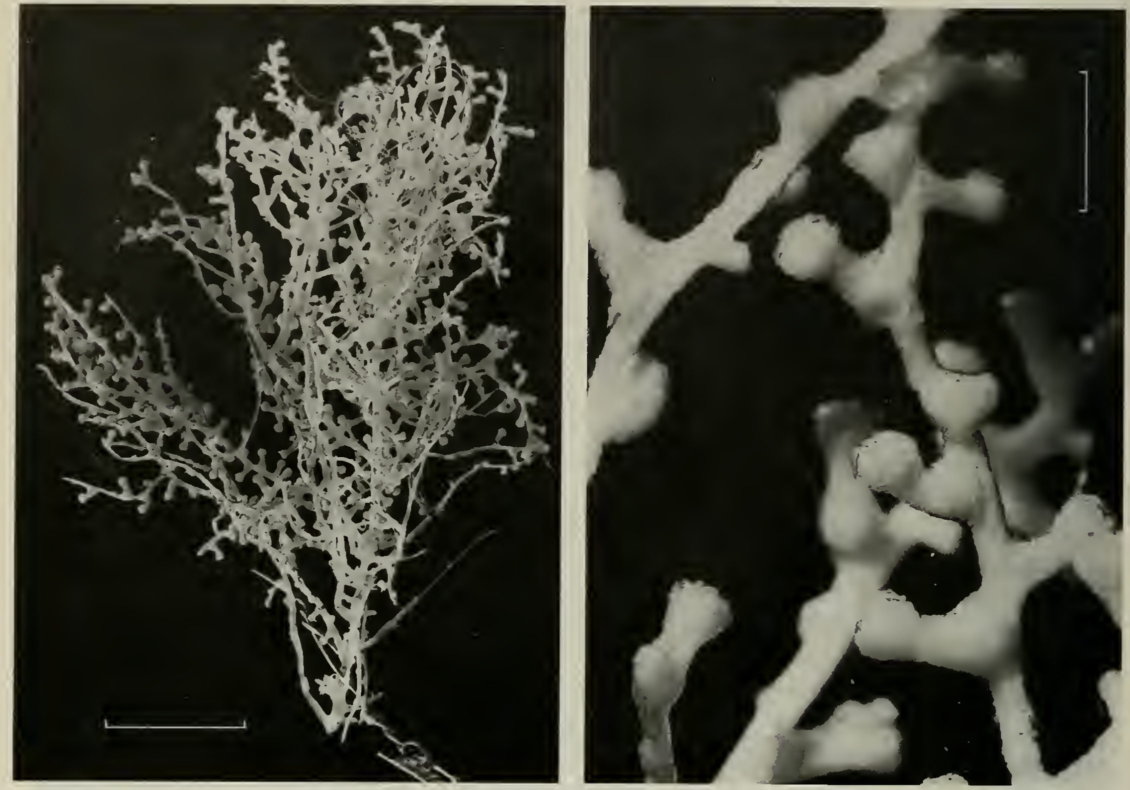


Fig. 2. *Primnoisis antarctica* (Studer), BM(NH) 1889.7.5.24: Left, colony, scale = 1 cm; right, detail of same, scale = 1 mm. Photographs courtesy of the Trustees of the British Museum (Nat. Hist.).

colonies, and branches, alcohol, USNM 78355.

Discussion.—Although described and illustrated by Wright and Studer (1889) in considerable detail, essential information about the size, distribution, and spiculation of the polyps was not presented. Consequently, we have examined the polyps and sclerites of a fragment from one of the *Challenger* specimens through the kindness of Dr. P. F. S. Cornelius, and here present illustrations (Figs. 2, 3a, 4) to supplement the description.

Neither Hickson (1907:6), Thomson and Rennet (1931:11), nor Broch (1965:20) provided enough information to confirm their reports of the species. The drawings given by Kükenthal (1912:340, figs. 55–57) are sufficient to demonstrate that his specimen probably was not the species taken by the *Challenger.*

One lot of specimens of bottle-brush form (USNM 78355) discovered among the Antarctic collections of the National Museum of Natural History can be referred to *P. antarctica* as represented by the *Challenger* specimen now examined. Although the latter was dredged near Prince Edward Island, the present lot from the Palmer Archipelago along the west coast of the Antarctic Peninsula is at least from the same general sector of the Antarctic even if not remotely topotypic. The polyps (Fig. 3b) are for the most part similar to those of the *Challenger* specimens (Fig. 3a) in size and shape and spiculation, but the fully developed polyps (as opposed to obviously young individuals) show considerable variation in size from one twig to another even on the same branch. Moreover, many polyps are misshapen owing to the presence of 1–4 large eggs, a condition not observed by Wright and Studer.

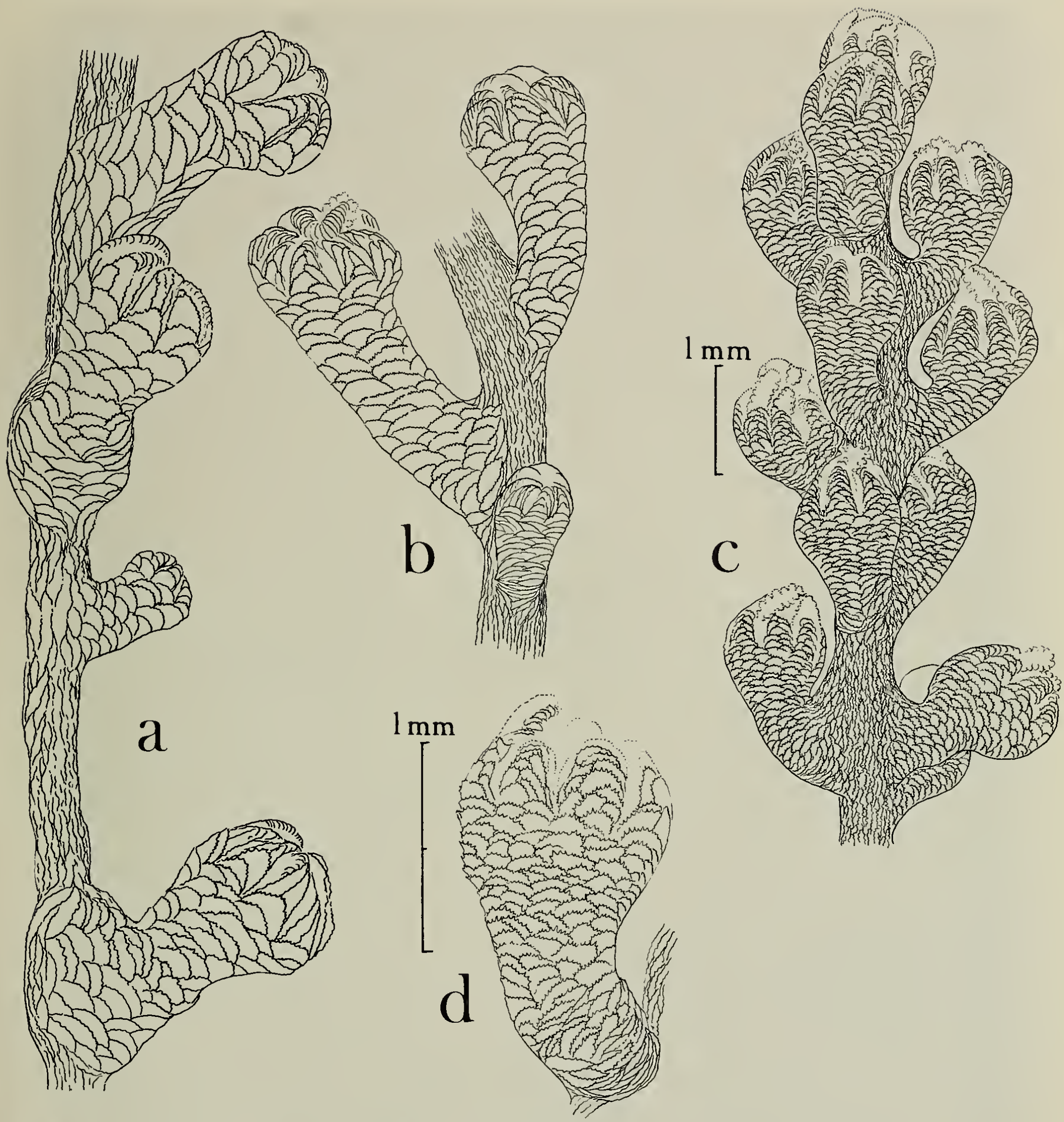


Fig. 3. a, *Primnoisis antarctica* (Studer) from *Challenger* sta 145A, BM(NH) 1889.7.5.24; b, *Primnoisis antarctica* from *Hero* sta 730, USNM 78355; c, d, *Primnoisis mimas* n. sp., USNM 78356. Scale at c applies to c only; that at d applies to a, b, d.

Primnoisis mimas, new species
Figs. 3c, d, 5, 6

Material examined.—Vicinity of South Georgia: 54°14.1′S., 37°54.2′W, depth 164–183 m. USARP, R/V *Islas Orcadas,* cruise 575, sta 101, 10 Jun 1975; 2 colonies without holdfast, USNM 78356 (holotype), USNM 78357 (paratype).

Vicinity of South Georgia: 53°51′–53°52′S, 37°38′–37°36′W, depth 97–101 m. USARP, USNS *Eltanin,* cruise 22, sta 1535, 7 Feb 1966; 1 colony without holdfast, USNM 78358 (paratype) and 1 small colony possibly juvenile or representing a different species (USNM 78359).

Diagnosis.—Bottlebrush-shaped *Primnoisis* with closely crowded clavate polyps

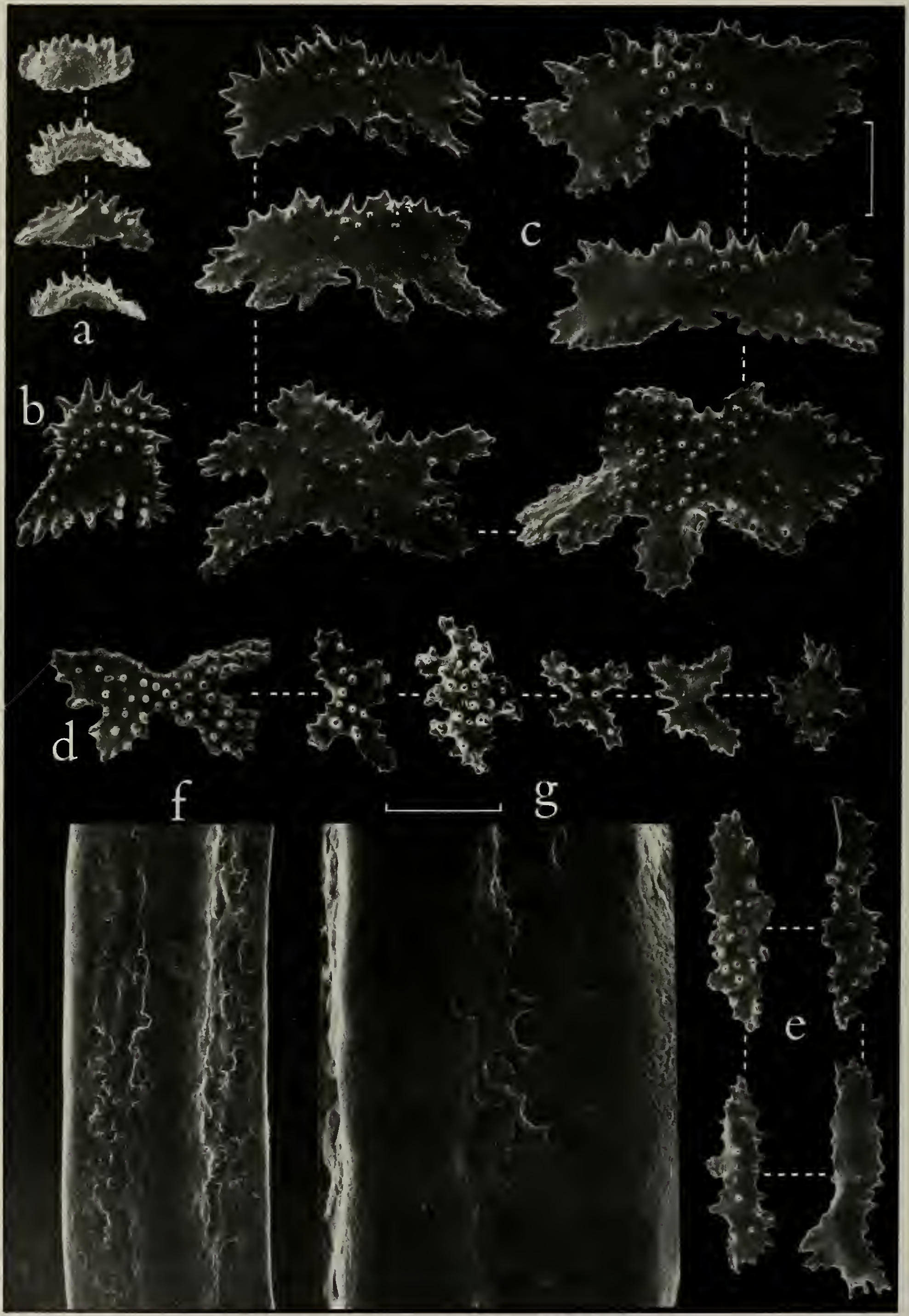


Fig. 4. *Primnoisis antarctica* (Studer) from *Challenger* sta 145A, BM(NH) 1889.7.5.24. a–e, sclerites: a, From tentacles; b, From base of tentacle; c, From body of polyp; d, e, From coenenchyme; f, g, Part of axial internode. 0.1 mm scale bar at c applies to a–f; 0.05 mm bar at g applies to g only.

Fig. 5. *Primnoisis mimas* n. sp., holotype colony, USNM 78356. Scale bar = 1 cm.

2 mm tall; verrucae armed with numerous, transverse, deeply serrated scales; coenenchyme with slender spinous rods and spindles commonly flattened and scale-like.

Description.—The holotype colony (Fig. 5) is approximately 43 cm high. It is shaped like a bottle-brush, with up to three upwardly directed branches arising from each internode of the main axis, measuring up to 7 cm in length, 0.7 mm in diameter (without polyps).

Proximally the axis lacks its holdfast; the basal node measures 4 mm in diameter, and 7 mm in length; subsequent nodes are at most 3 mm long, becoming much shorter distad. The internodes are between 2 and 4.5 mm in length, those at the base and summit of the stem shorter, those in the middle more consistently 4.0–4.5 mm in length; proximally the internodes are about 4 mm in diameter, decreasing to 3 mm about mid-height, and tapering to less than 0.5 mm apically. The internodes are sculptured with distinct longitudinal ridges and grooves (Fig. 6e); oval or circular pits marking the location of desmocytes in the axis epithelium are numerous and irregularly scattered in the grooves (Fig. 6f). Secondary branchlets and terminal twigs arise from the internodes of the branches, which average 2.5 mm in length, 0.7 mm in diameter.

The upwardly directed polyps are so crowded around the stem and branches that they overlap each other. They are club-shaped, 2 mm tall with tentacles folded over the mouth; at their base, they measure 1 mm in diameter, at the top, 0.6 mm. They tend to be more abundant on three of the four sides of the branches and twigs.

The sclerites of the verrucae are deeply serrated, translucent scales up to 0.3 mm long and 0.1–0.15 mm wide (Fig. 6c) transversely arranged in numerous irregular longitudinal rows (Fig. 3c, d). Smaller, transversely placed scales with more closely serrated margins extend along the backs of the tentacles, curved to fit the contour of the rachis (Fig. 6a); those extending into the pinnules show a peculiar twist (Fig. 6b). The coenenchyme contains slender, spinous spindles and rods 0.25–0.3 mm long, many distinctly flattened and scale-like (Fig. 6d).

The polyps and coenenchyme are dull brown; the lower nodes of the main stem are a rich reddish brown, becoming paler distad. The internodes are white.

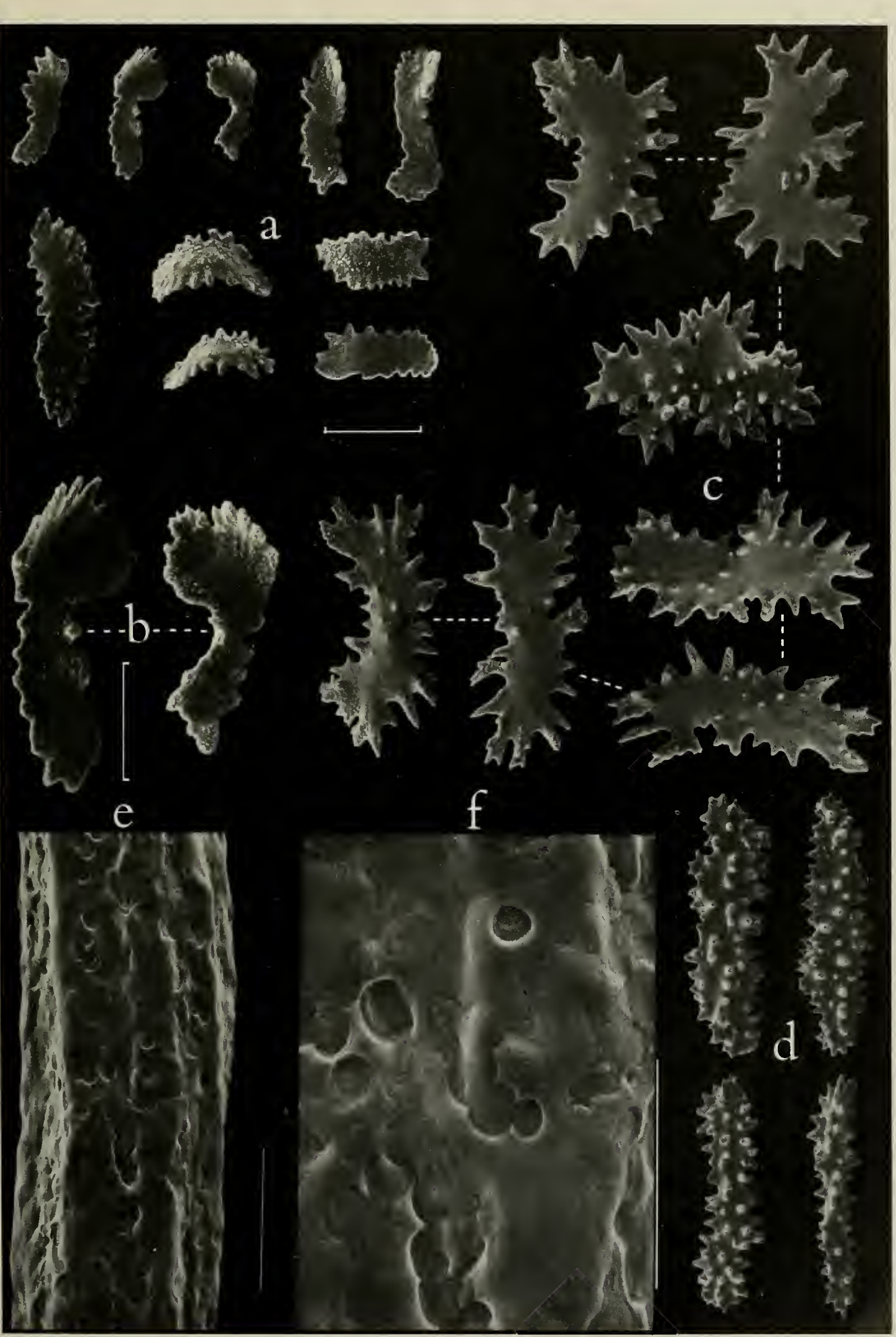
Comparisons.—In growth form this species is stouter and more robust than any *Primnoisis* heretofore described. The verrucal scales are more deeply and sharply serrated, and smaller than than those of *P. antarctica,* which may exceed 0.4 mm in length. A specimen illustrated by Grant (1976:37, fig. 32) and attributed to *P. antarctica* bears some resemblance to the material here described, but insufficient information is provided to determine its relationship. *Primnoisis formosa* Gravier (1913:453; 1914:31, pl. 1, figs. 3–5), also reported by Grant (1976:38), has a much more delicate growth form, and seems to be closer to *antarctica* than to the present material.

Etymology.—Greek Μίμασ, one of the giants, slain by Zeus (or perhaps Ares) during the war with the gods.

Remarks.—A specimen (USNM 78358) collected at *Eltanin* sta 1535, off South Georgia, is smaller and paler than the holotype and paratype from *Islas Orcadas* sta 101, but it agrees in all other details. A still smaller colony (USNM 78359) from *Eltanin* sta 1535 has polyps that are widely separated, slender and nearly straight like those

→

Fig. 6. *Primnoisis mimas* n. sp. a–d, sclerites: a, From tentacles; b, From pinnules; c, From body of polyp; d, From coenenchyme; e, f, Part of axial internodes. 0.1 mm bar at a applies to a, c, d; 0.05 mm bar at b applies to b only; 0.2 mm bar at e applies to e only; 0.1 mm bar at f applies to f only.


a
b
c
d
e
f

of *P. antarctica* on its lower branches, but on the upper branches and apex of the main stem clavate, recurved polyps are crowded as in the type material of *P. mimas.*

The variation among specimens from different stations and among colonies from the same haul suggests that intensive study of more abundant material will be necessary before Antarctic species of gorgonians can be adequately delimited and reliably recognized.

Echinisis Thomson and Rennet, 1931

Ceratoisis (part).—Hickson, 1907:5.
Primnoisis (part).—Kükenthal, 1915:122; 1919:611; 1924:432.
Echinisis Thomson and Rennet, 1931:15.—Grant, 1976:47.

Diagnosis.—Isididae with polyps covered by conspicuously lobed or branched scales having deeply serrate margins, those of 1 to 3 distal transverse rows bearing a strong projecting spine.

Type species.—*Ceratoisis spicata* Hickson, 1907, by subsequent designation.

Remarks.—This genus was established for colonies of essentially *Primnoisis* growth form, but in which the body sclerites of the polyps are irregularly stellate plates, those of the distalmost transverse rows below the tentacles having one ray developed as a strong projecting spike (Thomson and Rennet 1931). In one species (*E. spicata*), scales of the uppermost 2–3 rows develop such a spine; in the other (*E. armata*), only one row has the spines. Observations on variation of this character suggest that it is not wholly consistent (Thomson and Rennet 1931; Grant 1976). The three new species described herein, while clearly showing projecting spinous polyp scales as in *Echinisis,* depart from the bottle-brush growth form of the two species of that genus known heretofore. As we consider it undesirable to erect yet another genus, solely on the basis of growth form, we here place the new forms in *Echinisis* with a suitably emended diagnosis.

The recognition of *Echinisis spicata,* the type species of *Echinisis* Thomson and Rennet, 1931, on the basis of published data about the two species included in it is problematical. Kükenthal (1912) considered his *Primnoisis armata* to be close to, if not identical with, Hickson's *Ceratoisis spicata* (Hickson, 1907:7) but maintained the two as distinct species on the basis of the number of transverse rows of polyp sclerites bearing projecting spines and the different appearance of the body scales; the polyps of *spicata* also were considerably larger (2 mm) than those of *armata* (1.3 mm).

The species have subsequently been reported only infrequently, *armata* once when the genus *Echinisis* was established (Thomson and Rennet 1931), *spicata* once by Grant (1976) from six stations off New Zealand. Thomson and Rennet (1931) reported variation in the number of transverse distal scale rows developing strong spines and suggested intergradation between *spicata* and *armata* but retained both species as valid. Grant (1976:49) reported similar variation among his specimens, referring all to *spicata* while echoing Thomson and Rennet's doubt about the distinctness of the species.

We have examined specimens from Bahía Grande, Sta. Cruz, Argentina (USNM 77367), the South Shetland Islands (USNM 75651), Palmer Peninsula (USNM 58161, 76913, *Hero* 1022, *Hero* 26-1), Ross Sea (USNM 75222, *Eltanin* 2110), and off Cape Adare (USNM 77355), ranging in depth from 173 m to 2350 m. They show conspicuous differences in growth form, size of polyps, spiculation, and color of the polyps resulting from pigmentation of the mesenterial filaments, making unequivocal identification with either *spicata* or *armata* difficult. In no case is the circlet of spines of the polyps confined to the single distalmost row as reported by Kükenthal for *armata.*

The type locality of *Echinisis spicata* is McMurdo Bay in the Ross Sea, 175–218 m (96–120 fathoms), Scott Coast, Antarctica. Among the specimens that we have studied, three are from the Ross Sea, one from the

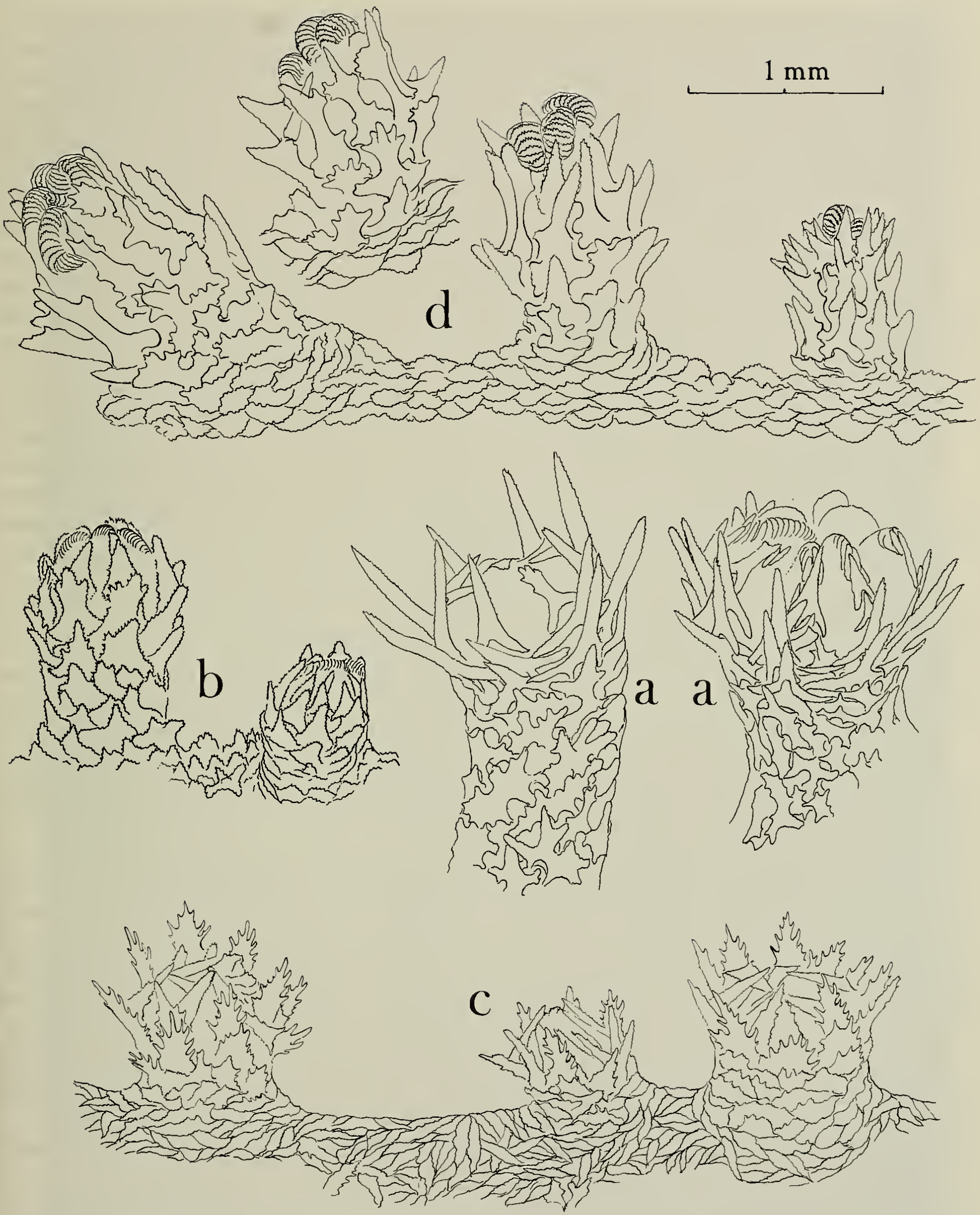


Fig. 7. a, *Echinisis spicata* (Hickson), two polyps; b, *Echinisis eltanin*, n.sp., two polyps; c, *Echinisis vema*, n. sp., three polyps; d, *Echinisis persephone*, n. sp., isolated polyp and twig tip wtih three polyps. Scale applies to all figures.

eastern part of the sea off Saunders Coast, depth unrecorded (USNM 75222), one from the middle part of the sea in 2350 m of water (USNM 78379), and one from the vicinity of Cape Hallett in 392 m (USNM 77355). In attempting to recognize *E. armata* with reasonable confidence the sample from 2350 m has been excluded on the basis of depth as well as size of the spines of the distal body scales. Those from the other two Ross Sea stations are in close agreement and they conform in all essentials with Hickson's original description; the station off Cape Adare is some 700 km north of the type locality in a similar depth. These two lots are here taken to represent *E. spicata* (Hickson).

Grant (1976) did not include this genus in any of the subfamilies that he recognized, owing to the presence of an "operculum" composed of eight triradiate sclerites (Thomson and Rennet 1931:12, 16).

Echinisis spicata (Hickson, 1907)
Figs. 1b, 7a, 8

Ceratoisis spicata Hickson, 1907:7, pl. 2, figs. 16–18.—Thomson and Rennet, 1931: 15.

Primnoisis spicata.—Kükenthal, 1919:613; 1924:433.

Echinisis spicata.—Grant, 1976:47, figs. 48, 49.

Material examined.—Ross Sea: 76°30′S, 156°19′W, Deepfreeze II, USS *Staten Island,* sta 21, coll. J. Q. Tierney, 26 Dec 1960; one colony with holdfast, one smaller colony without holdfast, one completely decorticated axis, and fragments; in alcohol. USNM 75222.—Ross Sea: off Cape Hallett, 72°05.8′S, 172°15.2′E, 392 m, Deep Freeze III, USS *Atka* sta 23, 12 Jan 1958; two small incomplete colonies, alcohol. USNM 77355.

Diagnosis.—Bottle-brush shaped *Echinisis* with body sclerites of the three distalmost transverse rows each prolonged into a strong, echinulate spike.

Description.—The colonies are branched on all sides in bottle-brush form, but the lateral branches tend to bend in such a way that the growth form becomes almost flabellate (Fig. 1b), as Hickson (1907:7) mentioned. The internodes of the principal axis are from 10 to 17 mm long, their length being rather consistent in any one colony; they give rise on all sides to about 10 to 13 lateral branches, which do not originate with a node. The first node of the lateral branches occurs at about 1 cm from the main axis, before which several secondary branchlets may be produced without articulating nodes. In the completely denuded axis from the eastern part of the Ross Sea, one lateral branch from the first main internode is developed as a secondary branch almost as long as the main axis, but less robust and with fewer branchlets. The fully developed polyps are up to 2 mm tall and 0.75 mm in diameter, mostly separated by at least their own diameter but tending to become more crowded toward the twig tips. The scales of the distalmost three circlets below the tentacles are produced as a stout spine arising from a bifurcated, lobed base (Figs. 7a, 8e); the sclerites of the proximal part of the polyps are stellate plates with elaborately lobed rays, often with one of the rays more sharply serrated and inconspicuously projecting from the body of the polyp (Fig. 8f). The bases of the tentacles are armed with triradiate scales of inverted Y-shape (Fig. 8c), the most proximal of which (Fig. 8d) fold inward over the tentacles in contraction, forming an "operculum" in the sense of Grant (1976). One or more smaller triradiate scales may follow the opercular scale, giving way distad to small flat rodlets and then transversely set crescentic scales (Fig. 8a, b) of the type that is of widespread occurrence also in *Primnoisis, Mopsea, Chathamisis* and *Sclerisis.* The coenenchyme is thin, filled with stellate plates (Fig. 8g).

The color is pale tan with darker brownish polyps.

Echinisis eltanin, new species
Figs. 7b, 9b, 10

Material examined.—Campbell Plateau south of New Zealand: 49°51′S, 178°35′E, 2010–2100 m, USNS *Eltanin,* sta 2143, 26

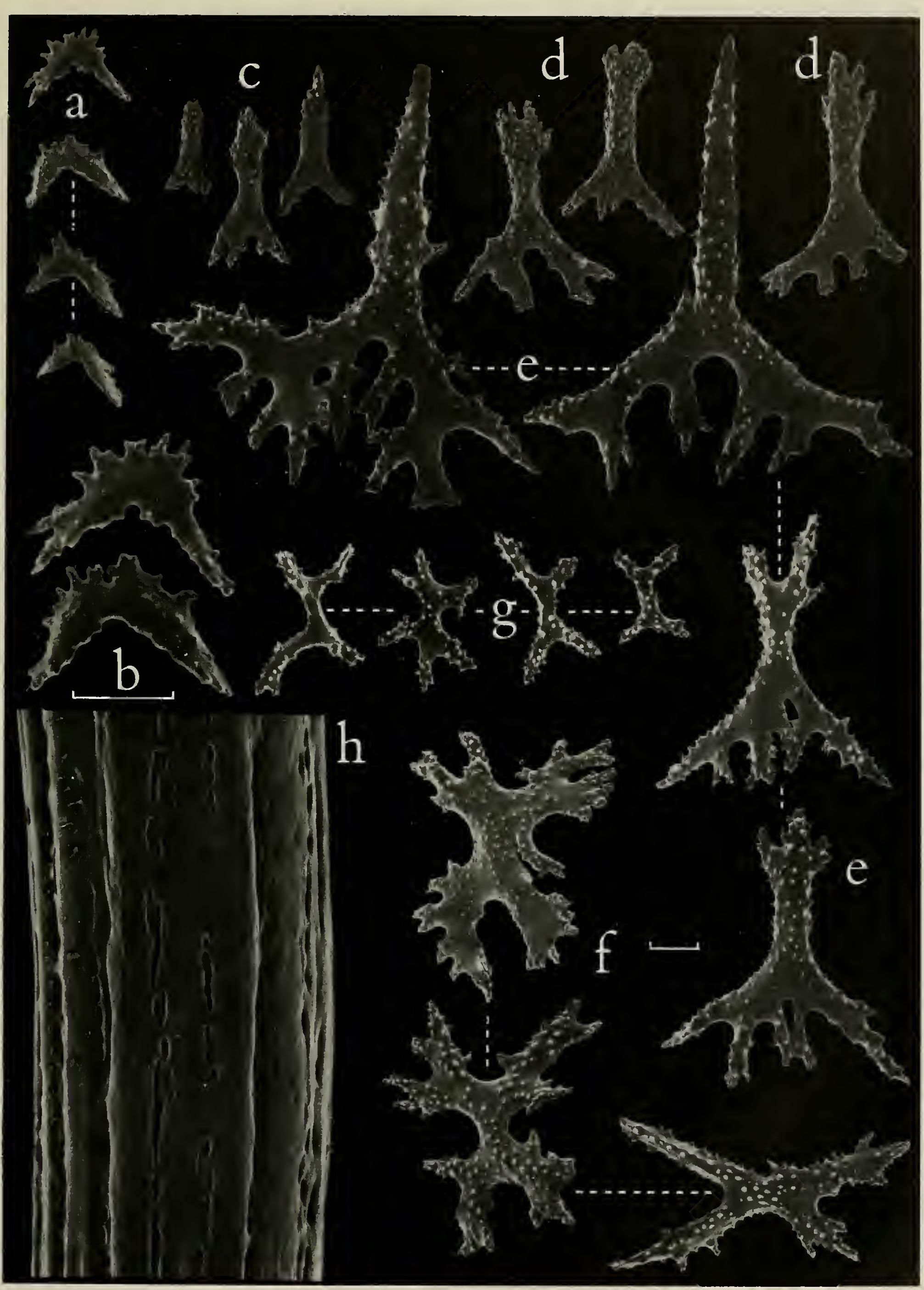


Fig. 8. *Echinisis spicata* (Hickson), USNM 77355. a–g, sclerites: a, b, From rachis of tentacles; c, From base of tentacles; d, Opercular sclerites from beneath tentacles; e, Thorn-stars from distal part of polyp; f, Stellate plates from body of polyp; g, From coenenchyme; h, Part of axial internode. 0.1 mm scale bar at b applies only to b; 0.1 mm bar at f applies to all others.

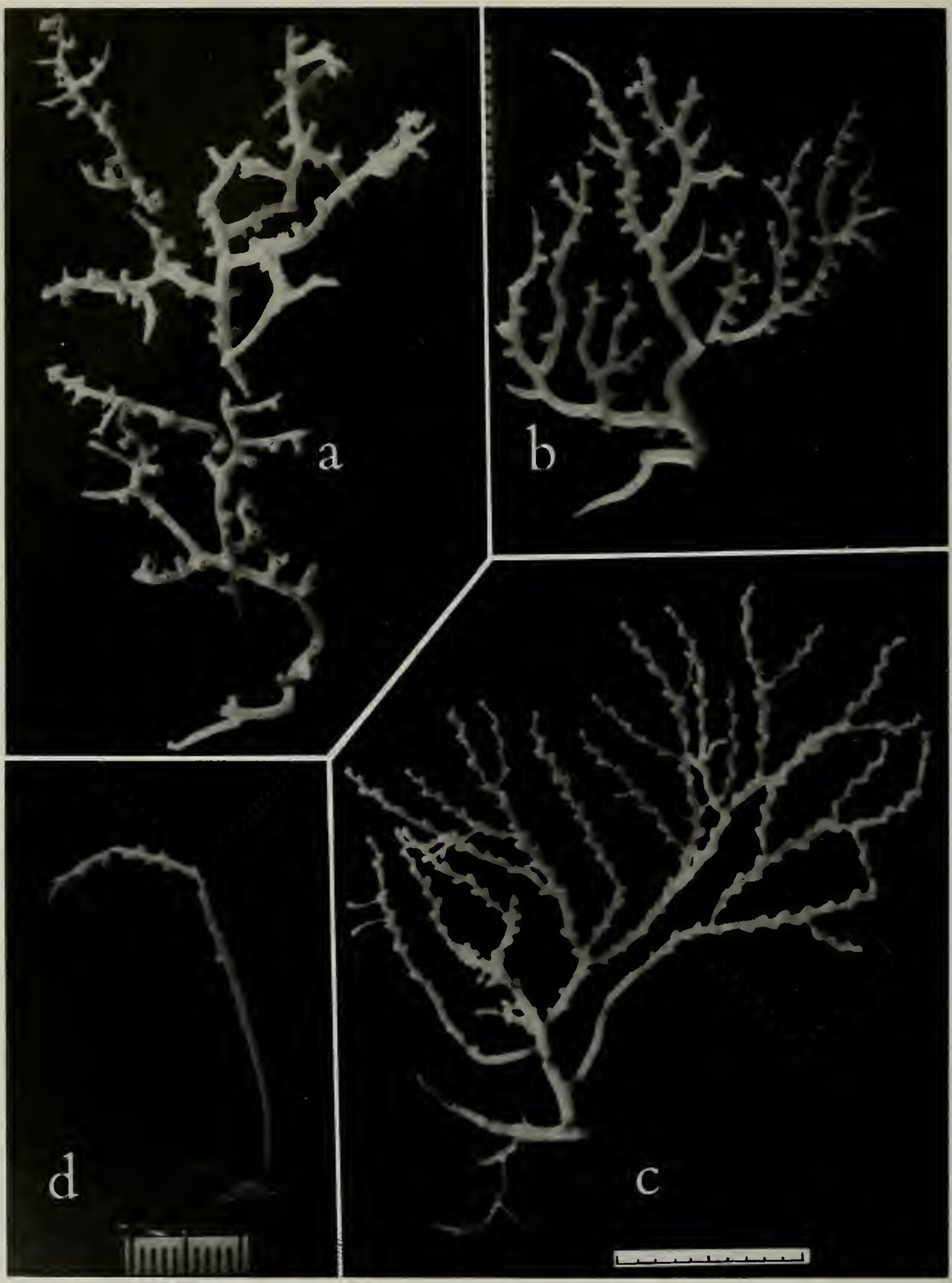


Fig. 9. a, *Echinisis vema,* n. sp., syntypic branches, USNM 78362; b, *Echinisis eltanin,* n. sp., holotype, USNM 78361; c, *Stenisis humilis* (Deichmann), n. gen., USNM 57287; d, *Caribisis simplex,* n. gen., n. sp., holotype colony USNM 57290. All scales = 1 cm; that at top applies to a and b.

Feb 1968; branch (of a larger colony?), now broken in two pieces; alcohol; holotype, USNM 78361.

Diagnosis.—*Echinisis* with branching planar, irregularly pinnate or lateral, without anastomoses. Internodes unusually long, forming tapering branches without nodes. Verrucae with sclerites of distalmost 2 or 3 transverse rows prolonged into a stout, echinulate, often 3-lobed projection.

Description.—Though the general growth-form is unknown because the colony is not

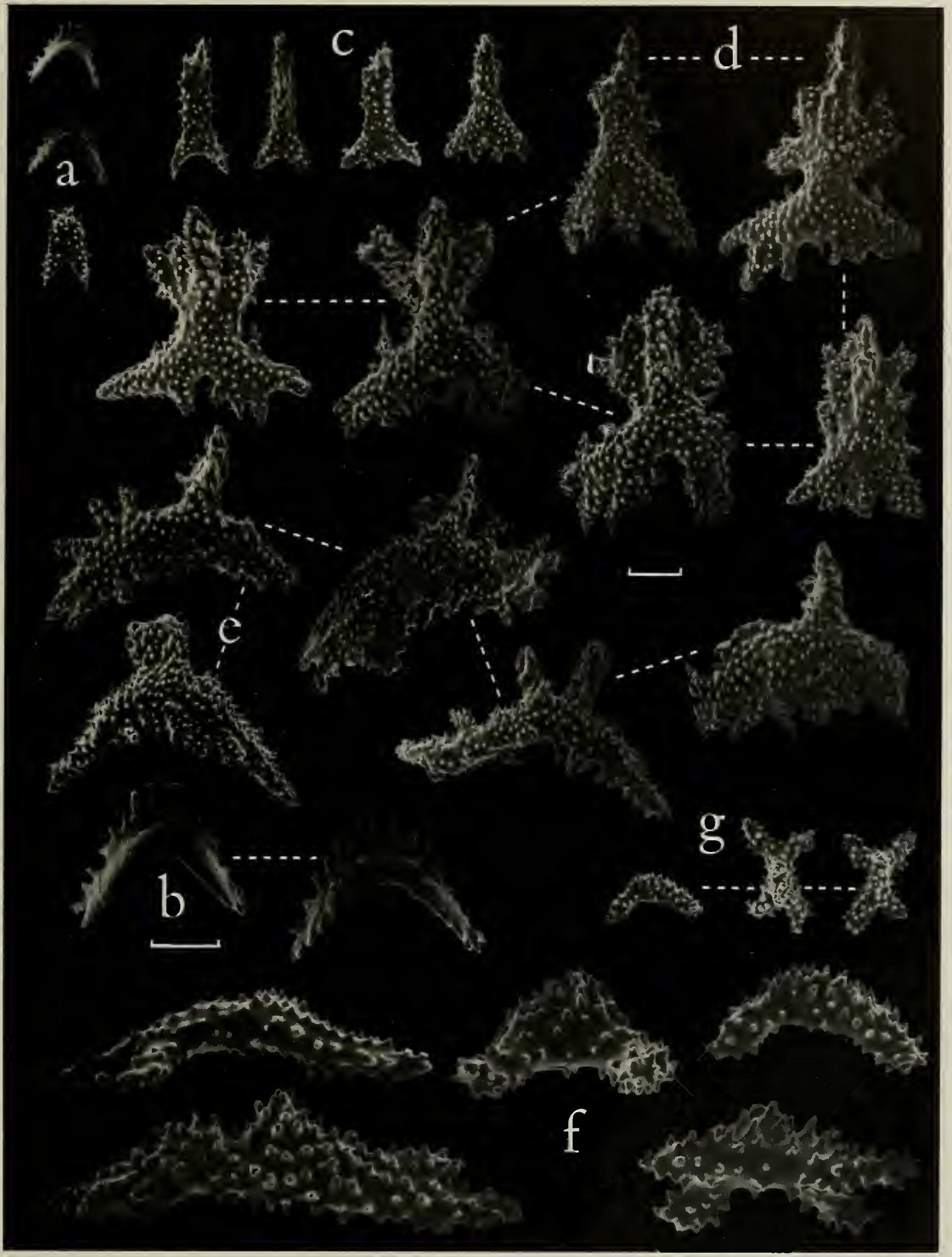


Fig. 10. *Echinisis eltanin,* n. sp., sclerites: a, b, From rachis of tentacles; c, From base of tentacle; d, Prickly thorn-stars from distal part of polyp; e, Prickly thornscales from proximal part of polyp; f, g, From coenenchyme. Scale bar at b = 0.05 mm applies to b only; bar between d and e = 0.1 mm, applies to all others.

complete, the specimen is in one plane (Fig. 9b) and suggests that the complete colony probably was planar. Long, stout branches curve toward the top of the colony. Branches occur laterally, mainly on one side of the colony. Terminal branchlets taper to a point, and are unbranched.

The axis is solid, with unusually long,

branched calcareous white internodes (3.5 cm high) tapering to the tips of the branches. Slight ribbing is visible along the entire internode, but the surface of the axis is quite smooth. The single horny node present in this specimen measures 1 mm in diameter, 0.5 mm in length.

The polyps (Fig. 7b) are prominent, cylindrical, non-retractile, perpendicular to the axis, when contracted forming verrucae that measure 1 mm in height, 0.6 mm in diameter. They are alternate, at intervals of about 0.75 mm, occurring only on one colonial face. The 8 triangular scales form a distinct operculum only when the tentacles are completely infolded.

In the polyps, the tentacles have elongated triradiate scales (Fig. 10c) proximally, measuring up to 0.2 mm, and sharply curved scales distally, the concave margins of which are smooth, while the convex margins are prominently serrated. These measure up to 0.2 mm in length. The body sclerites of the polyps include thorn-scales (Fig. 10d) measuring 0.35 mm in height, 0.5 mm in width, placed around the base of the tentacles in circular rows. In the body wall below this, the transversal thorn scales (Fig. 10e) become more complex, with their basic crescent shape becoming more apparent, finally assuming the shape of curved spindles in the coenenchyme at the base of the polyp.

The coenenchyme contains a thin layer of pale yellow sclerites (Fig. 10f), and appears bumpy owing to the presence of short spindles and 4-rayed bodies with a prominent blunt projection, and longer, more or less bent spindles measuring up to 0.4 mm in length, covered with conical spines, also often with a median hump or blunt projection, serrated along the edges, and 4-armed sclerites measuring 0.25 mm in length, also with blunt projections and serrated edges.

The colony in alcohol is pale yellow in color.

Etymology.—Named after USNS *Eltanin,* which operated in Antarctic waters under the U.S. Antarctic Research Program between July 1962 and December 1972.

Remarks.—The planar branching of the present material indicates that the colony could hardly have been in the bottle-brush shape of the previously described species of *Echinisis.* Assignment of this new species to that genus is made on the basis of the spinous development of the verrucal sclerites.

Echinisis vema, new species
Figs. 7c, 9a, 11

Material examined.—South Atlantic Ocean, Falkland Plateau: 54°44'S, 55°39'W, 1814–1919 m, R/V *Vema* sta 17-61, 11 May 1961; four branches (of a larger colony?). Syntypic branches, USNM 78362. Dry.

Diagnosis.—Irregularly branched *Echinisis* with repeatedly branched internodes infrequently interrupted by horny nodes; distal scales of verrucae prolonged into multiple serrated spikes.

Description.—The overall growth form is unknown because the colony is not complete. The specimen consists of 4 fragments irregularly branched, not planar and neither pinnate nor dichotomous (Fig. 9a). The axis consists of calcareous internodal material showing evidence of only 2 nodal articulations; examination by strong transmitted illumination fails to reveal nodes overgrown by internodal substance. The internodes are repeatedly branched, tapered toward the twig tips where longitudinal grooving becomes evident; elsewhere the surface is macroscopically smooth.

The contracted polyps (Fig. 7c) form short, cylindrical verrucae attaining about 1.75 mm in diameter; the tallest are about 2.5 mm tall, but most are less and some are only 1 mm tall. The body of the polyps is covered proximally by transversely arranged, irregularly lobed plates up to 0.7 mm long, curved in conformity with the body contours (Fig. 11f). The sclerites surrounding the oral end of the verrucae are basically triradiate scales about 0.7–0.8 mm in length, but with elaborately lobed margins. Those of the distalmost 2 or 3 transverse rows are prolonged as a strongly ser-

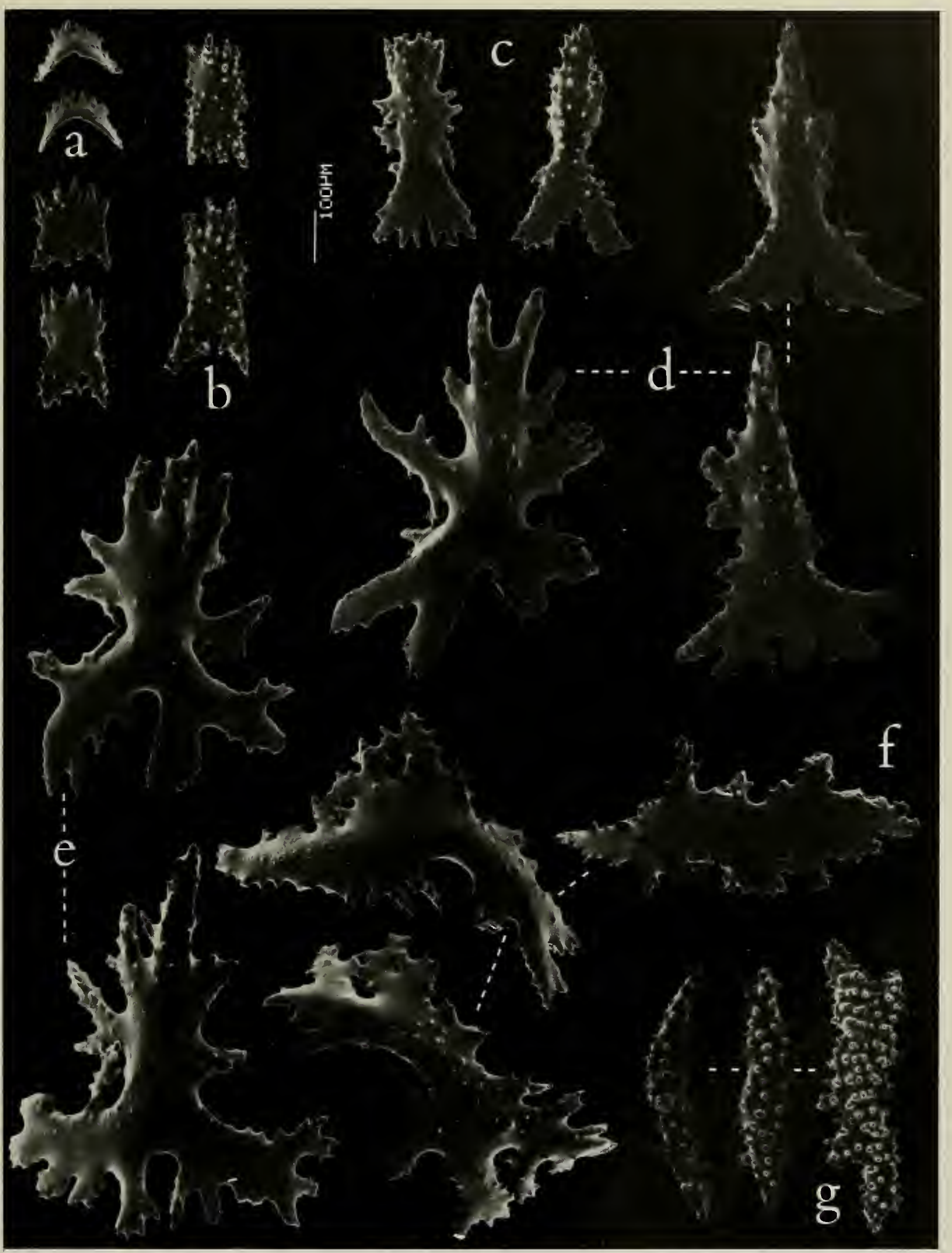


Fig. 11. *Echinisis vema,* n. sp., sclerites: a, b, From tentacles; c, From base of tentacle; d, Opercular scales from beneath tentacles; e, Thorn-stars from distal part of polyp; f, Lobate scales from proximal part of polyp; g, From coenenchyme. Scale applies to all figures.

rated spike; those of the sclerites immediately surrounding the tentacle bases may have on one or both sides one or more low, serrated lobes (Fig. 11d). In the sclerites of the lower transverse rows the lateral lobes of the central spike become prolonged as accessory spikes (Fig. 11e). The scales of the tentacles (Fig. 11a) progressively diminish in size distad, changing in shape from roughly triradiate scales at their bases, which fold over the oral region as an "operculum" (Fig. 11c), to curved, crescentic scales transversely placed along the distal part of the tentacle rachis (Fig. 11a). The coenenchyme contains a thin layer of irregularly oriented flattened spindles 0.5–0.6 mm long, ornamented with prominent tubercles (Fig. 11g).

The colony in dried condition is white; the sclerites are colorless, translucent.

Etymology.—Named after R/V *Vema* of Lamont Geophysical Observatory.

Remarks.—While adequate to demonstrate the distinctness of this species, the material is insufficient to permit conjecture about the overall branching of the colony. The irregular, crooked branchlets do not indicate the bottle-brush form assumed by *Echinisis spicata* and *E. armata,* so assignment to *Echinisis* is made on the basis of the spinous development of the distal sclerites of the verrucae.

Echinisis persephone, new species
Figs. 7d, 12, 13

Material examined.—Southwest Pacific Basin: 42°01′ to 41°57′S, 130°02′ to 130°01′W, 4831–4851 m, USNS *Eltanin* sta 1775, 14 Aug 1966; many fragments, alcohol, USNM 78363, syntypic branchlets.

Diagnosis.—*Echinisis* of unknown colonial form. Distal part of verrucae surrounded by 3 whorls of thornscales with a claw-like spine projecting obliquely from a divaricate or flattened lobate base; proximal part encircled by transverse, curved, flattened spindles sculptured by scattered conical projections. Coenenchyme with small, irregular spindles, many developing an outwardly directed hump.

Description.—The specimen is broken into many fragments, none longer than about 1.5 cm, some bifurcated or producing 1 or 2 short branchlets (Fig. 12a); the calcareous axis shows no trace of horny nodes among the numerous fragments, hence seems to consist solely of internodal material devoid of longitudinal grooves. The polyps form prominent cylindrical verrucae about 1 mm tall and 0.5 mm in diameter when fully developed (Fig. 7d), placed uniserially along the branchlets, mostly 1–2 mm apart but occasionally a little more or less. The distal part of the verrucae is surrounded by 3 (sometimes 2) whorls of thornscales with an obliquely projecting claw-like, serrated spike; the base of the verrucae is encircled by transversely placed, curved, rather flattened spindles (Figs. 7d, 12b); the tentacles of most polyps are loosely folded over the oral region. The coenenchyme has a pebbly appearance (Fig. 7d) resulting from a single layer of short spindles mostly with a prominent hump.

The verrucal thornscales, aligned in 8 vertical rows, are composed of a claw-like serrated spike projecting obliquely from a bifurcated or lobed, flattened base (Fig. 13d); in many cases the spike is apically enlarged and furnished with several strong diverging thorns (Fig. 13e). The spike is 0.3–0.4 mm long and the base 0.3–0.45 in width. Similar thornscales of smaller size (Fig. 13c) are present on the bases of the tentacles and are capable of folding over the inturned tentacles; distally on the tentacles they give way to transversely placed narrow scales curved to fit the contour of the rachis; these have a smooth concave margin and a convex margin with tall thorns (Fig. 13a, b) that project along the backs of the tentacles. The largest measure about 0.2–0.25 mm, decreasing in size distad along the tentacle. The curved spindles surrounding the base of the polyps are about 0.45 mm long, those merging with the coenenchyme as much as 0.7 mm and not so strongly curved. The coenenchymal sclerites (Fig. 13g) include irregular spindles mostly with a strongly humped projecting surface, sometimes reduced to a roughly hemispherical thorny body, sometimes distinctly fusiform and with or without a thorny projecting process. The stubby, humped bodies are 0.2–0.3 mm long, the narrower spindles up to about 0.5 mm.

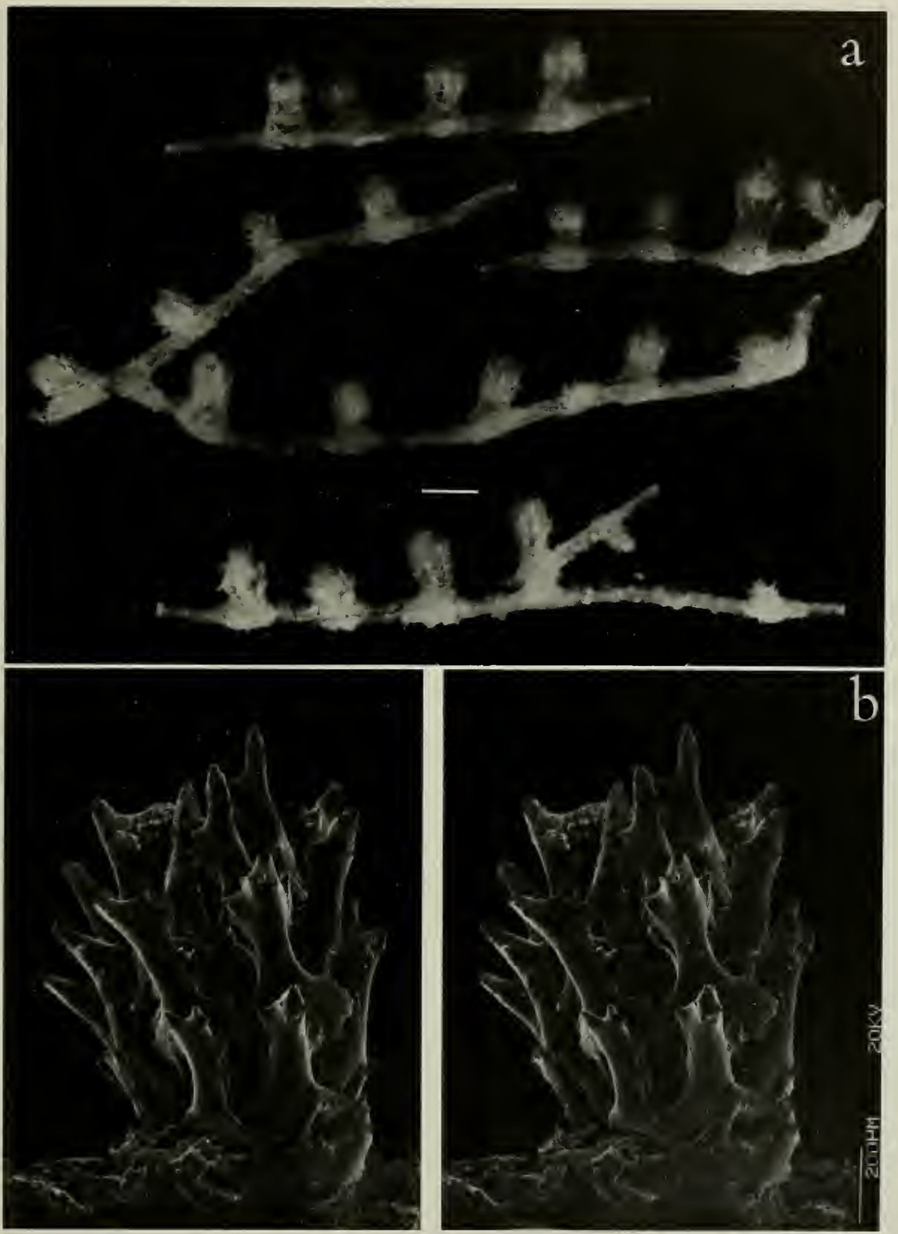


Fig. 12. *Echinisis persephone,* n. sp.: a, Broken branchlets; b, Profile of contracted polyp (stereoscopic view). Scale at a = 1 mm; that at b = 0.2 mm.

The axis is not longitudinally grooved but has faint short surficial striations (Fig. 13h); desmocyte pits are absent except near the extreme tips of the branchlets.

Comparisons.—In general shape the verrucal thornscales of *Echinisis persephone* are similar to those of both *Echinisis vema* and *E. eltanin,* the spike often having lateral lobes or accessory projections. At first sight, they are conspicuously different from the thornscales of *Echinisis spicata* and might be considered indicative of a distinct genus. However, it is by no means rare for the thornscales of *E. spicata* to be apically lobed,

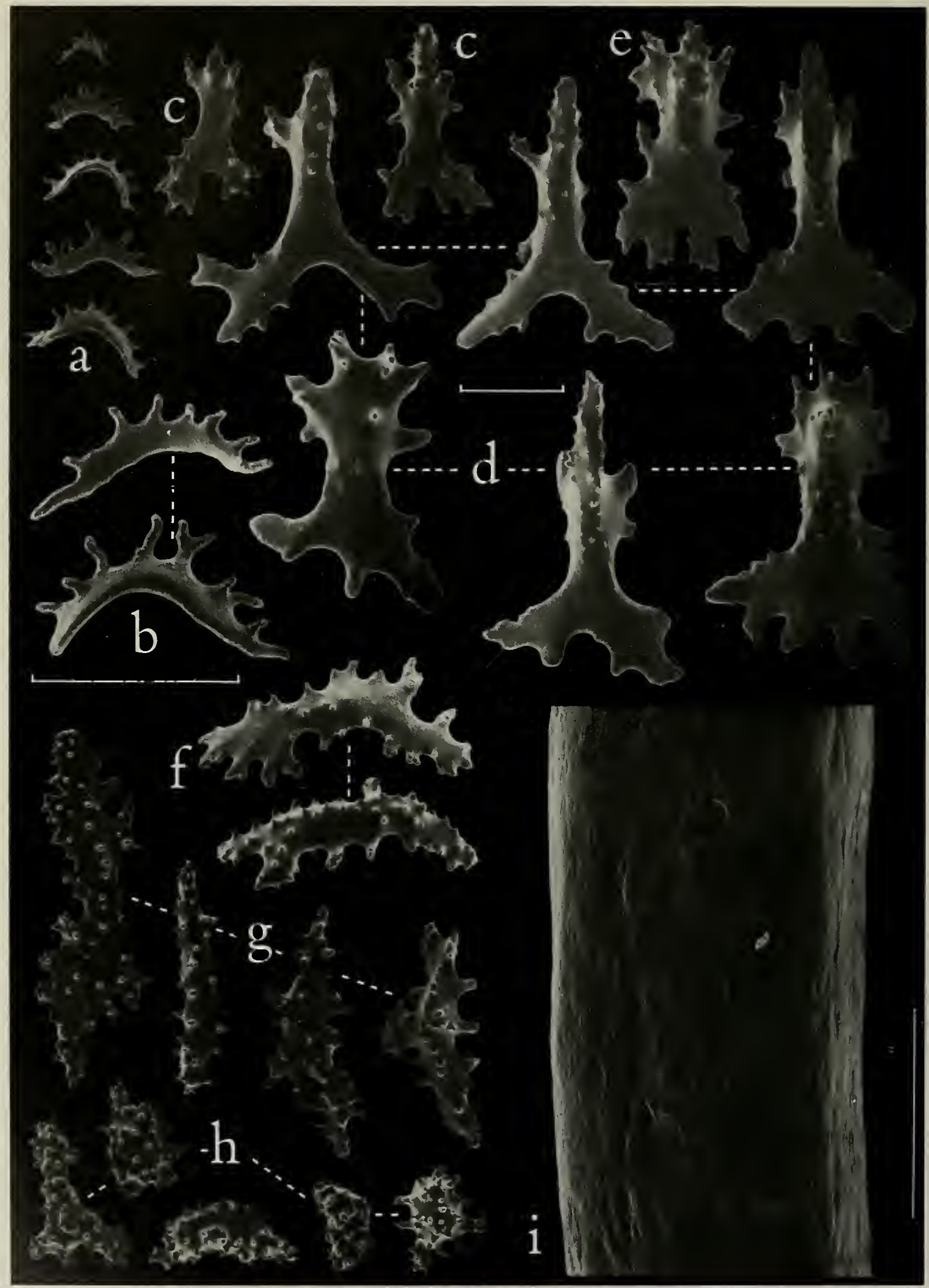


Fig. 13. *Echinisis persephone,* n. sp., sclerites: a, b, From rachis of tentacles; c, From base of tentacles; d, e, Thornscales form verrucal wall; f, Transverse scales from verrucal base; g, Coenenchymal scales transitional to verrucae; h, From coenenchyme; i, Part of axial internode. Bar scales at b and i apply to b and i only; scale at d applies to all others. All bars = 0.2 mm.

and the spike may have distinct, even strong, lateral spikes. Therefore, until more material is available to provide information about colonial characters, it seems preferable to treat all of the *Primnoisis*-like forms with verrucal thornscales or thornstars as a single genus *Echinisis.*

Etymology.—Persephone, mythological character, daughter of Zeus, wife of Hades and Queen of the lower world.

Remarks.—As numbers of sponge spicules were found on these fragments, it is possible that the colony was associated with a sponge, as was observed in *Primnoisis delicatula* by Hickson (1907:5). If the gorgonian was embedded in, or largely covered by, sponge tissue, this could account for the fragmentary condition of the sample obtained.

Sclerisis Studer, 1879

Sclerisis Studer, 1879:661.—Kükenthal, 1915:124.
Primnoisis.—Kükenthal, 1924:432 (part).

Since our reestablishment of this genus and description of *Sclerisis macquariana* were written (Bayer and Stefani 1987), we have located another specimen from Antarctic waters which provides additional information about this little-known genus. We interpret the specimen as conforming with all the salient characters mentioned by Studer (1879) in his brief original description of the genus *Sclerisis* and its sole species *Sclerisis pulchella.*

Sclerisis pulchella Studer, 1879
Figs. 13, 14c, 15

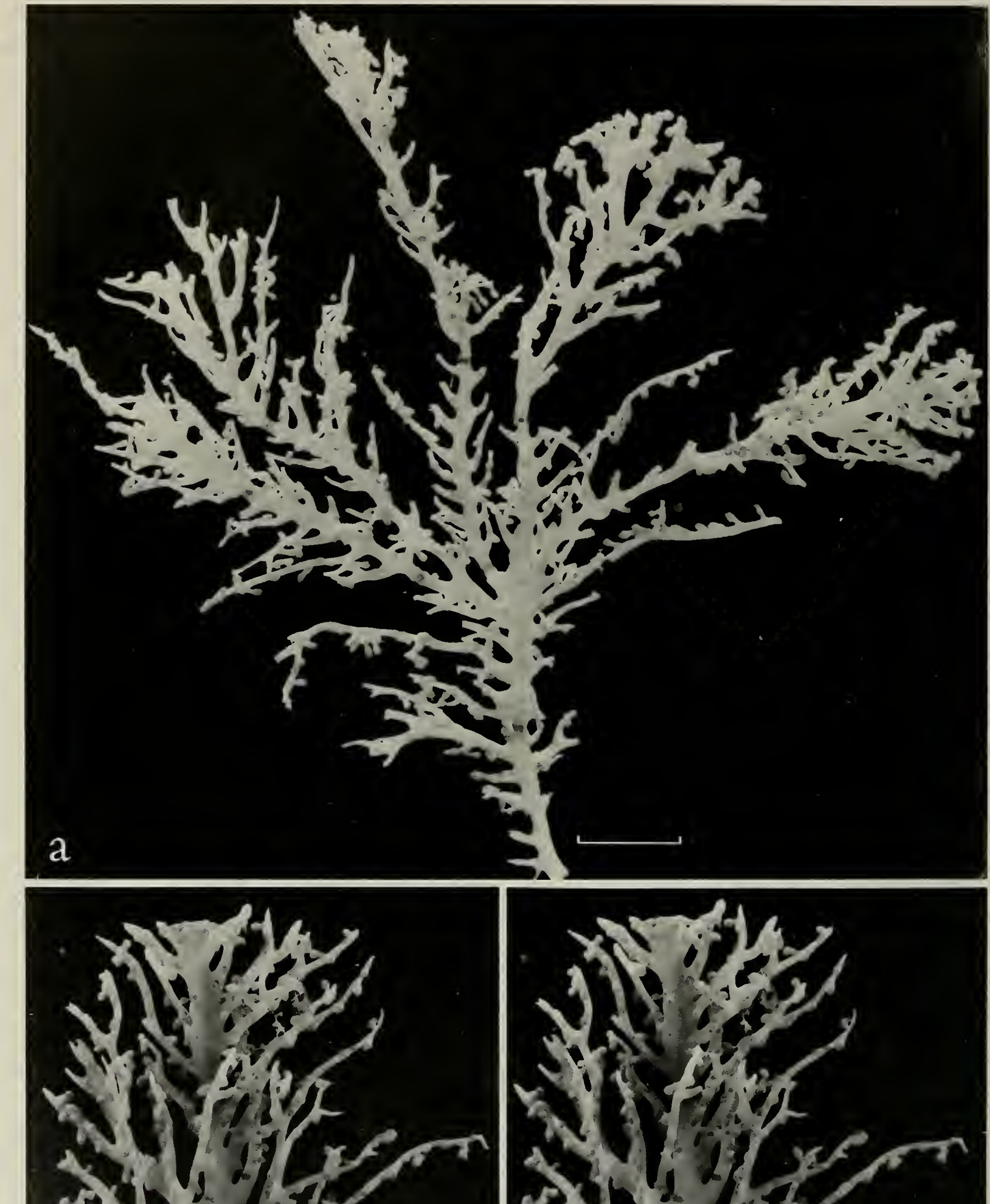
Sclerisis pulchella Studer, 1879:662, pl. 5, fig. 33 a, b, c.

Material examined.—South Atlantic Ocean: 61°04′S to 61°07′S, 39°55′W to 39°42′W, 2355–2897 m, USARP, USS *Eltanin* sta 1545, 11 Feb 1966; three large branches, possibly of a single colony; alcohol. USNM 78364.

Apart from being a much larger colony in better state of preservation (Fig. 13), the present specimen agrees with all important points in Studer's description: "Aufrecht verzweigt, die Kalkglieder sehr lang, fein gestreift, die hornigen Glieder kurz, scheibenförmig. Die Äste entspringen von den kalkigen Gliedern. Die Rinde, sehr dünn, entbehrt der Spicula. Die Kelche sind glockenförmig, mit eingeschnürter Basis und bedeckt mit grossen gebogenen, dornigen Spindeln, welche in Sklerenchym dicht aneinander liegen und sich mannigfach kreuzen und um die Kelchmündung, senkrecht stehend, einen achtklappigen Deckel bilden." (1879:661.) "Der Stamm ist gerade, und besteht aus einem kurzen, scheibenförmigen Hornglied und einem 35 mm. langen Kalkgliede. Das Kalkglied ist eigenthümlich missgestaltet durch die Anwesenheit einer Annelide, welche an dem Stamm lebt. Derselbe ist lamellenartig abgeplattet, die Ränder zusammengebogen, so dass eine tiefe Hohlrinne entsteht, in welcher der Wurm, eine Eunicide, lebt . . . Vom Stamme entspringen nach drei Seiten feine, dünne Zweige von höchstens 1 mm. Dicke an der Basis und bis 10 mm. Länge aus abwechselnd kurzen hornigen und langen kalkigen Gliedern. Die Kalkglieder sind fein längsgestreift. Die glockenförmigen Kelche sitzen vereinzelt an den dünnen Ästchen. Die Spicula, welche die Kelchmündung schliessen, sind lange, dornige, an der Basis am meisten verbreiterte Schuppen. Farbe weiss." (1879:662.)

In our specimen, the polyps are campanulate and basally constricted, directed downward, covered with large, bent, thorny spindles, which lie close together and variously cross one another, placed vertically at the distal end of the calyces to form an 8-lobed "operculum" (Fig. 15c).

The stem is straight and consists of short, discoidal horny nodes and long calcareous internodes that are about 35 mm long. The internodes of the principal branches are characteristically expanded to form con-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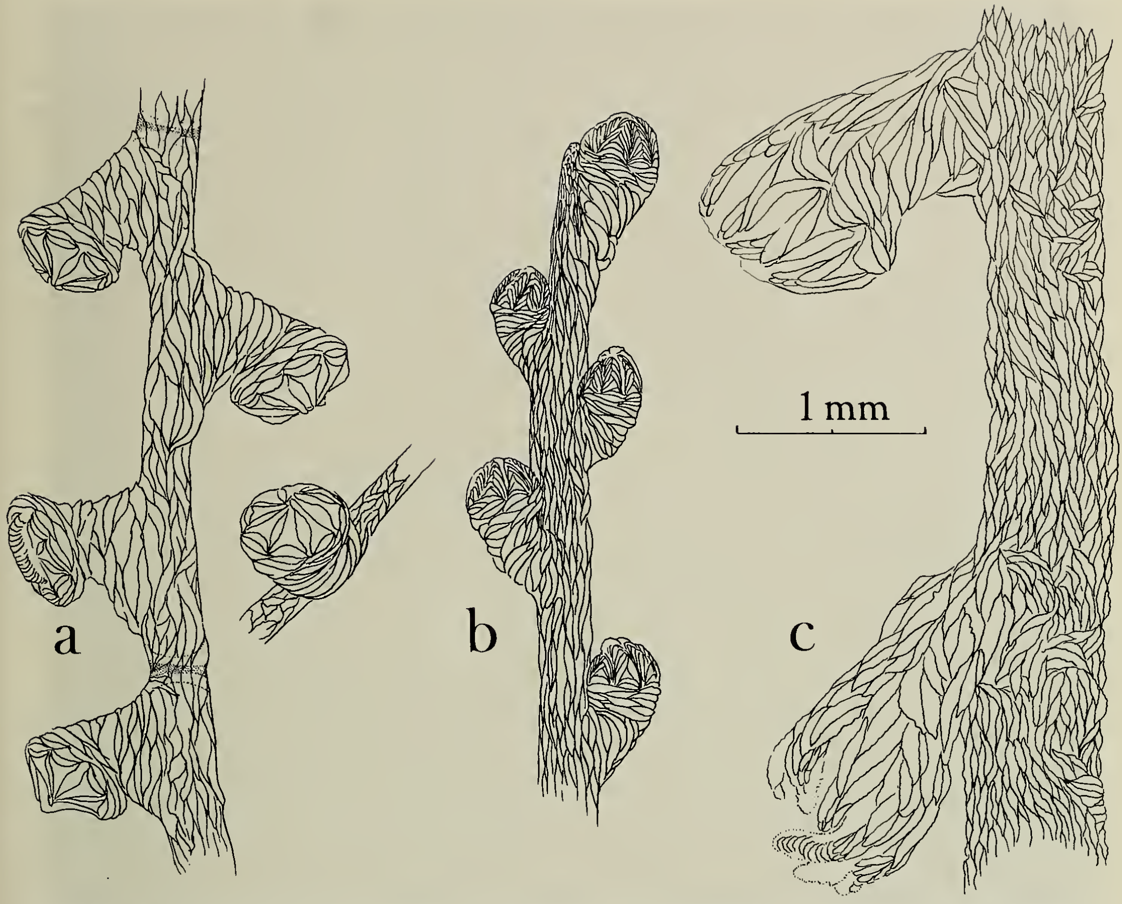

Fig. 15. a, *Chathamisis ramosa* (Hickson); b, *Stenisis humilis* (Deichmann); c, *Sclerisis pulchella* Studer.

cave, gutterlike structures from the upturned edges of which the lateral branchlets arise (Fig. 14b).

The slender lateral twigs, which leave one face of the colony free, contain horny nodes and calcareous internodes as described by Studer, but the nodes are infrequent and the internodes long, commonly branching repeatedly without intervention of horny nodes, so they are not composed of short nodes "alternating" with long internodes, but rather of long, branching calcareous internodes infrequently interrupted by horny nodes. Here it can be mentioned that Studer's figure (1879:pl. 5, fig. 33) illustrates rather few nodes in the branchlets, but it is unclear whether or not the internodes branch without intervening nodes.

The principal discrepancy between Studer's description and the specimen before us is Studer's statement that the spicules that close the calicular aperture are long, thorny scales mostly expanded toward the base. Strictly interpreted, this condition applies more closely to *Sclerisis macquariana* Bayer and Stefani than to the specimen at hand. However, the verrucal sclerites of this specimen (Fig. 16d) definitely are long,

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Fig. 14. *Sclerisis pulchella* Studer, USNM 78364: a, Broken colony; b, Branch (stereoscopic view). Scale bars = 1 cm.

thorny, distinctly flattened and commonly expanded at one end. Studer's drawing of the polyps of *pulchella* (1879:pl. 5, fig. 33b) does not suggest the strong projecting spines of *S. macquariana,* as it certainly would have had the spines been as conspicuous as in that species. Moreover, Studer's definition of "scales" is not clear, but the flattened thorny spindles of the present specimen could very easily qualify. Transversely arranged crescentic scales with serrated convex margin (Fig. 16a) extend along the rachis of the tentacles, the proximal ones becoming more or less asymmetrical (Fig. 16b) and obliquely placed. The coenenchymal sclerites are stubby rods covered with blunt projections (Fig. 16e).

Remarks.—Two pieces of denuded axis (USNM 78365) from *Eltanin* sta 1991 (south of New Zealand: 54°39'S to 54°44'S, 170°22'E to 170°25'E, in 1862–1940 m, 2 Jan 1968) are strikingly similar in growth form to the present specimen attributed to *Sclerisis pulchella.* A small piece of branch and two intact but dissociated polyps from the same haul (USNM 78366) are distinctly different from those of *S. pulchella* as here described. On the strength of the possibility that these polyps are conspecific with the axial fragments, we do not assign the latter to *S. pulchella.* If the polyps and axial fragments are not conspecific, the possibility remains that the latter are *S. pulchella,* so we here record that the largest, expanded, gutterlike internode, broken at both ends, is 65 mm long and 5 mm wide; from both edges it produces lateral branchlets, some of which are further branched, all without horny nodes. It is highly probable that the intact colony would have been closely similar in growth form to the colony of *pulchella* here reported.

It must be mentioned that the type locality of *Sclerisis pulchella* is northeast of New Zealand in 597 fathoms (1092 m), whereas the specimen from *Eltanin* sta 1545 is from the South Atlantic. Therefore, there is a possibility that the denuded axis from sta 1991 south of New Zealand is the real *pulchella,* regardless of whether it is or is not conspecific with the South Atlantic specimen. Studer's type specimen must be examined to resolve the question.

Chathamisis Grant, 1976

Chathamisis Grant, 1976:9, 10, 43.—Bayer, 1981:941 (in key).

Type species.—*Chathamisis bayeri* Grant, 1976: by original designation.

Diagnosis.—See Grant 1976:43.

Chathamisis ramosa (Hickson, 1904), new combination

Figs. 1c, 15a, 17

Ceratoisis ramosa Hickson, 1904:224, pl. 7, figs. 3, 4; pl. 8, fig. 12.—Thomson, 1911: 877, pl. 43, fig. 1.

Primnoisis ramosa.—Kükenthal, 1919:616; 1924:436.—Deichmann, 1936:251.

Not *Primnoisis ramosa* Thomson and Ritchie, 1906:851, pl. 1, fig. 2.

Material examined.—Vicinity of Durban, South Africa: 30°02'45"S, 31°03'25"E, 112 fathoms, 30 Jun 1930; one colony without holdfast, in alcohol, USNM 43071.

Description.—The original description (Hickson 1904) requires some amplification. Although the colony (Fig. 1c) is profusely bushy, the smaller branches strongly tend to ramify in one plane; some scattered anastomosis occurs. The calcareous internodes have several shallow longitudinal furrows separated by low ridges; the slender distal internodes are triangular or quadrangular in cross section, having 3 or 4 rounded ridges separating the shallow furrows that form the sides.

Many of the polyps have the squat, chalicelike aspect shown in Hickson's drawing (1904: pl. 8, fig. 12); for the most part, the polyps are strongly curved downward, away from the tips of the branches (Fig. 15a). The 8 large scales of the tentacle bases form a low conical operculum over the infolded tentacles, often lying almost flat. The tri-

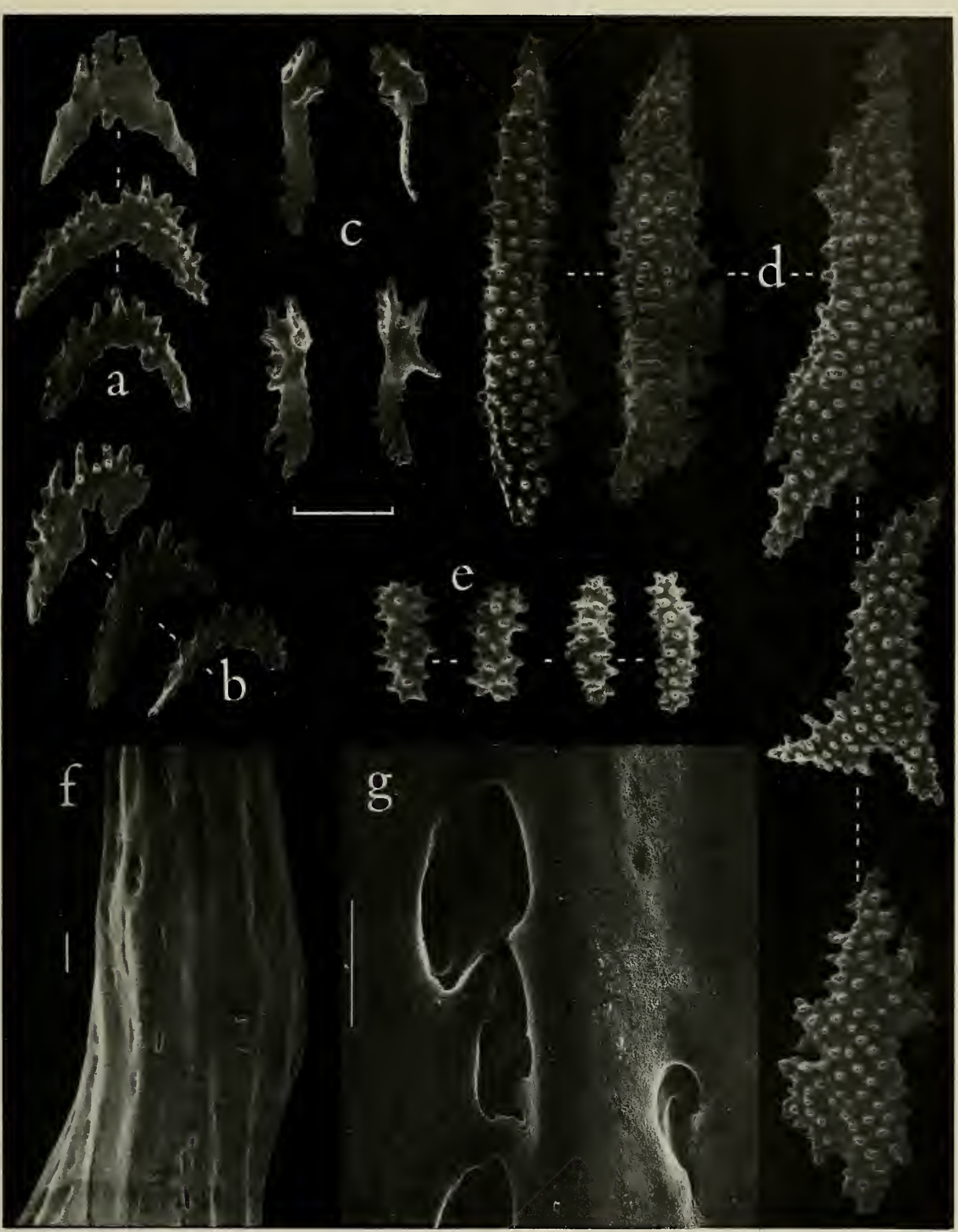

Fig. 16. *Sclerisis pulchella* Studer, a–e, sclerites: a, b, From rachis of tentacles; c, From pinnules; d, From verrucal walls; e, From coenenchyme; f, g, Part of axial internode. Upper scale = 0.1 mm, applies to all sclerites; scale at f = 1 mm; scale at g = 0.05 mm.

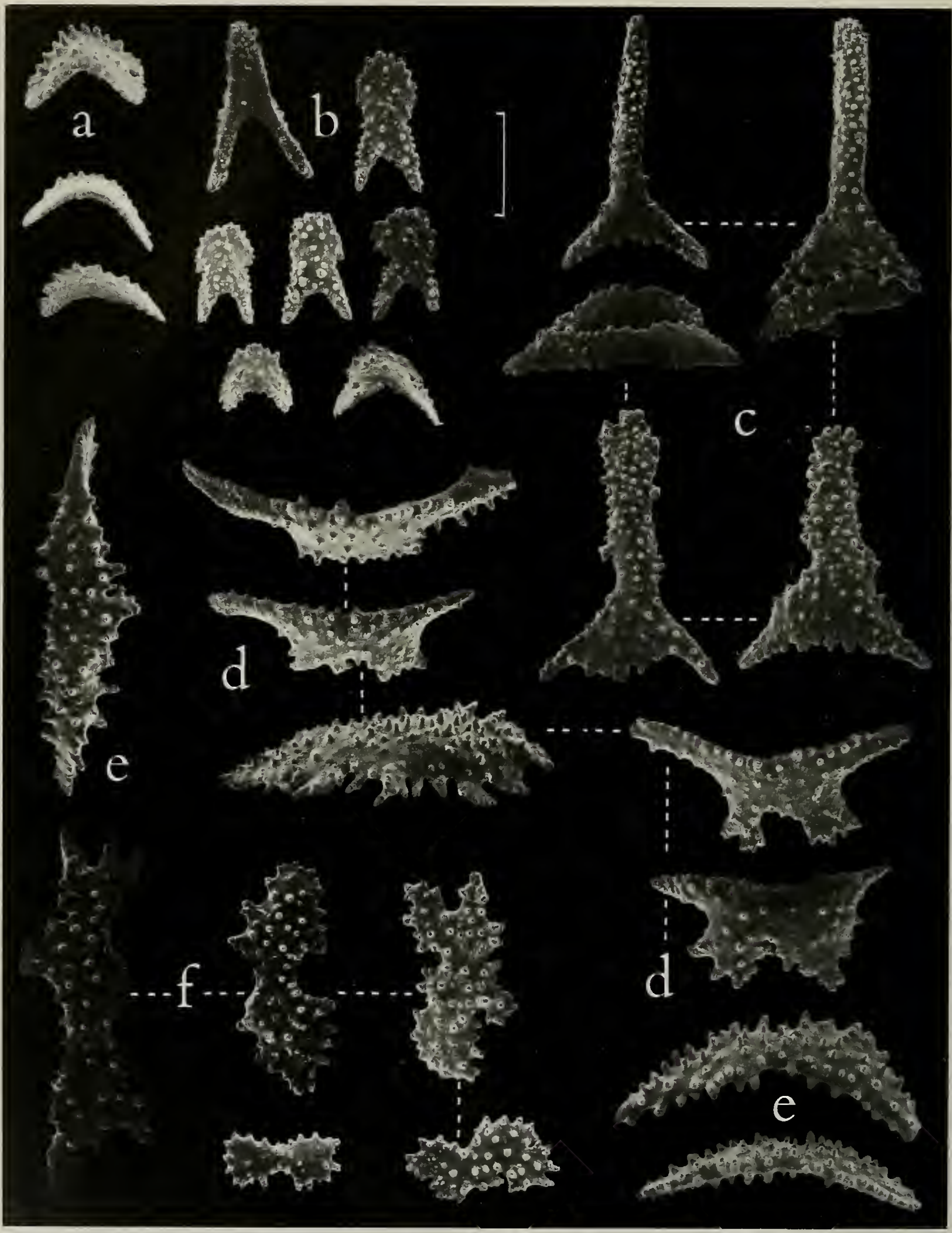

Fig. 17. *Chathamisis ramosa* (Hickson), a–f, sclerites: a, From rachis of tentacles; b, From base of tentacles; c, From opercular sectors; d, e, From verrucal wall; f, From coenenchyme. 0.1 mm scale bar at c applies to all figures.

radiate opercular scales typically rest upon a transverse lunate scale that occupies the basal concavity (Fig. 17c); non-fatal breakage and repair of the scales in one or more octant may result in an opercular segment with an irregular number of scales, and occasionally a narrow accessory sclerite lies along one or both sides of the apical spike of the opercular scales, but the opercular valves do not typically consist of several scales as depicted in Hickson's stylized drawing. The tentacles, which occasionally are preserved outside the opercular scales, have a series of small scales transversely placed along the back of the rachis (Fig. 17a). The more proximally placed of these have a bifurcated base that partially surrounds the tentacular rachis, resulting in forms intermediate between opercular and distal tentacular scales (Fig. 17b). A similar condition occurs in *Echinisis spicata* (see Fig. 8c). The body sclerites are transversely placed crescentic plates about 0.3 mm long, some with 2 broad diverging lobes on the proximal edge, others with several narrow lobes (Fig. 17d). The coenenchymal sclerites are elongated scales up to 0.35 mm long, the smaller individuals often with a median constriction (Fig. 17f).

Distribution.—South Africa.

Remarks.—There is no question but that the eight triradiate scales of the tentacle bases form an operculum in the sense of Grant (1976). However, the transverse scales immediately beneath each opercular scale tend to fold inward farther and farther with stronger degrees of contraction, the end result of which is a condition not unlike that seen in some species of *Mopsea*; the chief difference is that the uppermost scale is the largest and forms an opercular scale, whereas in *Mopsea* the scales become progressively smaller distad on the tentacles.

Stenisis, new genus

Primnoisis (part).—Deichmann, 1936:250 (not Studer [and Wright], 1887).

Type species.—*Primnoisis humilis* Deichmann, 1936.

Diagnosis.—Small, planar colonies branched from the internodes in a distantly pinnate manner, internodes without longitudinal grooves and ribs, covered with low, pointed thorns; polyps biserial, forming upturned verrucae weakly recurved toward axis, not retractile, tentacles folding over mouth; verrucal sclerites narrow, curved, spindlelike plates transversely arranged below tentacles.

Etymology.—Greek *στένοσ* = narrow + Isis, Egyptian goddess of the earth and the moon, whose name was applied to jointed octocorals by Linnaeus (1758).

Remarks.—The new species described by Deichmann (1936) as *Primnoisis humilis* was described and illustrated by Verrill in the unpublished manuscript on the *Blake* collection later rewritten and published by Miss Deichmann. Unfortunately, Verrill's original manuscript is no longer extant, but the surviving plates show that he recognized two species that he placed in a new genus *Stenisis,* one of them the *Primnoisis humilis* of Deichmann. Without access to Verrill's text it is impossible to say how the two species differed, but the illustrations reveal nothing significant. All of the specimens in the present collection can be attributed to one species, identical with Deichmann's *Primnoisis humilis.* The colonies branched in one plane, with biserial polyps armed with very narrow transverse plates of almost spindle-like form, are characters so at variance with *Primnoisis* that a separate genus is required, as recognized by Verrill a century ago. For this genus we here use the name *Stenisis* originally proposed for it by Verrill.

Stenisis humilis (Deichmann, 1936)

Figs. 9c, 15b, 18

Primnoisis humilis Deichmann, 1936:251.

Material examined.—Northwest Providence Channel, Bahamas: 26°32′N, 78°55′W, 183–549 m, R/V *Gerda*, sta G-493, 3 Feb 1965; one profusely subdivided branch, possibly a complete colony lacking holdfast, USNM 57287.—Yucatan Channel: 20°55′N, 86°28′W, 97–120 fathoms, R/V *Gerda* sta G-889, 10 Sep 1967; two profusely subdivided branches, possibly colonies without holdfasts; one extensively decorticated, USNM 57288.—Yucatan Channel: 21°04′N, 86°19′W, 185–200 fathoms, R/V *Gerda* sta G-898, 10 Sep 1967; ten more or less complete colonies and several broken branches, some partially decorticated and overgrown by epizoans, USNM 57289.

Diagnosis.—As for the genus.

Description.—The present specimens conform in all respects to Deichmann's description of the dried type specimen, but their better condition and greater number permit some minor amplification. The several colonies, some of which are complete (though partly decorticated and overgrown by epizoans), range from 2 to 5 cm in height, branched in a loosely pinnate or lateral manner chiefly in one plane and about as wide as high (Fig. 9c). The colonies are articulated to a discoidal holdfast by a basal horny node 1.5–4.5 mm long but only 0.4–0.5 mm wide. The first internode, which may or may not bear one or two lateral branches, is 3–4 mm long and 0.5–0.6 mm in diameter. The following nodes are 1–1.5 mm long, those of the smaller branches about 0.5 mm, and about 0.25 mm in diameter. In the finest terminal branchlets, the nodes may be only 0.15 mm in diameter and 0.5–0.6 mm long; the internodes vary in length from 0.5 mm to 3 mm or more. The internodes are not longitudinally furrowed but are covered by small, conical spinules (Fig. 18e).

The polyps (Fig. 15b) are 0.7–0.9 mm tall, somewhat larger than reported by Deichmann, but this may be explained by a difference in method of measurement. For the most part they are directed upward, although downward-pointing individuals are not rare. They are covered proximally by transversely and obliquely placed narrow, fusiform plates 0.2–0.25 mm long, sculptured externally by simple, blunt spines (Fig. 18c); these sclerites are more accurately described as curved spindles, flattened and smooth internally, sculptured externally by crowded, blunt spines. The bases of the tentacles are covered by smaller, straight spindles set en chevron (Fig. 18a); small, twisted, claw-like scales (Fig. 18b) occur distally in the tentacles, probably in the pinnules, but their exact position could not be determined.

The coenenchyme contains a layer of spindles (Fig. 18d) similar to those of the polyps but not strongly curved, up to 0.2 mm long.

Remarks.—The planar branching, spindle-like sclerites, and unfurrowed prickly internodes preclude assignment of this species to the genus *Primnoisis.*

The exceptional length of the basal node suggests that conditions of the habitat call for greater flexibility of the axis than would be afforded by the short, disk-like nodes more usual in small isidids.

Deichmann's assertion that this species is closely related to *Primnoisis rigida* Wright and Studer (1889:37) and might be nothing more than a shallow-water form of it is without justification. *Primnoisis rigida* is a densely bushy form that appears to be a true *Primnoisis.*

Australisis, new genus

Type species.—Australisis sarmentosa, n. sp.

Diagnosis.—Bushy isidids branched from the internodes; internodes round in cross-section, tapered, not longitudinally grooved, but covered with low prickles or thorns; polyps on all sides, not retractile but forming prominent cylindrical verrucae; verrucal walls filled with thorny spindles arranged distinctly en chevron in eight longitudinal tracts.

Etymology.—Latin *australis* = southern + *Isis,* in allusion to the geographic range of the type species.

Remarks.—This genus cannot be accommodated in any of the subfamilies as now defined. The polyps are not retractile into the coenenchyme as those of *Isis* are, but form prominent cylindrical verrucae. The

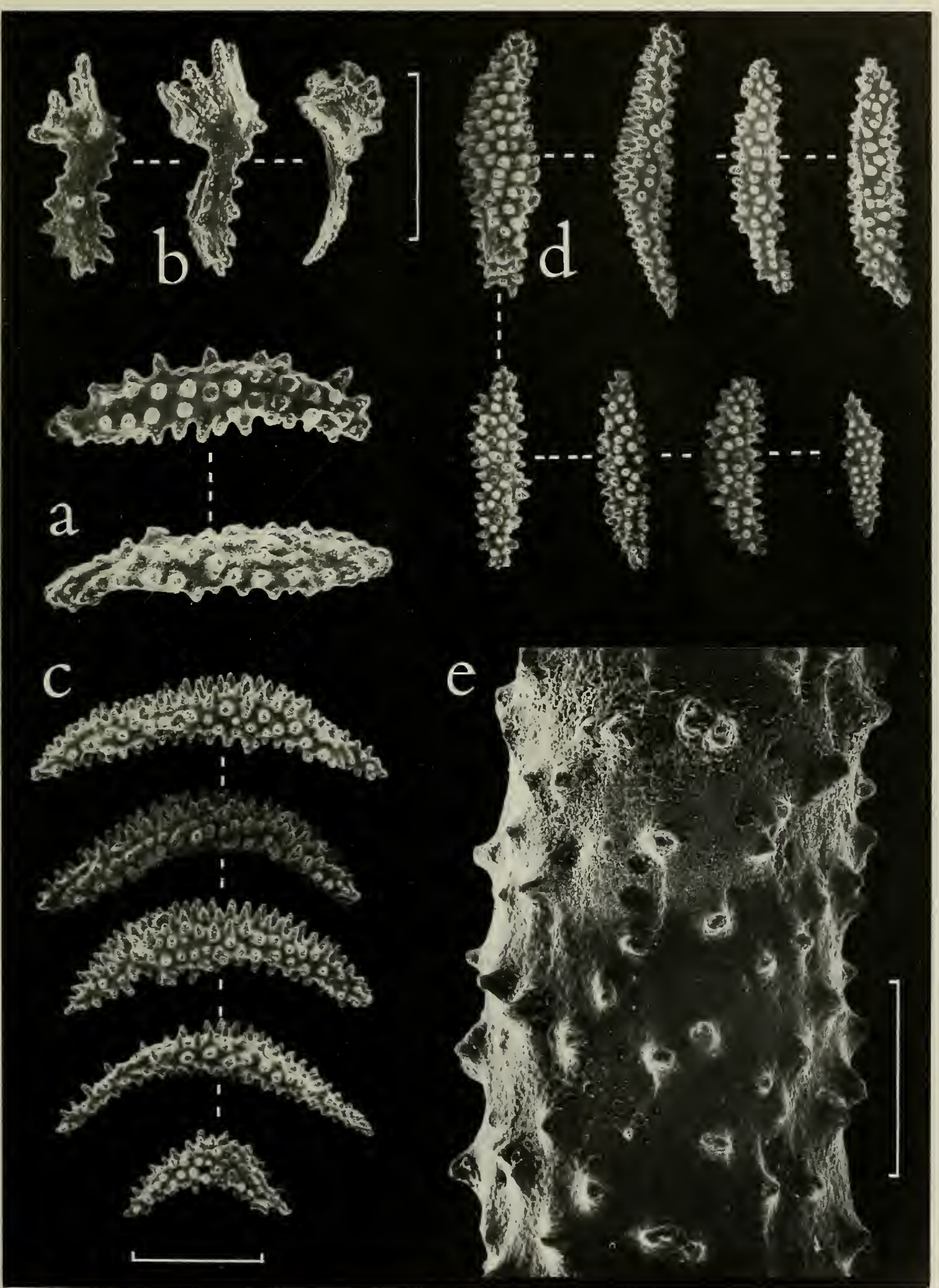

Fig. 18. *Stenisis humilis* (Deichmann), a–d, sclerites: a, From base of tentacles; b, From pinnules; c, From verrucal wall; d, From coenenchyme; e, Part of axial internode. 0.05 mm bar at b applies to a and b; 0.1 mm bar below c applies to c and d; 0.1 mm bar at e applies to e only.

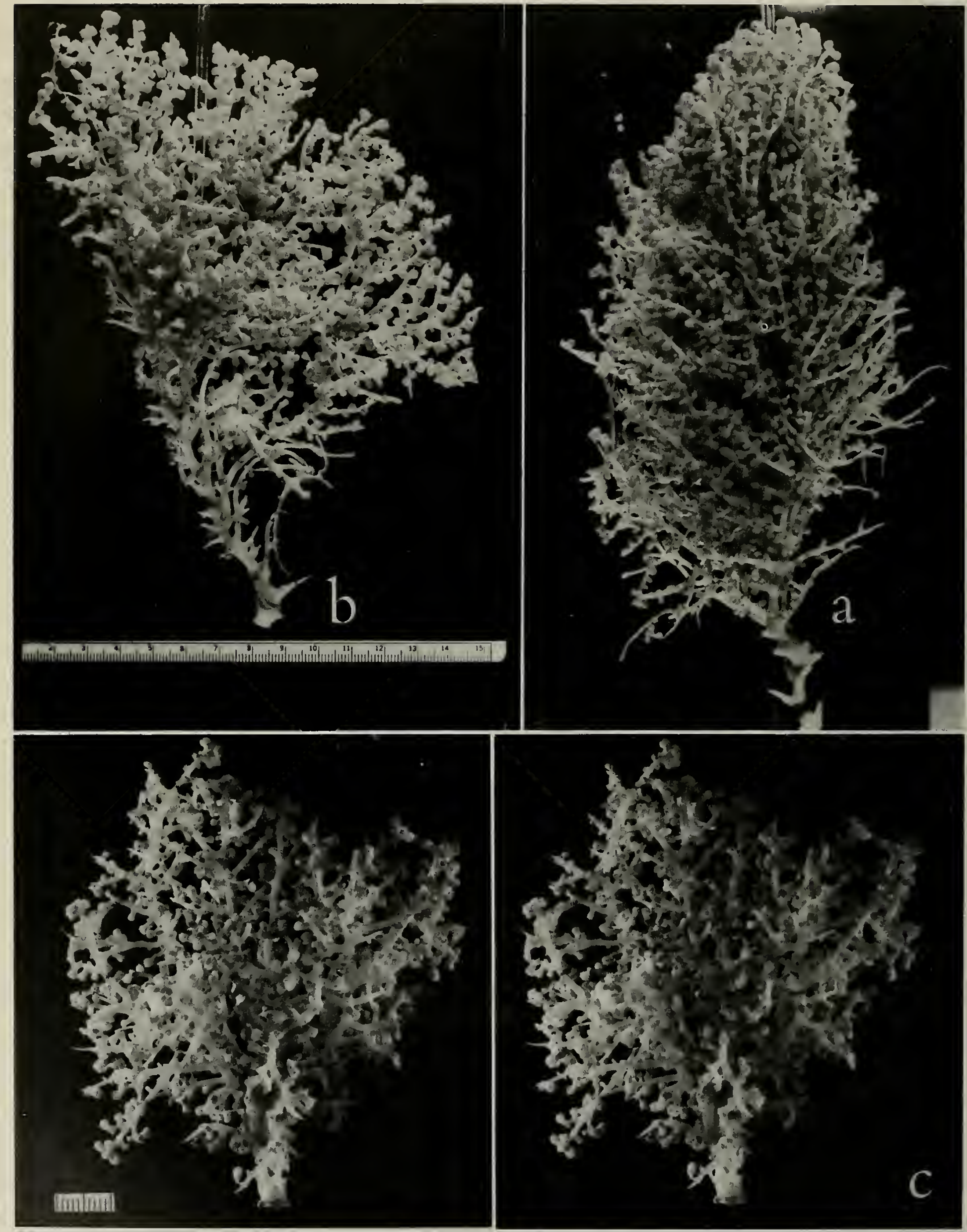

Fig. 19. *Australisis sarmentosa,* n. gen., n. sp.: a, Paratype, USNM 78370; b, Holotype, USNM 78368; c, Paratype, USNM 78371, stereoscopic pair. Scale at b applies to a and b.

verrucal sclerites are distributed without interruption from base to tentacles, so the polyps are not divided into an anthostelar and an anthocodial part as in *Muricellisis,* and therefore lack crown and points. The verrucal sclerites are exclusively spindles arranged conspicuously en chevron.

Australisis sarmentosa, new species
Figs. 19, 20, 21d–i

Material examined.—South Shetland Islands: 61°19′ to 61°21′S, 56°28′ to 56°27′W, 403 m, 5′ Blake Trawl, USNS *Eltanin* sta 992, 13 Mar 1964; fragments, USNM 78367.—Off South Georgia: 54°29′S, 39°22′W, 659–686 m, 5′ Blake Trawl, USNS *Eltanin* sta 1536, 8 Feb 1966; one colony, holotype, USNM 78368; 4+ colonies, paratypes, USNM 78369.—Off South Georgia: 55°00.6′S, 37°42.6′W, 494–501 m, USARP, R/V *Islas Orcadas,* cruise 575, sta 91, 7 Jun 1975; one colony complete except for holdfast, paratype, USNM 78370.—Off South Georgia: 53°27.1′S, 41°39.2′W, 371–424 m, USARP, R/V *Islas Orcadas,* cruise 575, sta 102, 11 Jun 1975; one complete colony and several partly denuded branches, paratypes, USNM 78371.

Diagnosis.—As for the genus.

Fig. 20. *Australisis sarmentosa,* n. gen., n. sp. Part of branchlet with contracted verrucae.

Description.—The colony branches abundantly in all directions from the internodes to form a dense, upright bush (Fig. 19). Most internodes produce 1, often 2 or 3 lateral branches that diverge in various directions but rarely if ever coalescing, even when they come in close proximity; the few internodes that fail to branch are usually terminal or subterminal. The lateral branches arise from the parent internode without a nodal articulation, and the branch may itself branch again before producing a horny node. The internodes are round in cross-section except in the immediate vicinity of branch origins, where some flattening may occur; when branches originate at an angle of 45° or less, the axils may be extensively filled in to produce even greater flattening. The internodes are not longitudinally grooved, but are covered with small, sharp prickles (Fig. 21i), most conspicuous on the more distal internodes, becoming lower and obscure on the larger, proximal internodes. The minute pits marking the position of desmocytes in the axis epithelium are irregularly scattered over the surface (Fig. 21h).

Most of the specimens have been de-

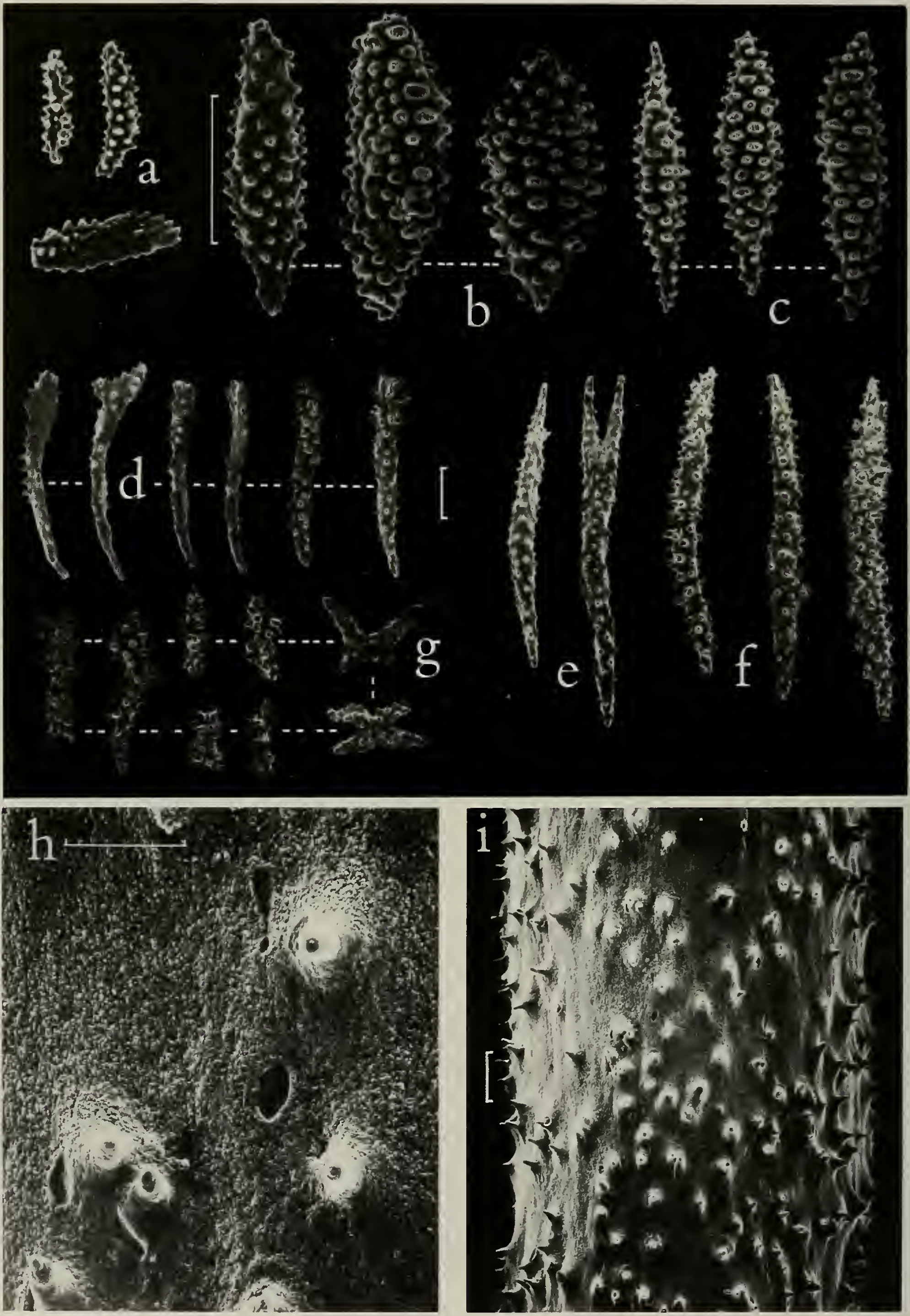

Fig. 21a–c, *Caribisis simplex,* n. gen., n. sp., sclerites: a, From tentacles; b, From verrucal wall; c, From coenenchyme. d–i, *Australisis sarmentosa* n. gen., n. sp., a–g, sclerites: d, From pinnules; e, From base of tentacles; f, From verrucal wall; g, From coenenchyme; h, Surface of axial internode; i, Part of axial internode. Upper scale bar = 0.1 mm, applies to a–c; scale at d = 0.1 mm, applies to d–g; scale at h = 0.05 mm; scale at i = 1 mm.

tached from their holdfast at the basal articulation, but one small colony attached to a pebble, and another to a fragment of dead scleractinian coral, show that the holdfast is a thin calcareous disk from which the colony arises by way of a basal node.

The contracted polyps (Fig. 20) are prominent, cylindrical, and sometimes slightly enlarged distally, 2–3 mm tall depending upon the degree of contraction. They are situated on all sides of the branches, 2–4 mm apart but with a tendency to occur in opposite pairs; often they are more closely placed near twig tips, and twigs commonly end with an opposed pair. The tentacles are folded over the mouth and may be turned inward to a greater or lesser extent.

The sclerites of the body wall are narrow, pointed spindles up to about 0.65 mm long, usually curved or bent, ornamented with low, sharp thorns (Fig. 21f); they are arranged in closely crowded chevrons converging on the bases of the tentacles. The spindles on the base of the tentacles are less sharply sculptured (Fig. 21e) and decrease in size distally, assuming a longitudinal direction; smaller, slender spindles about 0.3 mm long, somewhat twisted and more or less distinctly expanded at one end (Fig. 21d) extend into the pinnules, expanded end outermost. The coenenchyme contains shorter, thorny spindles about 0.45 mm long, whose thorns are somewhat stronger on one side, and rather flattened, irregular forms of smaller size (Fig. 21g).

The colonies are pale tan or dark cream-colored, the nodes light brown and the internodes white.

Etymology.—Latin *sarmentosus* = full of twigs, in allusion to the bushy growth form.

Remarks.—The densely branched, compact growth form, the prominent cylindrical verrucae with sclerites conspicuously en chevron, and the prickly cylindrical internodes without longitudinal fluting of *Australisis sarmentosa* are features unlike those of any isidid heretofore reported. The character of the internodes is shared with *Caribisis simplex* n. gen., n. sp. and *Primnoisis humilis* Deichmann (now reassigned to a new genus *Stenisis*). Although the former is further similar in having only spindle-shaped sclerites, these are only indistinctly arranged in chevrons in verrucae that are distinctly up-turned and recurved toward the axis as in several species of *Mopsea,* and the unique type colony is unbranched. The internodes of *Stenisis humilis* (Deichmann) are similarly prickly and ungrooved, but the colonies are small and planar, and the up-turned and recurved verrucae are armed with narrow, transverse plates similar to those of some species of *Mopsea* and *Acanthoisis.*

Caribisis, new genus

Diagnosis.—Unbranched isidids with non-retractile polyps biserially placed, directed upward and recurved toward the axis. Sclerites exclusively spindles, those of verrucae longitudinally arranged in eight tracts irregularly en chevron. Internodes not longitudinally grooved, covered with low prickles.

Type species.—*Caribisis simplex,* n. sp.

Caribisis simplex, new species

Figs. 9d, 21a–c, 22

Material examined.—Windward Islands, Lesser Antilles; off St. Vincent: 13°20.8′N, 61°02.5′W, 576–842 m, 5′ Blake Trawl, R/V *John Elliott Pillsbury* sta P-881, 6 Jul 1969; one colony, holotype, USNM 57290.

Diagnosis.—Unbranched colonies with biserial polyps directed upward and recurved toward the axis; sclerites exclusively tuberculate spindles, in the verrucae arranged indistinctly en chevron in 8 longitudinal tracts.

Description.—The holotype (Fig. 9d) is an unbranched colony 4.5 cm in height consisting of 4 internodes articulated by horny nodes, arising from a conical, calcareous holdfast. The polyps are biserial and variably alternate (Fig. 21a), directed obliquely upward, and measuring 1.1 mm in height,

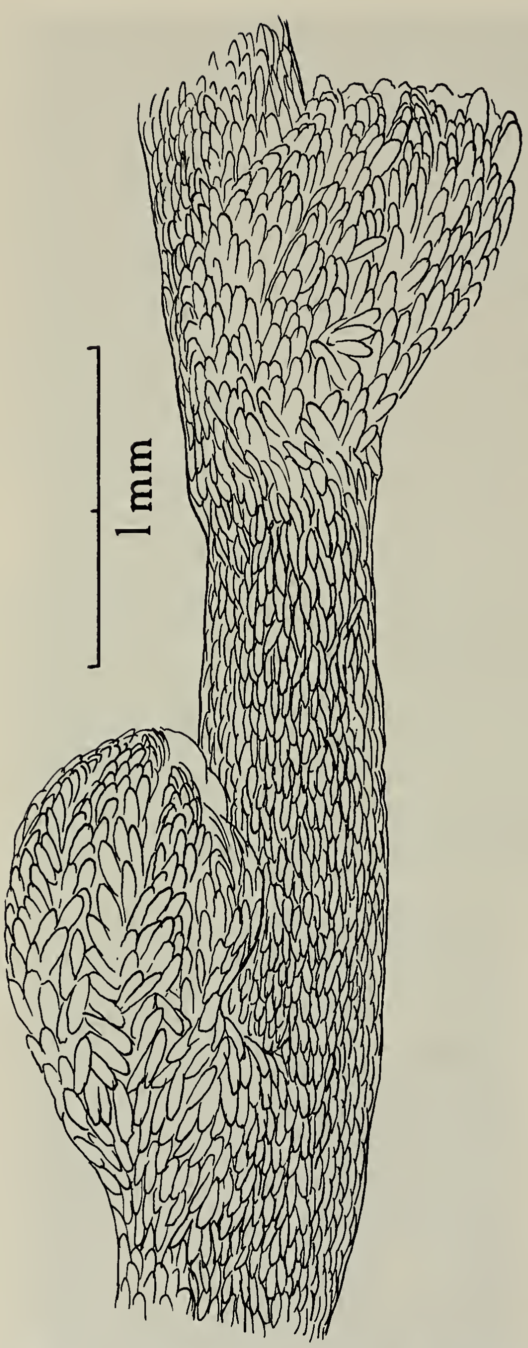

Fig. 22. *Caribisis simplex*, n. gen., n. sp. Part of colony with two contracted verrucae.

0.6 mm in width, placed at intervals of 3 mm proximad, 2 mm distad. There is no distinct operculum at the top of the verrucae. The first polyp occurs 1.4 cm from the base, although tissue is missing from the base of the colony.

The axis consists of calcareous internodes measuring between 0.7 and 1.95 cm in length, and 0.7 mm in diameter, alternating with horny nodes the most proximal of which measures 3 mm in length, compared to 1 mm for the others. The terminal internode tapers a little, but the end is broken off. The internodes are cylindrical, not longitudinally ribbed, the surface covered by scattered sharp granules or low prickles.

The coenenchymal sclerites are tapered, slender spindles (Fig. 21c), those of the verrucae mostly stouter and blunt (Fig. 21b), with complex tubercles arranged in irregular rows; some tubercles may fuse together transversely, but they are not arranged in regular girdles around the sclerite. Both verrucal and coenenchymal spindles measure up to 0.2 mm in length, but the calicular spindles are consistently narrower than their coenenchymal counterparts. Smaller sclerites, about 0.1 mm in length, extend onto the tentacles, those of the tentacle backs slightly curved, with prominent blunt projections, some becoming distinctly flattened, with the projections forming a serrated margin (Fig. 21a).

In alcohol the colony is pure white, including the internodes; the long basal node is light yellowish brown but the subsequent nodes are only faintly yellowish.

Etymology.—Latin *simplex* = simple, uncompounded; in allusion to the unbranched colonial form.

Remarks.—The growth form, spiculation, and axial characters as combined in *Caribisis simplex* are unlike those of any isidid described heretofore. The shape and arrangement of the verrucal spindles are unique and attributable to no known genus; the axial internodes resemble those of *Australisis* and *Stenisis,* both of which have quite different verrucae, arrangement and shape of sclerites, and colonial form. It is impossible to state whether older colonies develop branches as they grow larger but, if so, it is

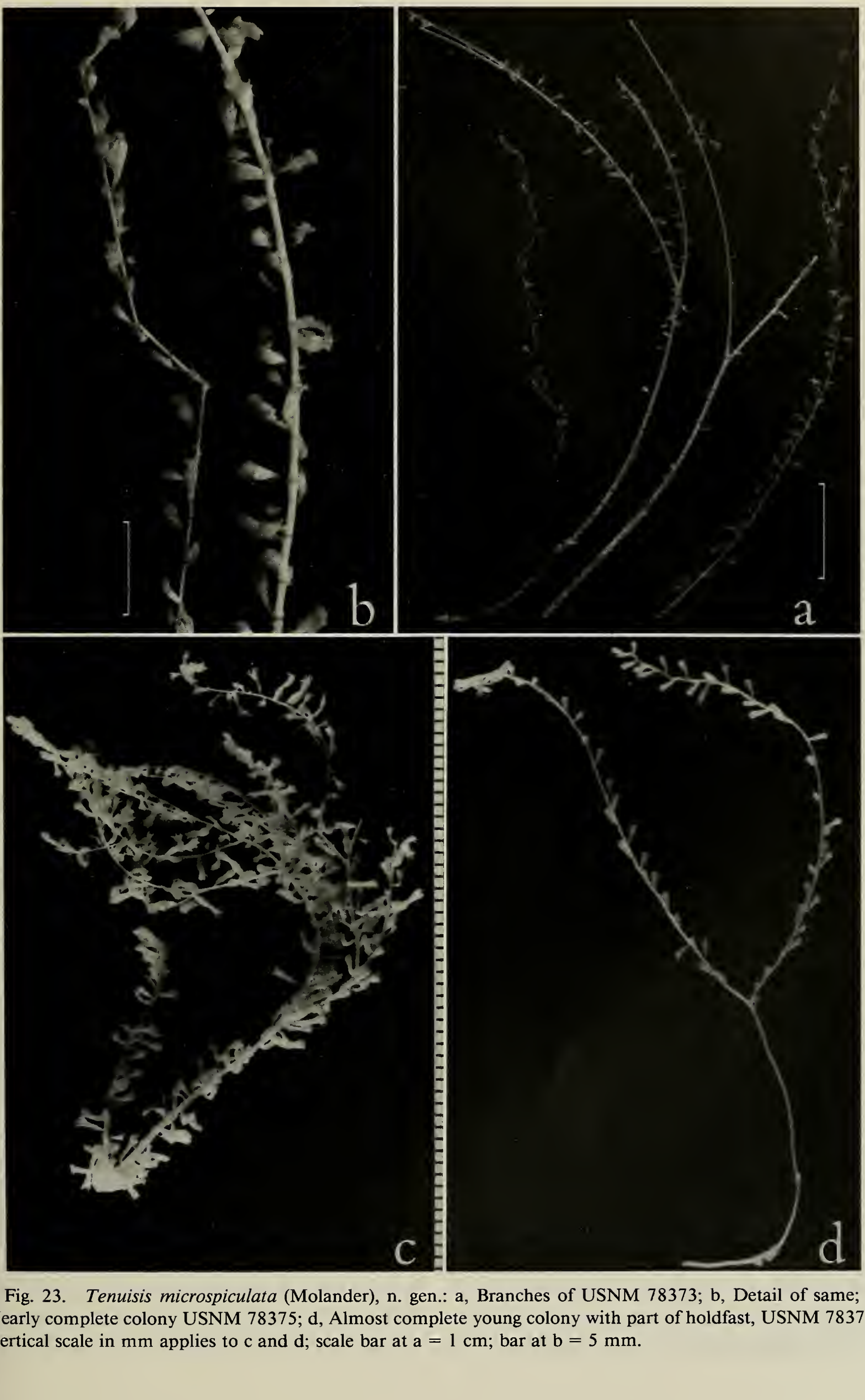

Fig. 23. *Tenuisis microspiculata* (Molander), n. gen.: a, Branches of USNM 78373; b, Detail of same; c, Nearly complete colony USNM 78375; d, Almost complete young colony with part of holdfast, USNM 78374. Vertical scale in mm applies to c and d; scale bar at a = 1 cm; bar at b = 5 mm.

strange that no larger, branched specimens have been taken by any of the hundreds of trawling stations occupied in the same general vicinity during the past century of exploration.

Tenuisis, new genus

Ceratoisis.—Molander, 1929:78.
not *Ceratoisis.*—Verrill, 1883:10.—Wright and Studer, 1889:26.—Kükenthal, 1915: 120; 1919:585; 1924:423.
not *Keratoisis* Wright, 1869:23.—Bayer, 1956:222; 1981:941.—Grant, 1976:15.

Diagnosis.—Very slender isidids sparsely dichotomously branched chiefly from the internodes, occasionally from the nodes; internodes cylindrical, solid, slightly enlarged at each end, smooth or with only faint longitudinal striation confined to the larger branches and main stem. Polyps tall, narrowly campanulate, usually 1 or 2 per internode. Sclerites exclusively scales, those of the polyps narrow, more or less tapered, marginally serrated, longitudinally placed in the body wall; tentacles with crescentic scales transversely placed and curved to fit the rachis, and delicate, narrow scales or rodlets extending into the pinnules. When present, sclerites of the coenenchyme are small, thin scales with dentate margins, many with a median constriction.

Type species.—*Ceratoisis microspiculata* Molander, 1929, here designated.

Remarks.—In his report on the octocorals of the Swedish Antarctic Expedition, Molander (1929:78) described a new species of isidid, *Ceratoisis* [sic] *microspiculata.* Six samples from Antarctic waters in the collections of the National Museum of Natural History, one of which was reported by E. Deichmann (1945:294) as *C. microspiculata,* can now be attributed to that species. However, the material at hand differs from *Keratoisis* in many respects and clearly cannot be accommodated in that genus. Colonies of *Keratoisis* are large and robust, even very large—sometimes exceeding a meter in height (Verrill 1922:43). The characteristic sclerites are stout, cylindrical rods or tapered spindles, longitudinally arranged in the polyps and more or less strongly projecting around the oral end, sometimes with an admixture of smaller scales; the pharyngeal walls contain small double stars or thorny rods.

The specimens at hand agree with *Keratoisis* only in their sparse dichotomous branching. The sclerites are exclusively scales, not spindles or rods, do not project around the distal end of the polyps, and may be wholly absent from the coenenchyme; the pharyngeal walls are devoid of sclerites. Molander's description of the sclerites as "short, flat spindles, cylinders and clubs" must in part reflect faulty observation, as no sclerites in the present material can be described as cylindrical; some are tapered and could be called flat spindles, and some have one end expanded and might be described as clubs, but they are scales without exception. Consequently, this material is here treated as a distinct new genus, for which we propose the name *Tenuisis.*

Tenuisis microspiculata (Molander, 1929)
Figs. 23–27

Ceratoisis microspiculata Molander, 1929: 78, fig. 26; pl. 5, fig. 8.—Deichmann, 1945: 294.

Material examined.—South Shetland Islands: Discovery Bay, at Anchorage off Greenwich Island, 62°28'S, 59°37'W; 31 fathoms, dredge, W. L. Schmitt coll., sta 62–63, 26 Feb 1963; one colony now broken into several pieces, USNM 78373.—South Shetland Islands: 62°05.00'S, 58°23.7'W; 58 m, Petersen grab, R/V *Hero* cruise 721, sta 806, 15 Jan 1972; one colony with holdfast, alcohol, USNM 78374.—Antarctic Peninsula, Graham Land: Palmer Archipelago, 64°49.4' to 64°49.5'S, 62°51.9'W, 120–148 m, R/V *Hero* cruise 721, sta 730, 27 Dec 1971; several terminal branches, in alcohol, USNM 78375.—Antarctic Peninsula, Palmer Land: Neny Fjord, 68°16′S, 66°50′W, 15 fathoms, dredge, 20 Mar 1940; one colony much broken, USNM 51279.—Knox Coast, Antarctica: Vincennes Bay, 66°55.5′S, 110°58.5′E, 120 m, USS *Glacier,* sta G1.-1, dredge, 18 Mar 1956; two colonies, somewhat broken; in alcohol, USNM 78376.—Wilkes Land, Antarctica: off Wilkes Station, 66°16′38″–66°16′20″S, 110°30′48″–110°31′24″E, 128–146 m USARP, VIMS sta AZ, 12 Feb 1961; trawl, many broken branches; in alcohol, USNM 78377.

Diagnosis.—As for the genus.

Remarks.—The specimens in hand agree in the main with Molander's original description, but differ in some particulars. The specimen from Schmitt sta 62–63 (Fig. 23a, b) bears a strong resemblance to the material from South Georgia described by Molander (1929:78, pl. 5, fig. 8). The polyps as described by Molander are of similar size but the scale of his illustration (1929:plate 5, fig. 8), given as 1:1, must be wrong if the measurements are correct as given in the text. The polyps are shown at least 5 mm tall and the specimen 15 cm, but the largest fragment was stated in the text to be 7 cm tall and the polyps 1–1.5 mm tall. The internodes (Fig. 27) are similar in size to those described by Molander, but in his material they were sculptured by "fünf deutlichen Rippen" which are not present here. The polyp sclerites of *microspiculata* were reported to be short, flat spindles, cylinders and clubs, sparsely thorned, 0.15 to 0.25 mm long, but in this specimen they are narrow scales up to 0.4 mm long. The polyps (Fig. 24c, d, e) are tall, trumpet-shaped, 1.5–1.8 mm in height, about 0.3 mm in diameter proximally and 0.5 mm distally, usually one or occasionally two per internode, all around the branches. The intact individuals are covered by a thin layer of epidermal tissue probably overlain by cuticle (Fig. 24d, e), but in many cases this was torn off during collection so most polyps are flayed. The distal half of the polyp body, beneath the tentacles, contains a single layer of flat, elongated scales longitudinally arranged, the distalmost sclerites weakly converging in 8 indistinct points. The sclerites of the body are not continuous with those of the tentacles, the backs of which are filled with narrow, flat scales transversely arranged and curved to fit the rachis (Fig. 26a, b). The large scales of the polyp body (Fig. 26c) are as long as 0.4 mm and about 0.05 mm wide, not uncommonly wider and marginally lobed at one end, tapering to a narrower blunt point at the other; they are sparsely ornamented with low, rather sharp granules, those along the edge more prominent and producing a toothed or serrated margin. A few smaller scales, sometimes twinned, occur among the large body scales. The tentacular scales (Fig. 26a) are mostly small, transversely placed crescents, but a few are flat, bilobed, with a distinct median waist, resembling the scales of some chrysogorgiids; all are nearly smooth. They diminish in size toward the tip of the tentacles; the pinnules contain minute rodlets about 0.03–0.04 mm in length, the larger ones flattened and marginally lobate (Fig. 26d). The nature of the holdfast is not known as the base of the colony was not collected. However, the lowest part of the axis obtained is denuded and overgrown by epizoans, so it probably constitutes the main trunk just above the holdfast. A species of diatom found attached to the denuded trunk (Fig. 27e) was also observed in whole mounts on the axis of distal twig tips with coenenchyme intact.

The specimen taken by the U.S. Antarctic Service Expedition at Neny Fjord in Palmer Land, reported by Deichmann (1945), agrees with that from the South Shetland Islands in all respects except that the body scales of the polyps are somewhat smaller, more nearly in accord with the measurements given by Molander (1929) for *microspiculata.* The branches are conspicuously thickened in several places by elongated swellings containing a parasitic copepod. The tissue over these galls contains sclerites present no-

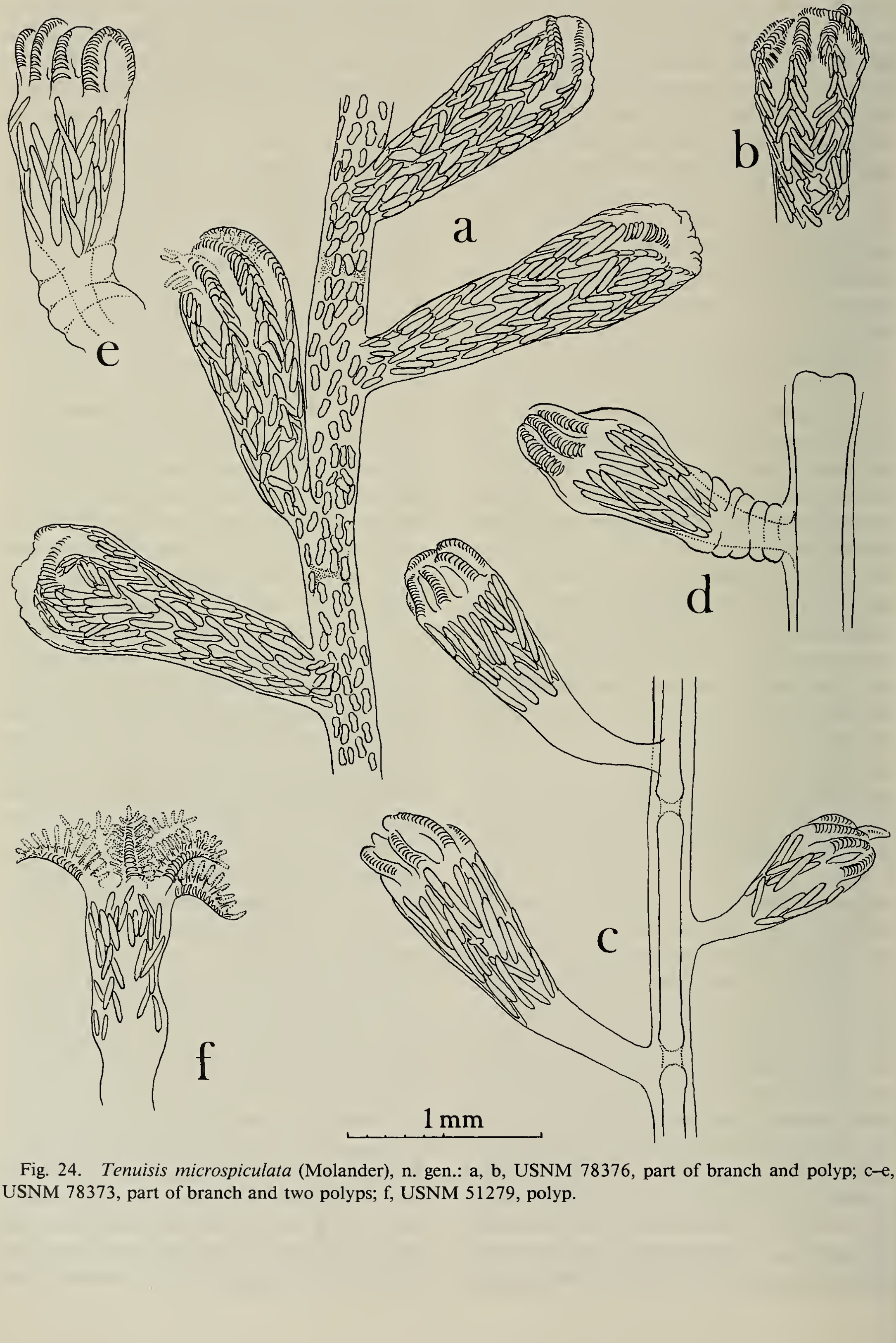

Fig. 24. *Tenuisis microspiculata* (Molander), n. gen.: a, b, USNM 78376, part of branch and polyp; c–e, USNM 78373, part of branch and two polyps; f, USNM 51279, polyp.

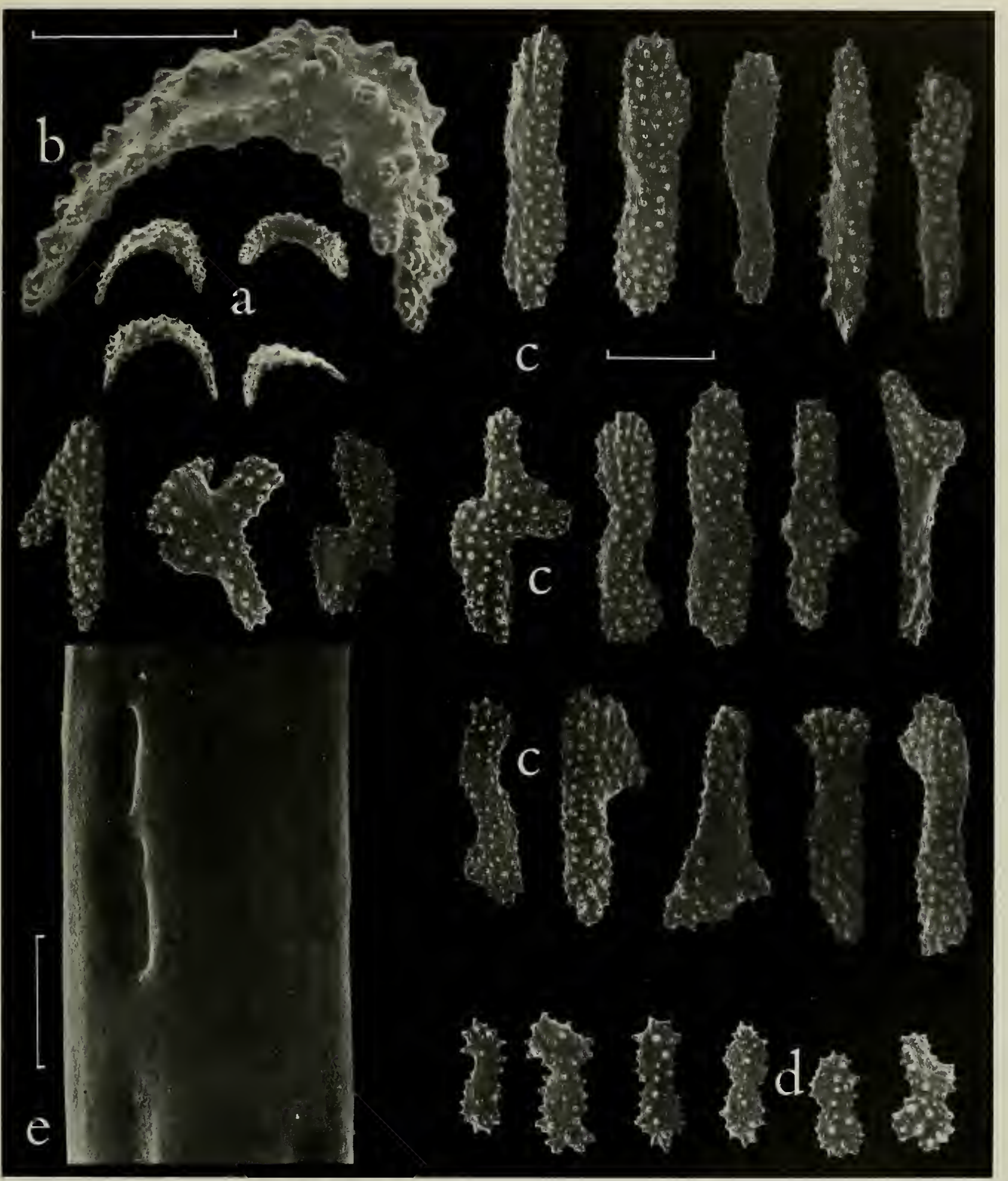

Fig. 25. *Tenuisis microspiculata* (Molander), n. gen. USNM 78376: a–d, Sclerites: a, b, From tentacles; c, From verrucal wall; d, From coenenchyme; e, Part of axial internode. Scale bar at b = 0.05 mm, applies to b only; bar at c = 0.1 mm, applies to a, c, d; bar at e = 0.05 mm, applies to e only.

where else in the coenenchyme. As the entry of the copepod into the gorgonian tissue is most likely through the polyp that ingested it in larval stage, this condition is not surprising. Owing to differences in preservation, many polyps of this specimen are preserved with tentacles extended (Fig. 24f).

The taller colony from *Glacier* sta 1 at Vincennes Bay, Knox Coast, somewhat broken and lacking the proximal parts and holdfast, is more than 10 cm in height. Reaching a length of slightly more than 0.2 mm, the scales of the polyps (Fig. 25c) are similar in size to those reported by Molander, but the coenenchymal scales (Fig. 25d) are much smaller, about 0.1–0.13 mm long,

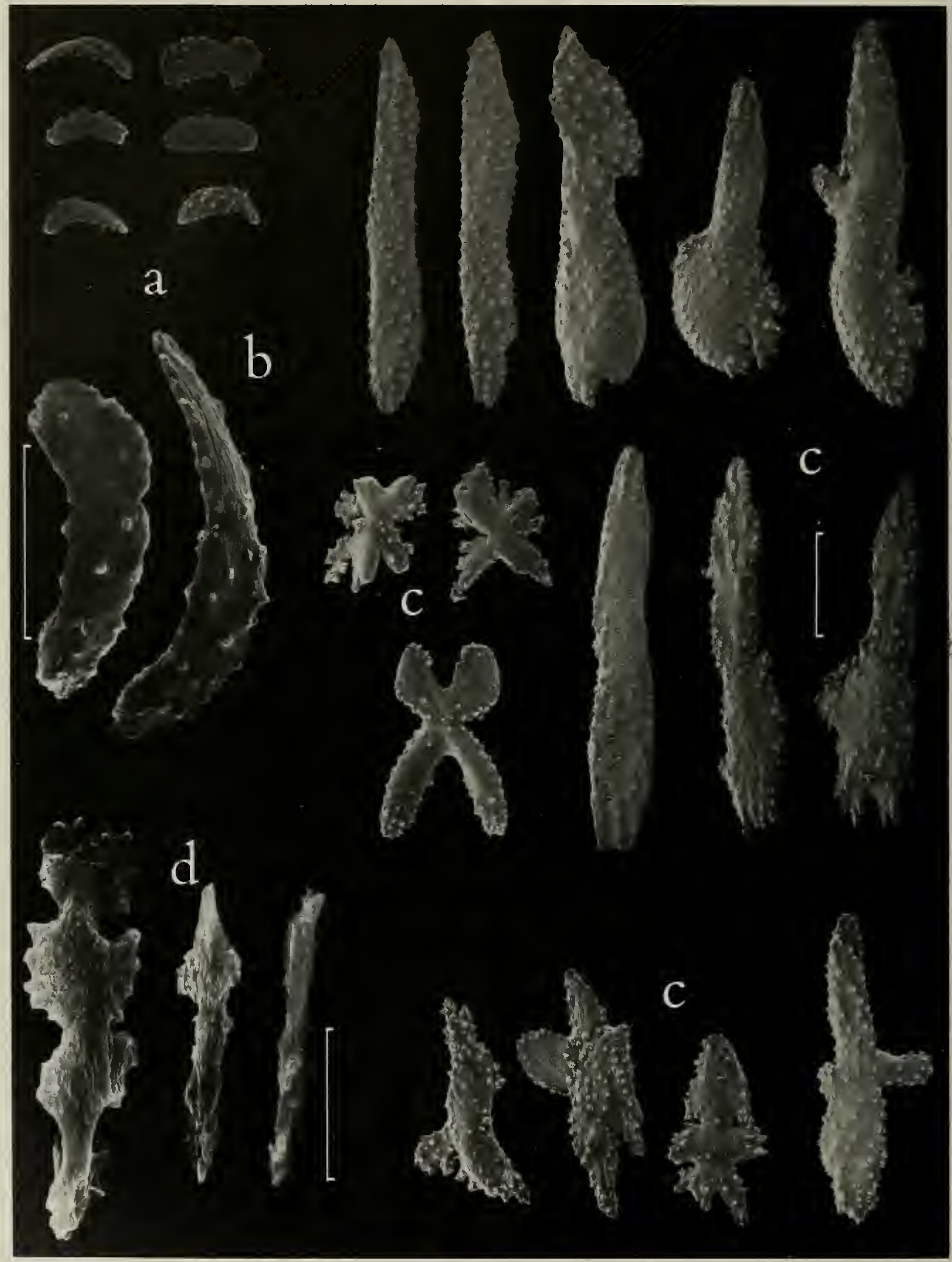

Fig. 26. *Tenuisis microspiculata* (Molander), n. gen., USNM 78373, a–d, sclerites: a, b, From tentacles; c, From verrucal wall; d, From pinnules. Scale bar at b = 0.05 mm; scale bar at c = 0.1 mm, applies to a and c; scale bar at d = 0.02 mm.

never as much as 0.21 as recorded by Molander. The body scales are longitudinally arranged in interseptal tracts irregularly converging toward the bases of the tentacles (Fig. 24a, b), where somewhat smaller scales converge toward the tips; these are followed by transversely placed crescentic scales (Fig. 25a, b) curved to fit the rachis of the ten-

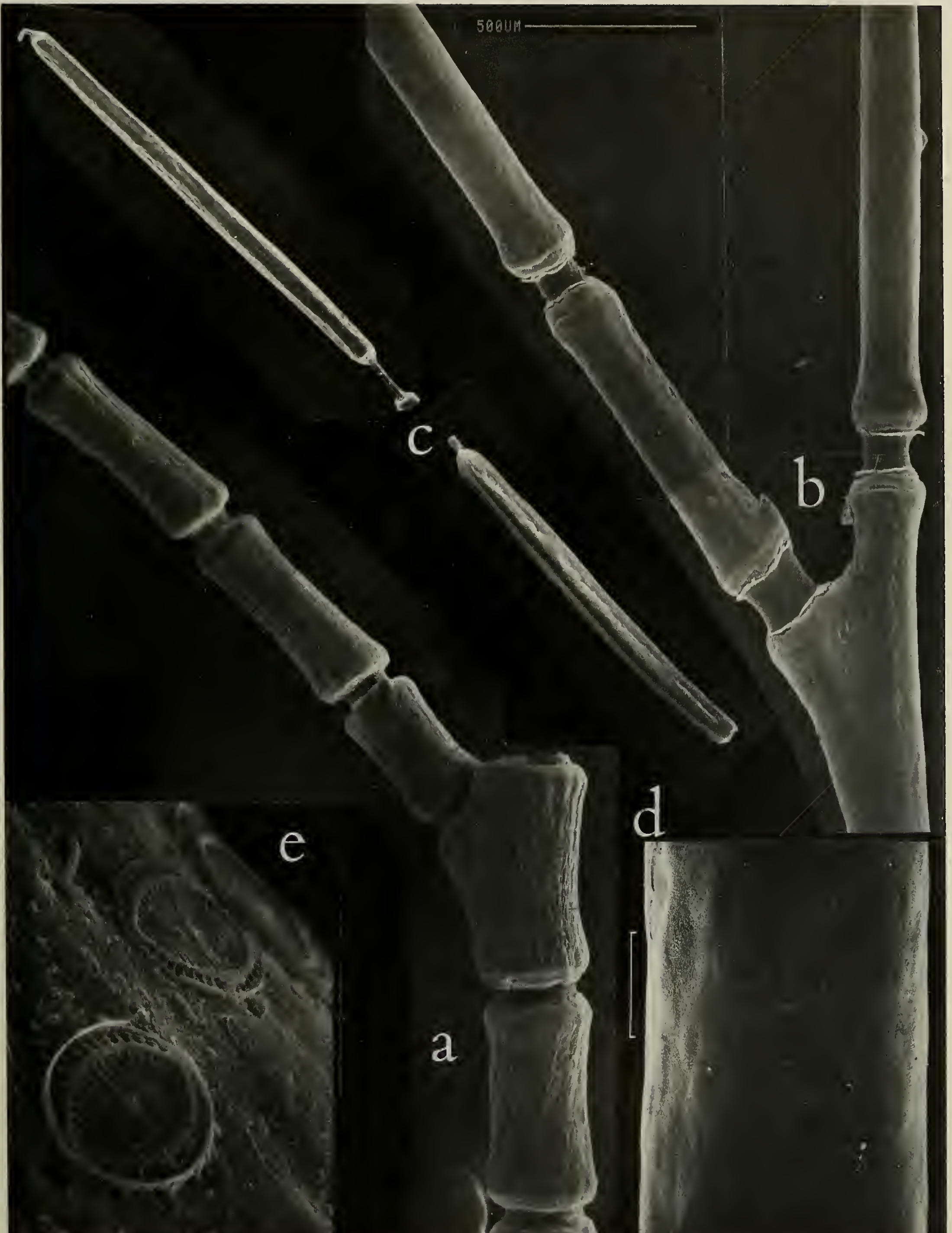

Fig. 27. *Tenuisis microspiculata* (Molander), n. gen., USNM 78373: a, Proximal, b, Intermediate, and c, Distal segments of axis; d, Surface of internode; e, Surface of denuded proximal internode showing attached diatoms. 1 mm, scale at a applies to a only; 0.5 mm scale at b applies also to c; scale at d = 0.05 mm.

tacles. Groups of minute, narrow rods extend into the pinnules. The axis is without conspicuous longitudinal fluting (Fig. 25e).

The colony from *Hero* sta 806 (USNM 78374) has most of its discoidal calcareous holdfast, detached from the substrate. The basalmost three internodes are overgrown by horny nodal material, above which the next six or seven internodes show irregular longitudinal ridges. The internodes of the upper part of the colony are not ribbed.

The specimen from *Hero* sta 730 (USNM 78375) has the polyps more closely placed than in the other specimens examined (Fig. 23c).

Distribution.—Molander's original material was collected in the vicinity of South Georgia in the South Atlantic. Four of the lots now recorded, including that reported by Deichmann (1945), are from the Antarctic Peninsula in the same Antarctic sector. Two of the lots (USNM 78376 and 78377) are from the diametrically opposite side of the Antarctic continent, indicating a widespread Antarctic distribution for this species.

Chelidonisis Studer, 1890

Chelidonisis Studer, 1890:553; 1901:38.—Kükenthal, 1915:118, 124; 1919:631; 1924:444.—Deichmann, 1936:252.—Bayer, 1956:F224; 1981:941.—Tixier-Durivault and d'Hondt, 1974:1415.—Grant, 1976:10.

Type species.—*Chelidonisis aurantiaca* Studer, 1890; by monotypy.

Diagnosis.—Isidids dichotomously branched in one plane, occasionally anastomosing; branching from the distal end of the internodes; internodes longitudinally grooved, the ridges serrated. Polyps forming hemispherical or bluntly conical verrucae distributed mostly on 2 sides of the branches in the plane of ramification. Coenenchyme thin. Sclerites predominantly in the form of 6-radiates.

Remarks.—The 6-radiate sclerites of *Chelidonisis* (Fig. 29b) are unique in the family. Studer's statement that the sclerites "ont tout-à-fait la forme de celle du genre *Isis* proprement dit" is clearly incorrect. Tuberculate spindles and clubs do not occur in *Chelidonisis.*

The ornamentation of the axial internodes (Fig. 29a) also is unique in the family. Although longitudinal fluting by ridges and furrows occurs in several genera, as do prickles or thorns aligned or scattered on the ridges, and pits marking the location of desmocytes are present in all, the internodal sculpture of *Chelidonisis* is distinct from that of all other genera.

Studer's observation (1890:553) that the upper part of the polyp with its tentacles can be withdrawn within the verrucae must be based upon a misinterpretation of the verrucal structure. In contraction the tentacles are merely folded inward over the oral region and enclosed by the eight verrucal lobes—actually the bases of the tentacles.

The specimens from the Gulf of Mexico and the Philippines are so similar to the eastern Atlantic material that there can be no doubt about their identification. However, among these geographically scattered specimens there are subtle differences in the form of the sclerites and the distribution of the polyps that defy adequate description and quantification. Although it is possible that populations on opposite sides of the North Atlantic could maintain a continuous gene pool, it seems highly improbable that an interbreeding population could include colonies as geographically remote as the Philippines. Consequently, we are here considering the population in the Gulf of Mexico to be a geographical subspecies of the eastern Atlantic *aurantiaca,* and are treating that in the Philippines as a distinct species.

Distribution.—Heretofore this genus has been known only from isolated records in the eastern North Atlantic (Studer 1890; Stephens 1909; Tixier-Durivault and d'Hondt 1974; Grasshoff 1982, 1986), although Deichmann (1936:252) stated that

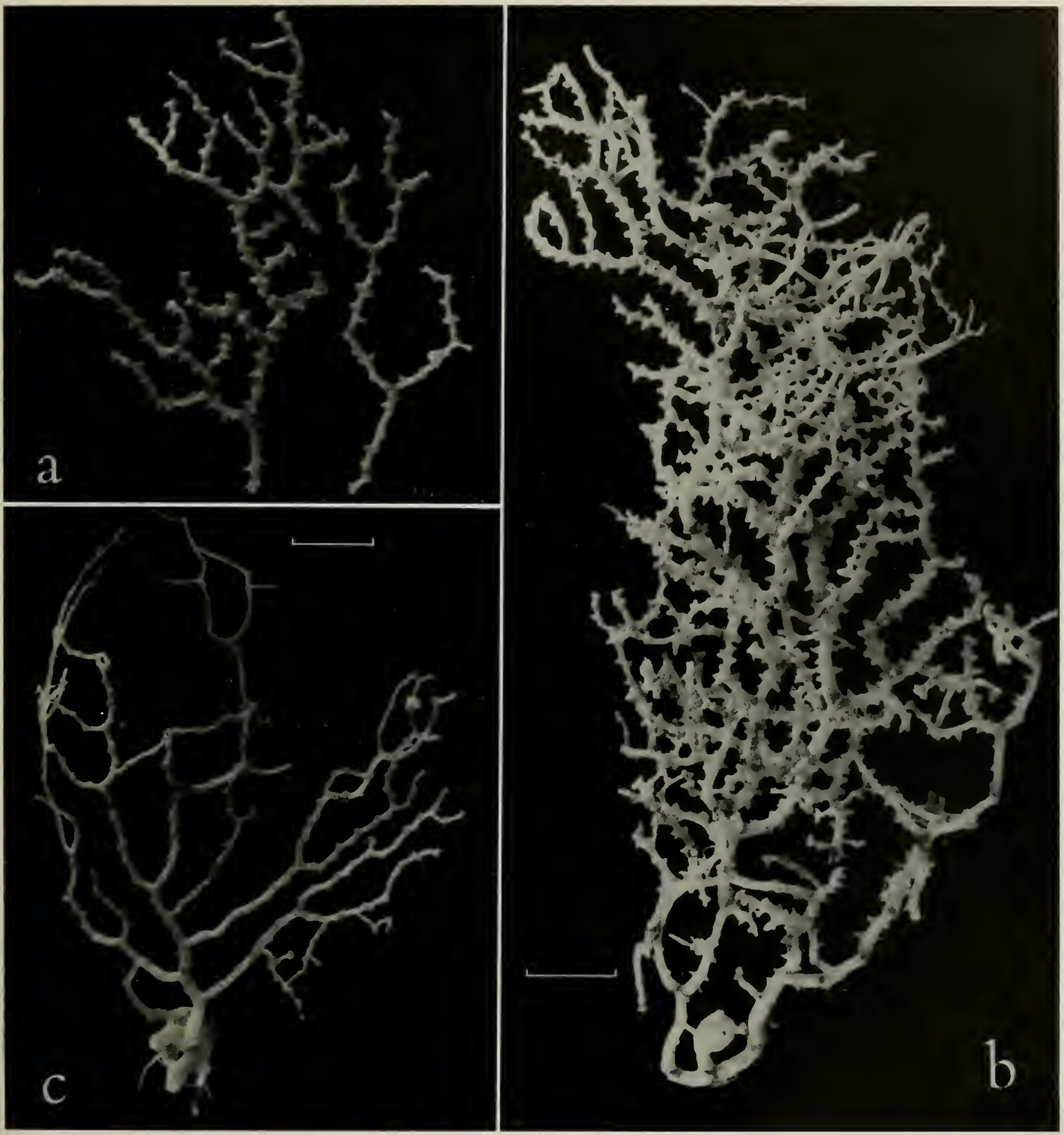

Fig. 28. a, *Chelidonisis aurantiaca aurantiaca* Studer, USNM 28238; b, *Chelidonisis aurantiaca mexicana,* n. subsp., USNM 56564, holotype; c, *Chelidonisis philippinensis,* n. sp., USNM 60389, holotype. Scale bars = 1 cm; that at b applies also to a.

Verrill, in his unpublished report on the "Blake" alcyonarians, described a specimen, now lost, of *Chelidonisis aurantiaca* taken by the University of Iowa Bahamas Expedition off Sand Key, Florida. No illustration of it is to be found among the surviving unpublished plates from Verrill's report, and his original manuscript describing it seems no longer to be extant. While it is strange that none of the many trawling and dredging stations occupied in that area by research vessels of the University of Miami obtained it, a specimen trawled by M/V *Oregon* at sta 4708 in the Gulf of Mexico lends credibility to Verrill's record from the Florida Keys.

The specimen obtained by the U.S. Fish Commission steamer *Albatross* at sta

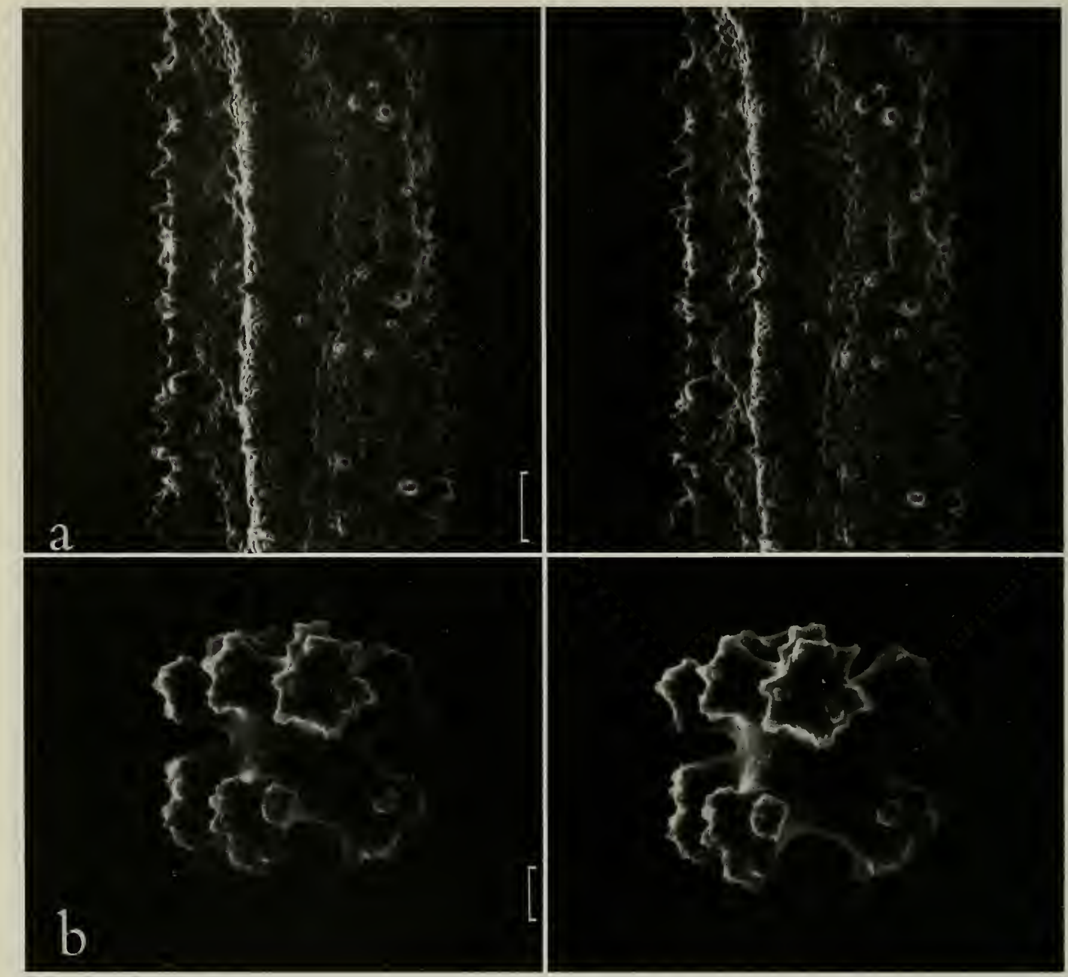

Fig. 29. *Chelidonisis aurantiaca* Studer: a, Part of axial internode, stereo pair, scale bar = 0.1 mm; b, Sclerite, stereo pair, scale bar = 0.01 mm.

D-5423 in the Philippine Islands is the first and only known record of *Chelidonisis* from the Indo-Pacific.

Kükenthal's (1915:124; 1919:637; 1924: 445) contention that *Isidella capensis* Studer, 1878, belongs to this genus is not convincing and is completely refuted by Stiasny's (1941:87, fig. 11) illustrations of sclerites from Studer's type specimen. Even though the axis is not described, the sclerites are those of a melithaeid, probably *Acabaria*. Hickson's (1900:86, pl. 6, figs. A, A') specimen identified as *Primnoisis capensis* (Studer) appears from the illustrations to be some melithaeid rather than an isidid, and may be Studer's species.

Chelidonisis aurantiaca aurantiaca Studer, 1890

Figs. 28a, 29, 30a, 31a

Chelidonisis aurantiaca Studer, 1890:553; 1901:38.—Stephens, 1909:9.—Kükenthal, 1919:631; 1924:444.—Deichmann, 1936:253.—Tixier-Durivault and d'Hondt, 1974:1415.—Grasshoff, 1982: 965; 1986:35.

Material examined.—Southwest of Ireland: 50°42′N, 11°18′W, 627–728 fathoms,

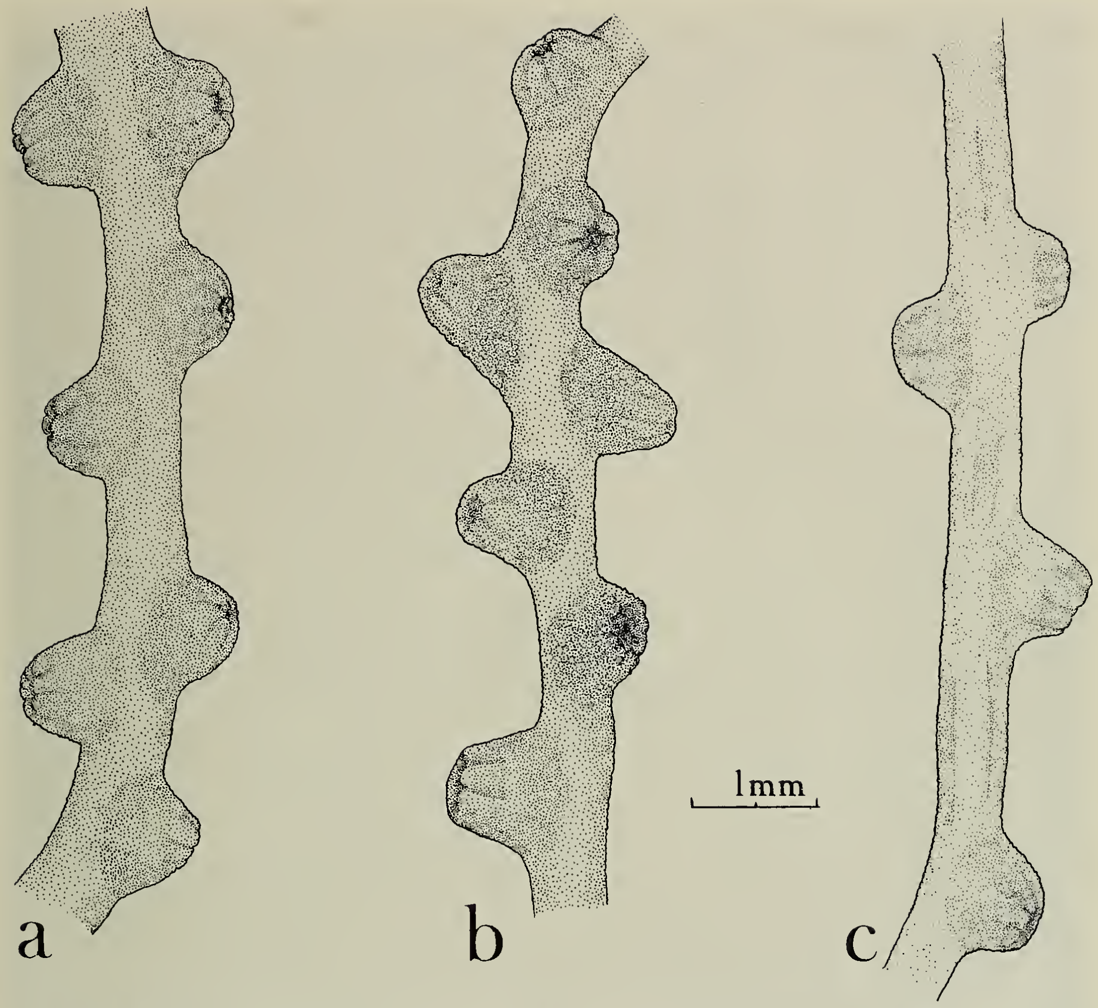

Fig. 30. a, *Chelidonisis aurantiaca aurantiaca* Studer; b, *C. aurantiaca mexicana,* n. subsp.; c, *C. philippinensis,* n. sp.

Fisheries of Ireland, Scientific Investigation S.R. 504, 12 Sep 1907; several branches without holdfast, USNM 28238, received from the National Museum of Dublin.

Diagnosis.—As for the genus.

Remarks.—The present material (Figs. 28a, 30a), part of that recorded by Stephens (1909:9), agrees in every respect with the original description so its authenticity is not open to question. Examination of the sclerites by scanning electron microscope shows that some of the 6-radiates are asymmetrically developed (Fig. 31a) in a way similar to that occurring in *Corallium* and *Paragorgia.* Such asymmetrical forms were illustrated, although not very clearly, by Studer (1901:pl. 4, fig. 9).

Chelidonisis aurantiaca mexicana, new subspecies

Figs. 28b, 30b, 31b

Material examined.—Gulf of Mexico, south of the Mississippi Delta: 27°45′N, 91°12.5′W, 230 fathoms; R/V *Oregon* sta 4708, 23 Feb 1964; one colony, USNM 56564.

Diagnosis.—*Chelidonisis* having colonies

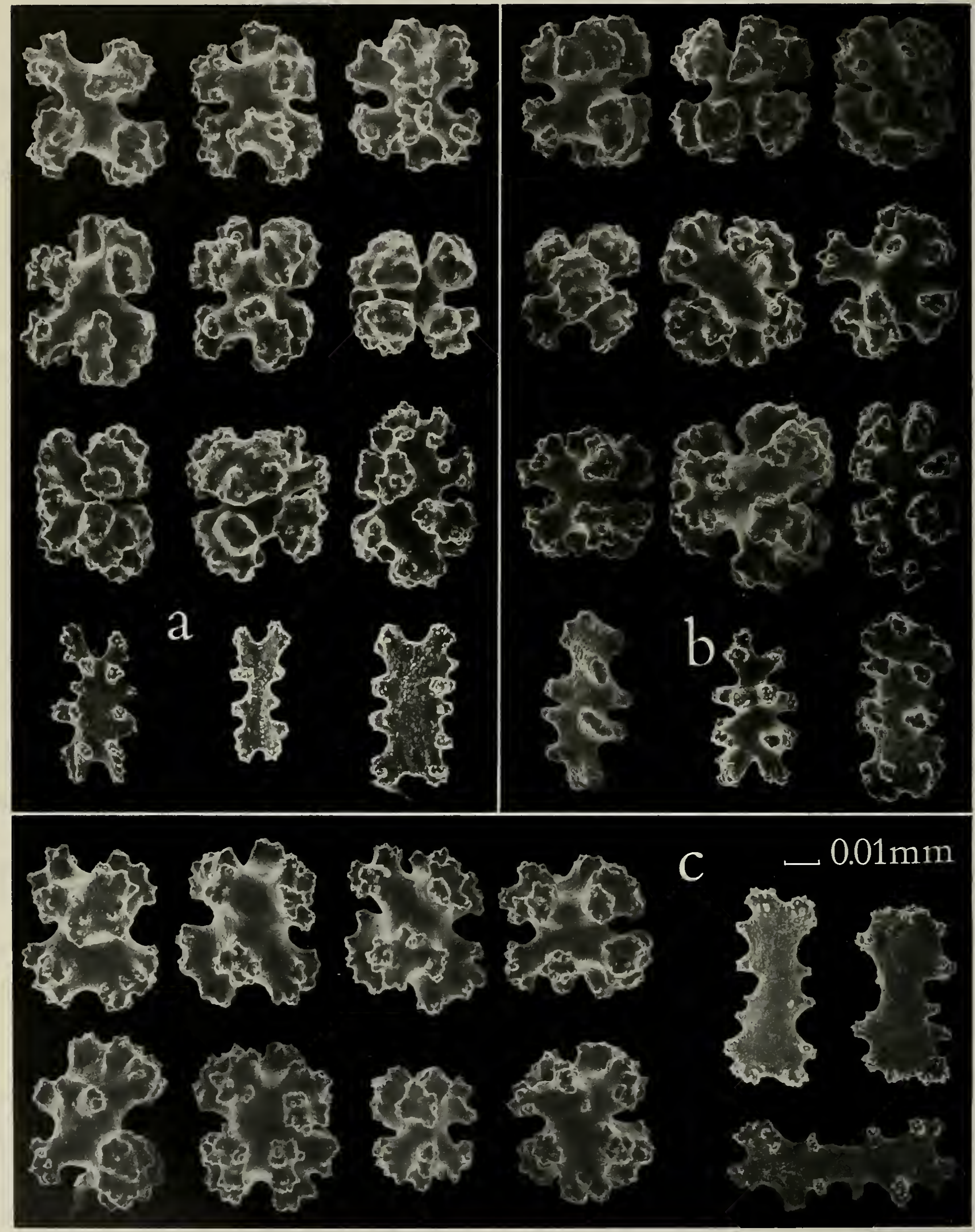

Fig. 31. Sclerites of a, *Chelidonisis aurantiaca aurantiaca* Studer; b, *Chelidonisis aurantiaca mexicana,* n. subsp.; c, *Chelidonisis philippinensis,* n. sp.

abundantly branched, with occasional anastomosis; polyps commonly less than 2 mm apart.

Description.—The holotype (Fig. 28b) as preserved is a colony, probably incomplete, about 11.5 cm tall and 5 cm wide, in the form of a profusely branched compressed bush produced by a combination of dichotomous and lateral branching with occasional anastomosis. In many cases, an internode gives rise to 2 branches, each beginning with a horny node, so close to its distal end that they seem to arise from a single node. Between such bifurcations, one or both internodes may give rise laterally to one or more side branches in approximately the same plane, each commencing with a horny node. These branches may in turn bifurcate or produce further lateral branchlets, resulting in an irregular multiplanar thicket. The middle of the colony is traversed by a vague principal axis formed by the dominance of one branch of successive bifurcations; the thickest internodes are about 2 mm in diameter, whereas those of the smaller branches are only 0.2 mm wide, or even less. The longest internodes are about 1 cm long between dichotomies, and the side branches from them are 3–5 mm apart.

The polyps tend to a biserial arrangement, rather widely separated, on the smaller branches; some incline toward one face of the colony, and on the older branches they occupy 2 sides and one face of the branches, leaving one side of the colony almost free of polyps. They contract to form obtusely conical verrucae 0.2–0.35 mm tall and 0.5–0.6 mm wide at the base; the infolded tentacles produce a blunt, obscurely 8-lobed apex (Fig. 30b).

The sclerites (Fig. 31b) are similar to those of eastern Atlantic material.

Chelidonisis philippinensis, new species

Figs. 28c, 30c, 31c

Material examined.—Philippine Islands, off Cagayan Island: 9°38′30″N, 121°11′E, 508 fathoms; USFC steamer *Albatross* sta D-5423, 31 Mar 1909; one nearly complete colony with holdfast and some detached branchlets; holotype, USNM 60389; one colony lacking holdfast, and detached branchlets; paratype, USNM 78378.

Diagnosis.—*Chelidonisis* with flabellate colonies openly branched, polyps widely spaced, commonly 2.5 mm or more apart.

Description.—The holotype (fig. 28c) is a nearly complete colony about 6 cm in height and width, arising from a multilobed holdfast adapted for anchoring the colony in soft substrate. The colony is essentially uniplanar but the flabellum is distinctly convex. Branching is chiefly dichotomous, each internode giving rise at its distal end to 2 branches each arising from a short horny node; a few internodes produce 1 or 2 side branches articulated by a horny node, and a few fail to bifurcate, instead producing only a single new internode in its own direction of growth. Anastomosis may occur fortuitously where the courses of 2 branches coincide, but does not appear to be a consistent feature of ramification. Most internodes are 1 cm in length, but a few may be as long as 1.2 cm or as short as 0.7 cm. The basal internodes of the main stem are 1.5 mm in diameter, those of the principal branches 1 mm, and of the terminal branches only 0.2–0.5 mm.

The polyps are biserially arranged, widely spaced and often in pairs, probably owing to the fact that branchlets always end with an opposed pair of polyps. Distance between polyps is usually 3–4 mm, but somewhat greater or lesser distances are not uncommon. In most parts of the colony the contracted polyps form hemispherical verrucae 0.25–0.3 mm in height, with blunt, indistinctly 8-lobed apices formed by the bases of the infolded tentacles (Fig. 30c); near the tips of branches, the verrucae may be scarcely raised above the coenenchymal surface.

The sclerites (Fig. 31c) differ from those of Atlantic material in no significant way.

Acknowledgments

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FIRST FLOWERING DATES FOR SPRING-BLOOMING PLANTS OF THE WASHINGTON, D.C., AREA FOR THE YEARS 1970 TO 1983

Stanwyn G. Shetler and Susan K. Wiser

Abstract.—The first-flowering dates for spring-blooming plants (both native/naturalized and cultivated species) have been recorded by volunteers in the Department of Botany, National Museum of Natural History, since 1970. The first fourteen years (1970–1983) of these observations are tabulated, and the native/naturalized records are analyzed briefly. Over 100 persons contributed observations, recording 397 native/naturalized species and 704 cultivated species. Bar graphs of first-flowering dates are presented for all native/naturalized species for which there are four or more years of records, and comparisons of cumulative numbers of woody, perennial, biennial, and annual species coming into flower by a certain date are graphed. Variation in first-flowering dates from year to year within and among species is described and possible explanations are discussed.

Phenology is the study of periodic cycles in biological events and their relation to climate. One important phenological cycle is flowering in plants. In temperate areas, such as the mid-Atlantic region, this cycle is an annual one. Flowering plants are generally dormant throughout the winter but renew growth in spring. Many species flower in the spring within a few weeks after growth resumes. Several factors, which are seasonal themselves, are well known to correlate with flowering time. Among these are (1) temperature, (2) day-length, (3) degree of canopy closure, (4) potential for pollination, i.e., availability of pollinators or suitability for wind-pollination, and (5) microclimate. Recently, Fagerström and Agren (1980) have proposed that competition for seedling establishment may also influence the phenological spread of flowering. While flowering time may vary greatly from year to year, each species has its own approximate timetable, and there is an overall flowering pattern as the season progresses.

This study was begun by Shetler in 1970 as an informal effort to record the first dates of blooming for as many spring-flowering woody and herbaceous species as possible in the immediate Washington, D.C., area. To ensure as wide a coverage as possible, he enlisted the help of other interested persons by posting a recording chart outside his office in the Department of Botany at the Smithsonian Institution, and soon others were contributing regularly. The project quickly proved popular as a means of following the progress of spring and became an annual tradition, which has been continued down to the present. Each year the chart is put up at the beginning of the calendar year, and recording is continued through May 31st. At the outset, June 1st was selected as the arbitrary cutoff for the spring season.

After the annual observations had accumulated for several years, it became apparent that they were adding up to a unique phenological record for the area, and efforts were begun to computerize the data. Despite the large number of observers and recording variability introduced thereby, the flowering dates were becoming predictable and the species comparisons reliable as the years of data accumulated.

In 1983, after 14 springs of recording first-flowering dates in the manner described, it seemed obvious that the annual observations were beginning to yield diminishing returns and that the time had come to summarize what had been learned. Accordingly, the authors began to process and analyze the first 14 years of records, and the results of the analysis are presented in this paper.

Lester Ward, in his important early flora of Washington and vicinity published in 1881, included observations of flowering dates for 122 species of native and naturalized plants. More recently, two studies of spring flowering times have been made in this area. Terrell (1970) produced an annotated list of spring-flowering plants of the Chesapeake and Ohio (C&O) Canal with general flowering information on 342 species. Thomas (1963, 1965) made detailed studies of 286 species flowering on Theodore Roosevelt Island in the Potomac River at Washington, D.C.

The Washington, D.C., area lies on the juncture of the Piedmont and the Coastal Plain, with the Piedmont to the northwest and the Coastal Plain to the southeast. The Piedmont has a marked intrusion of Appalachian Mountain and northern plants, while the Coastal Plain area, i.e., lower Potomac River, is rich in marsh species (Hitchcock and Standley 1919).

A record of first-flowering dates provides a practical guide for such activities as teaching, planning fieldtrips, and collecting research materials during the spring season. Such a list serves as a basis for determining when the bulk of the species begins to bloom in the spring season and in detecting how the number of species coming into flower changes through the course of the season. Other aspects of spring flowering that we wished to examine were (1) the relationships of peaks of first bloom to life-form and to native and naturalized vs. cultivated species, (2) the patterns of year-to-year variation in first-flowering dates within individual species, and (3) the types of species that are the most or least variable.

Methods

The data analyzed here are dates of first-flowering or anthesis recorded for the years 1970 through 1983 for species coming into bloom between January 1st and June 1st. A species was not always observed in its initial flowering stage. If flowering was more advanced when first observed, then the approximate stage of flowering (e.g., peak-flowering, late-flowering) was recorded. Any given species was recorded only once in any given year.

"Date of first-flowering," as used in this study, requires explanation. "Flowering" is taken to mean the stage at which a perfect flower or a male flower is shedding pollen or a female flower is receptive to pollen. "First-flowering," literally, would be the moment at which the very first flower begins to shed pollen or display receptive stigmas. A "first-flowering date," therefore, would be the date for a given species within the study area on which the first flower of the season begins to shed pollen or display receptive stigmas. The study also includes some gymnosperms and other non-flowering plants. The date of "first-flowering" for these species is the date when spore- or pollen-shedding began.

Because, for a region as large as the D.C. area, it is impossible in virtually all cases to establish this date on an absolute basis, in actual practice "date of first-flowering" becomes the date on which a species is first *observed* to be in flower. The validity of the concept of first-flowering depends, therefore, on observing the species as early as possible in their annual flowering cycles, i.e., as close as possible to the absolute dates of first-flowering. In this study most of the species (more than 90 percent) recorded each year were actually observed in very early, though not necessarily the absolute earliest, stages of flowering. Each year, however, some of the species recorded were in more advanced stages of flowering when first observed. For the purposes of this paper, we eliminated all records based on flowering stages beyond what was deemed to be the peak-flowering stage. Ranges of first-flowering dates (earliest and latest ever recorded) and averages of first-flowering dates were computed on the basis of all the remaining dates, including some that were recorded for species that had already reached peak-flowering by the time that they were observed.

All observations were made by volunteers, and the species recorded each year are the ones that the volunteers happened to observe in first- or early-flowering stage in the given year. Because it was an entirely informal, voluntary project, there was no systematic effort to include all spring-flowering species or even the same set of species every year. Thus, while many species were recorded year after year, they were not necessarily recorded from the same localities or by the same observers every year, and many species happened to be recorded only once during the entire 14-year period. Many other spring-flowering species never happened to be reported even once during this 14-year period. This was particularly true of grasses and sedges. Altogether, 109 persons contributed one or more observations to the flowering records over the 14 years.

All observations were recorded from localities within about a 35-mile radius of the center of the District of Columbia. The localities are plotted on Fig. 1 for all first-flowering records of native and naturalized species only.

From the outset, first-flowering dates were recorded for exotic species (e.g., hyacinth, *Hyacinthus orientalis*) growing under cultivation as well as for native and naturalized species. The status of the species, whether "cultivated" or "native or naturalized," was coded into the computer record, and the two groups of records were analyzed separately. The complete list of the native and naturalized species that were recorded over the 14-year period (397 spp.) is presented in Appendix 1, and the list of cultivated species that were recorded more than once (401 spp.) is presented in Appendix 2. In these appendices, the range of first-flowering dates, the average first-flowering date, and the number of observations used in these determinations are presented.

For certain native and naturalized species, some of the flowering dates were recorded from plants being cultivated as ornamentals (e.g., as shade trees or as wildflowers). A native or naturalized species was treated as a "cultivated" species and analyzed with the cultivated group only when *all* recorded dates were for plants growing in cultivation. This explains why a few locally native or naturalized species appear in Appendix 2. In the case of native or naturalized plants, therefore, no distinction was made between flowering observations from the wild and from cultivation when both kinds of observations had been made for the same species; all observations were treated as though made in the wild. Native and naturalized species of eastern North America that are unknown in the wild from the local area of this study automatically were treated as "cultivated" species and appear in Appendix 2.

Except for the inclusion of Appendix 2, we have confined our analysis in this paper to the native and naturalized species. Because all of the records are sight records without preserved specimen vouchers, the cultivated taxa, in particular, present major taxonomic and nomenclatural problems. Many were not identified to species in the first place, while in other cases the identifications are debatable. With cultivated plants there also is the problem of cultivars. The nomenclature for the cultivated plants in Appendix 2 follows *Hortus Third* (Bailey and Bailey 1976), as far as possible. Otherwise, the names were retained as recorded by the observers, and the validity of the identifications rests on the authority of the observers. Varietal names are retained only

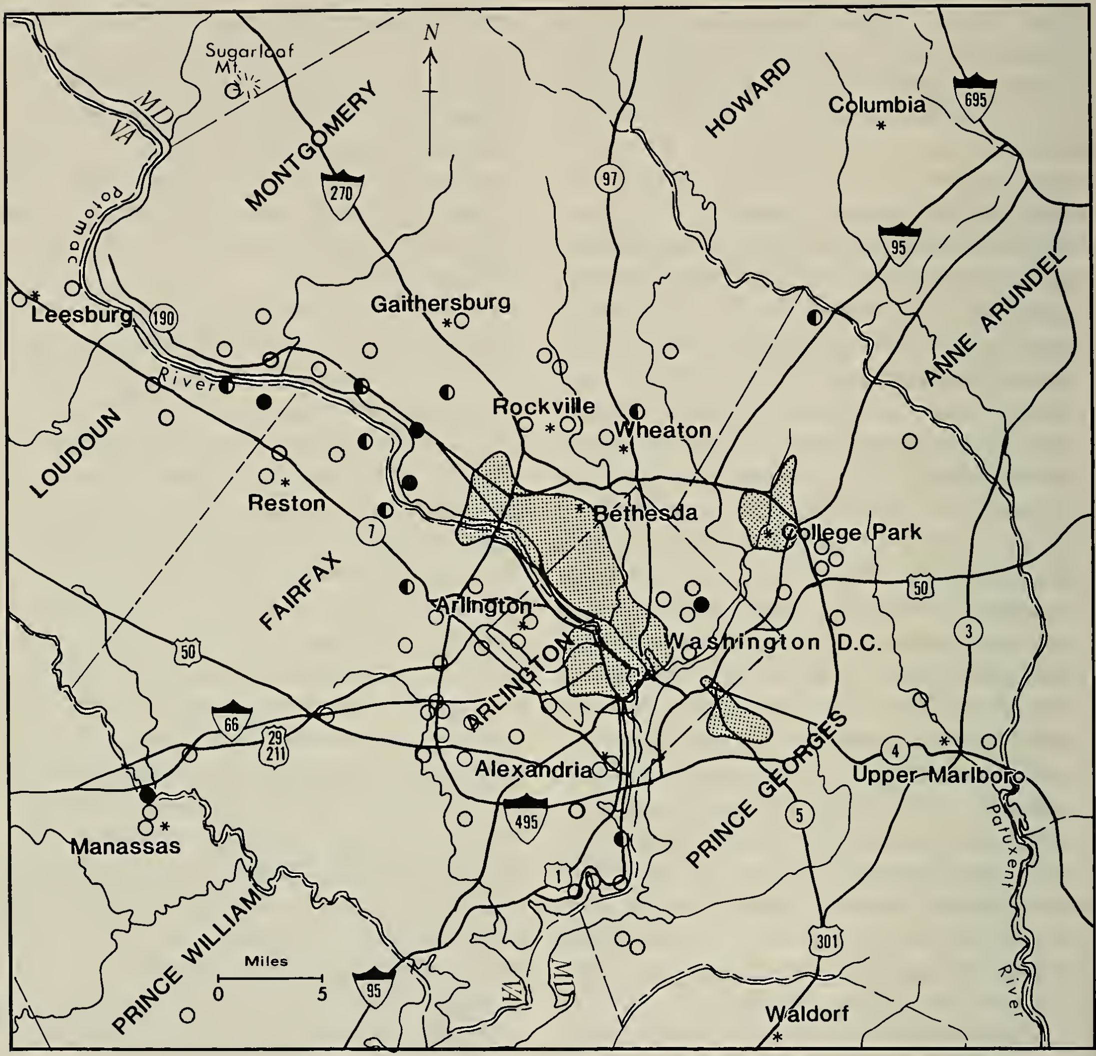


Fig. 1. Map of recording localities of spring-flowering plants, 1970–1983. The number of records from each locality is indicated by the following symbols: Open circle = 1–10 records, Half circle = 10–50 records, Solid circle = 50 or more records. Stippled areas are locations of heavy observation, with cited localities too dense to map.

in the cases where more than one variety was recorded for the same species.

For the native and naturalized species, the taxonomic circumscriptions and nomenclature largely follow the eighth edition of *Gray's Manual of Botany* (Fernald 1970). In some cases, the more recent interpretations of the *National List of Scientific Plant Names* (United States Soil Conservation Service 1982) were adopted. No infraspecific names were retained for native or naturalized species.

To determine whether a species was native or naturalized in the study area, we consulted Hermann's (1946) *Checklist of Plants in the Washington-Baltimore Area* and the separate Washington-Baltimore Herbarium in the U.S. National Herbarium (US) at the Smithsonian Institution. Any records for species not previously reported from the wild in the study area were dropped from the database because of their doubtful status.

Throughout the life of the project, Shetler has served as the final authority for identifications of native and naturalized species when there has been any doubt. He personally identified many specimens brought in by observers who were unable to name them and corrected or verified many other doubtful determinations made by unsure observers. In the vast majority of cases, however, the observer made his or her own identification, which was accepted by Shetler, as recorded, unless there was good reason for questioning the identification. Nonetheless, Shetler accepts ultimate responsibility for the identifications, taxonomic interpretations, and nomenclature in this paper.

Computer analysis and graphing were done using a Honeywell 6680 mainframe, Calcomp 1051 Drum Plotter, and a custom built CPM microcomputer using DBASE II software.

Results

The records include observations on plants from 95 different plant families, although 40% of the records are for species of the following eight families: Asteraceae, Brassicaceae, Ericaceae, Fabaceae, Liliaceae, Ranunculaceae, Rosaceae, and Violaceae.

Figure 2 is a bar graph of the first-flowering dates of all the individual species for which there are four or more years of records. The species are arranged chronologically in order of their average first-flowering dates. The computer-generated bar for each species plots the first-flowering dates of the species on a calendar scale. Dates for other than the initial flowering stage are plotted with special symbols, as defined in the legend.

Cumulative numbers of species coming into flower by a given date are graphed according to certain categories (e.g., woody plants) in Figs. 3 and 4. These graphs were generated by plotting the species totals in one-week intervals. Each point on a particular graph represents the sum of all species of the given category that came into flower over the whole 14-year period during the given week. A weekly rather than a daily interval was chosen so as to balance out year-to-year variability produced by the obvious weekend peaks in date recording.

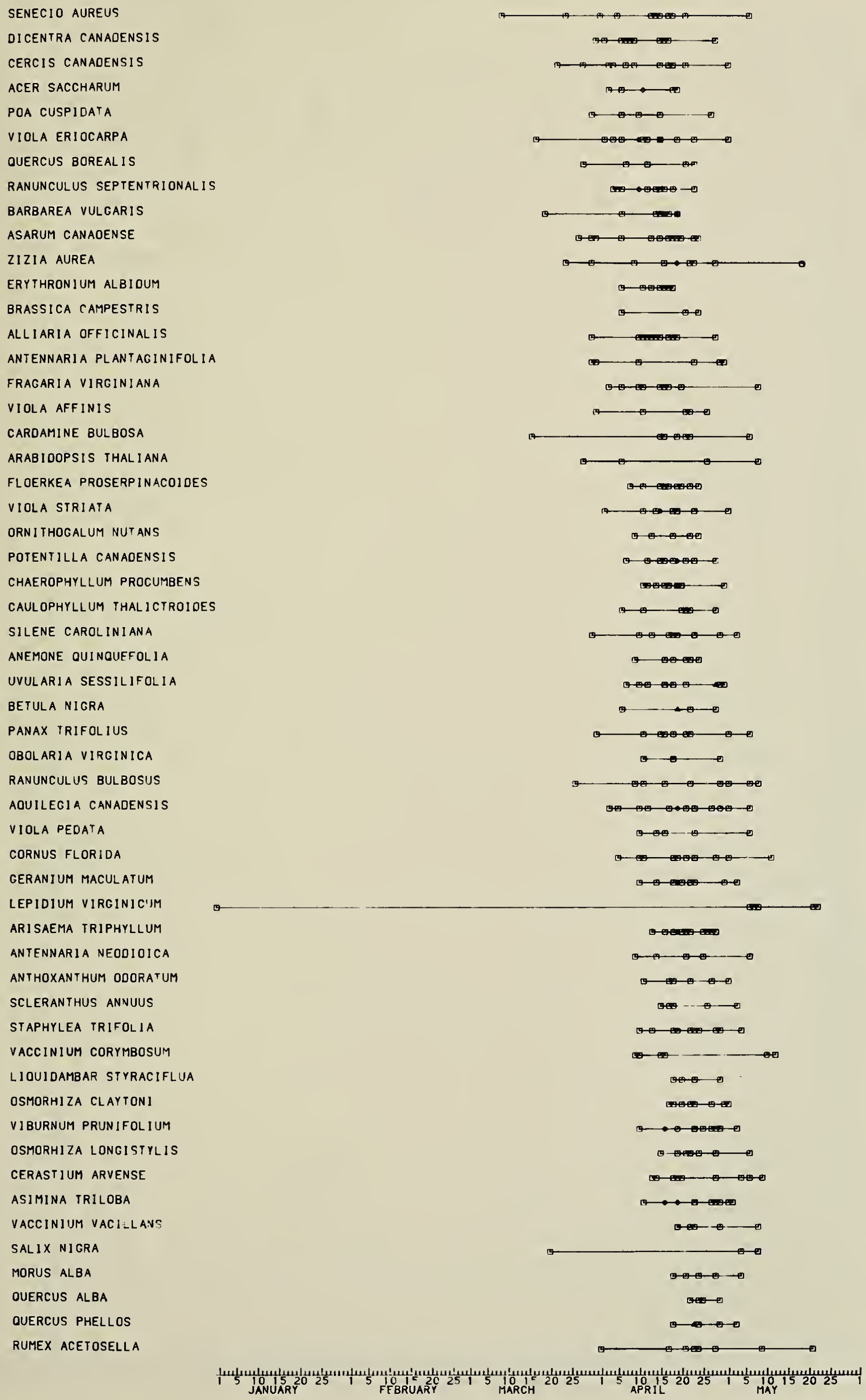
The top curve of each figure cumulates all species, regardless of category, by the weekly intervals of first-flowering. The other curves represent different categories of species. For this purpose, the species were classified in terms of life-form (Fig. 3: annual, biennial, perennial, or woody) and nativeness (Fig. 4). This information was gathered primarily from *Gray's Manual of Botany* (Fernald 1970) and the *Manual of Vascular Plants of Northeastern United States and Adjacent Canada* (Gleason and Cronquist 1963).

Discussion

The regular flowering season in the Washington area begins in late February or early March. Some plant species flower earlier in the year, however, especially when there are mild spells in the weather or when they occur in sheltered places. Figures 3 and 4 show 29 species coming into flower in early January over the 14-year period. Because the recording of flowering dates did not start until January 1st of each year, species that had begun to flower in the previous autumn and had remained in flower through the new year often were recorded as beginning to flower on or soon after January 1st. Consequently, the initial peak of first-flowering in January is an artifact of the method of data collection.

The species that appear to begin flowering in January and February are primarily widespread weedy introductions, such as common chickweed (*Stellaria media*), dandelion (*Taraxacum officinale*), henbit *La-*

Fig. 2. List of recorded native or naturalized species with line graphs of actual dates of first-flowering. The species are listed in order of flowering, from earliest to latest, based on average first-flowering dates.


SENECIO AUREUS
DICENTRA CANADENSIS
CERCIS CANADENSIS
ACER SACCHARUM
POA CUSPIDATA
VIOLA ERIOCARPA
QUERCUS BOREALIS
RANUNCULUS SEPTENTRIONALIS
BARBAREA VULGARIS
ASARUM CANADENSE
ZIZIA AUREA
ERYTHRONIUM ALBIDUM
BRASSICA CAMPESTRIS
ALLIARIA OFFICINALIS
ANTENNARIA PLANTAGINIFOLIA
FRAGARIA VIRGINIANA
VIOLA AFFINIS
CARDAMINE BULBOSA
ARABIDOPSIS THALIANA
FLOERKEA PROSERPINACOIDES
VIOLA STRIATA
ORNITHOGALUM NUTANS
POTENTILLA CANADENSIS
CHAEROPHYLLUM PROCUMBENS
CAULOPHYLLUM THALICTROIDES
SILENE CAROLINIANA
ANEMONE QUINQUEFOLIA
UVULARIA SESSILIFOLIA
BETULA NIGRA
PANAX TRIFOLIUS
OBOLARIA VIRGINICA
RANUNCULUS BULBOSUS
AQUILEGIA CANADENSIS
VIOLA PEDATA
CORNUS FLORIDA
GERANIUM MACULATUM
LEPIDIUM VIRGINICUM
ARISAEMA TRIPHYLLUM
ANTENNARIA NEODIOICA
ANTHOXANTHUM ODORATUM
SCLERANTHUS ANNUUS
STAPHYLEA TRIFOLIA
VACCINIUM CORYMBOSUM
LIQUIDAMBAR STYRACIFLUA
OSMORHIZA CLAYTONI
VIBURNUM PRUNIFOLIUM
OSMORHIZA LONGISTYLIS
CERASTIUM ARVENSE
ASIMINA TRILOBA
VACCINIUM VACILLANS
SALIX NIGRA
MORUS ALBA
QUERCUS ALBA
QUERCUS PHELLOS
RUMEX ACETOSELLA
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JANUARY
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PODOPHYLLUM PELTATUM
PHACELIA RANUNCULACEA
POTENTILLA SIMPLEX
CYPRIPEDIUM ACAULE
POA PRATENSIS
GALIUM APARINE
DACTYLIS GLOMERATA
RHODODENDRON NUDIFLORUM
LEPIDIUM CAMPESTRE
ORNITHOGALUM UMBELLATUM
PAULOWNIA TOMENTOSA
KRIGIA DANDELION
UVULARIA PERFOLIATA
SEDUM TERNATUM
VICIA CAROLINIANA
ORCHIS SPECTABILIS
HYBANTHUS CONCOLOR
CHRYSOGONUM VIRGINIANUM
PLANTAGO LANCEOLATA
ERIGERON PHILADELPHICUS
PLANTAGO VIRGINICA
TRIFOLIUM PRATENSE
VIOLA PRIMULIFOLIA
PHACELIA DUBIA
CONOPHOLIS AMERICANA
PRUNUS SEROTINA
VACCINIUM STAMINEUM
RANUNCULUS RECURVATUS
VICIA ANGUSTIFOLIA
ROBINIA PSEUDO-ACACIA
PINUS VIRGINIANA
COMANDRA UMBELLATA
MAZUS JAPONICUS
OROBANCHE UNIFLORA
GERANIUM CAROLINIANUM
LIRIODENDRON TULIPIFERA
OXALIS STRICTA
TRIFOLIUM HYBRIDUM
HYDROPHYLLUM VIRGINIANUM
SMILACINA RACEMOSA
SOLANUM DULCAMARA
CHIONANTHUS VIRGINICUS
TRADESCANTIA VIRGINIANA
RUBUS FLAGELLARIS
SALVIA LYRATA
HYPOXIS HIRSUTA
LEUCOTHOE RACEMOSA
LONICERA JAPONICA
OXALIS VIOLACEA
HIERACIUM VENOSUM
SISYRINCHIUM SP
MELILOTUS OFFICINALIS
GAYLUSSACIA BACCATA
JUGLANS NIGRA
ILEX OPACA
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JANUARY
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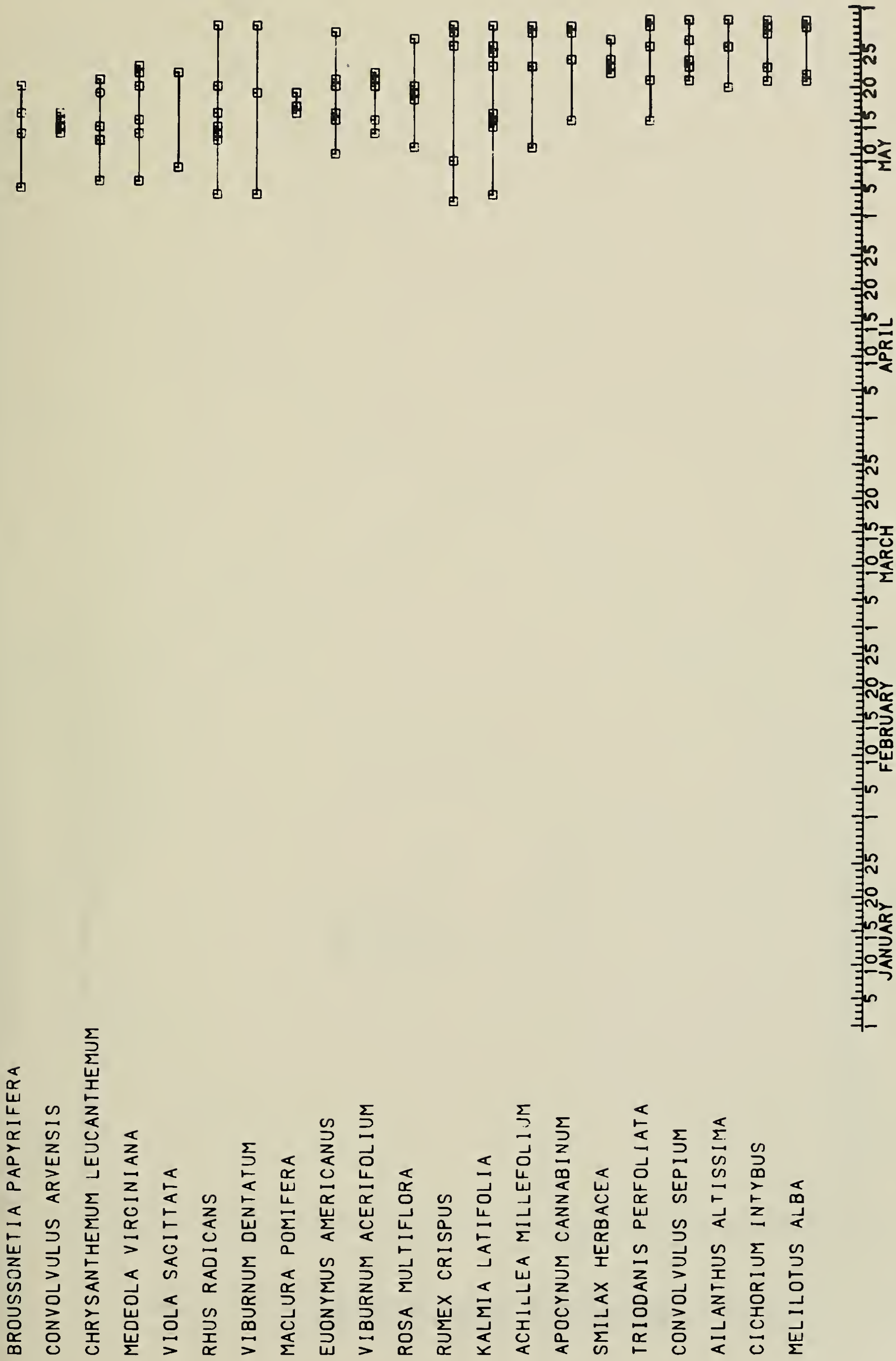
BROUSSONETIA PAPYRIFERA
CONVOLVULUS ARVENSIS
CHRYSANTHEMUM LEUCANTHEMUM
MEDEOLA VIRGINIANA
VIOLA SAGITTATA
RHUS RADICANS
VIBURNUM DENTATUM
MACLURA POMIFERA
EUONYMUS AMERICANUS
VIBURNUM ACERIFOLIUM
ROSA MULTIFLORA
RUMEX CRISPUS
KALMIA LATIFOLIA
ACHILLEA MILLEFOLIUM
APOCYNUM CANNABINUM
SMILAX HERBACEA
TRIODANIS PERFOLIATA
CONVOLVULUS SEPIUM
AILANTHUS ALTISSIMA
CICHORIUM INTYBUS
MELILOTUS ALBA
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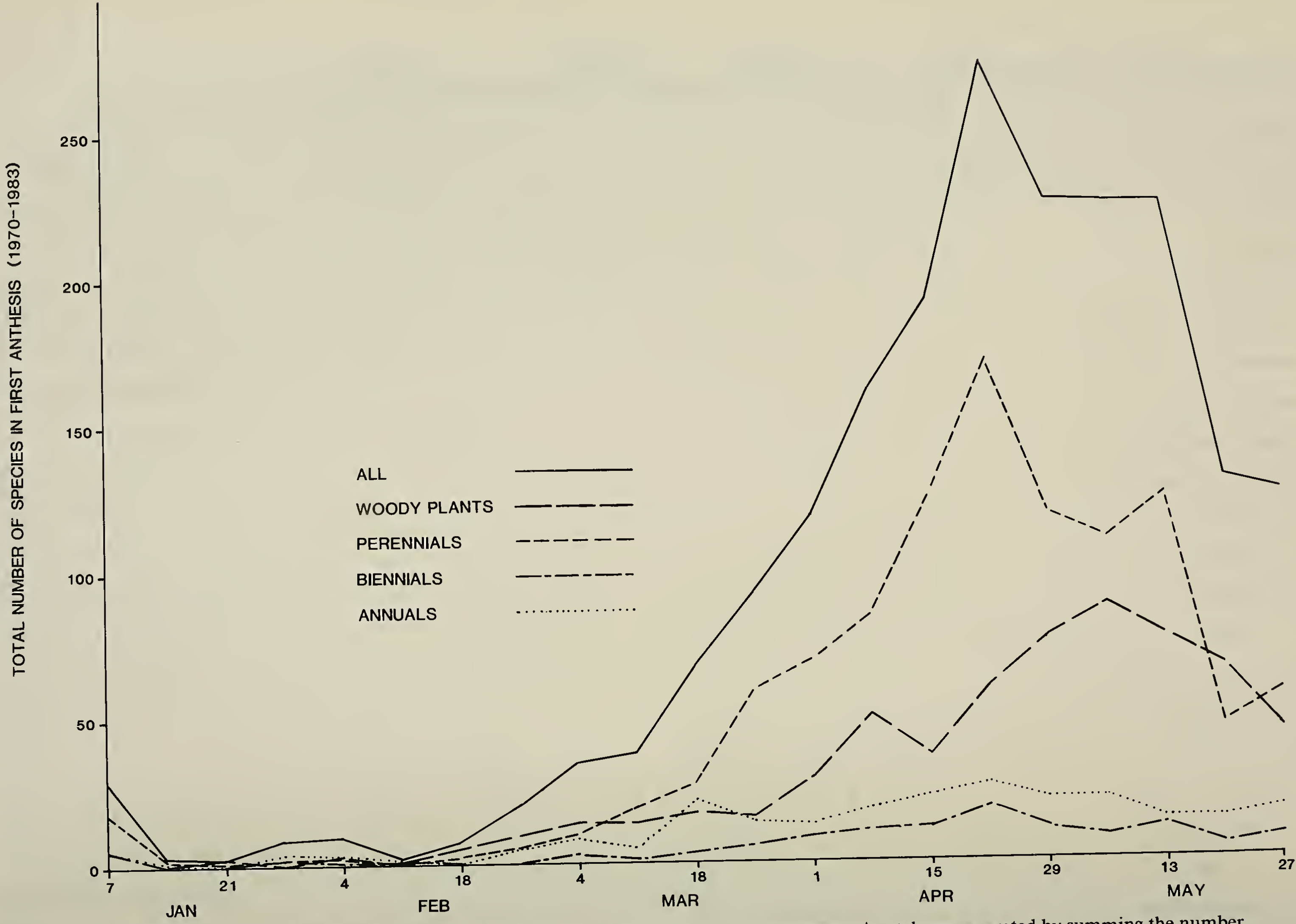

Fig. 3. Graphs of cumulative totals of species coming into flower week by week during the season. A total was generated by summing the number of species coming into flower over a prescribed one-week period in all 14 years studied. The top, solid line shows the total number of species coming into flower during a given one-week period. The other lines indicate the first-flowering progression for each of the different life-forms of plants

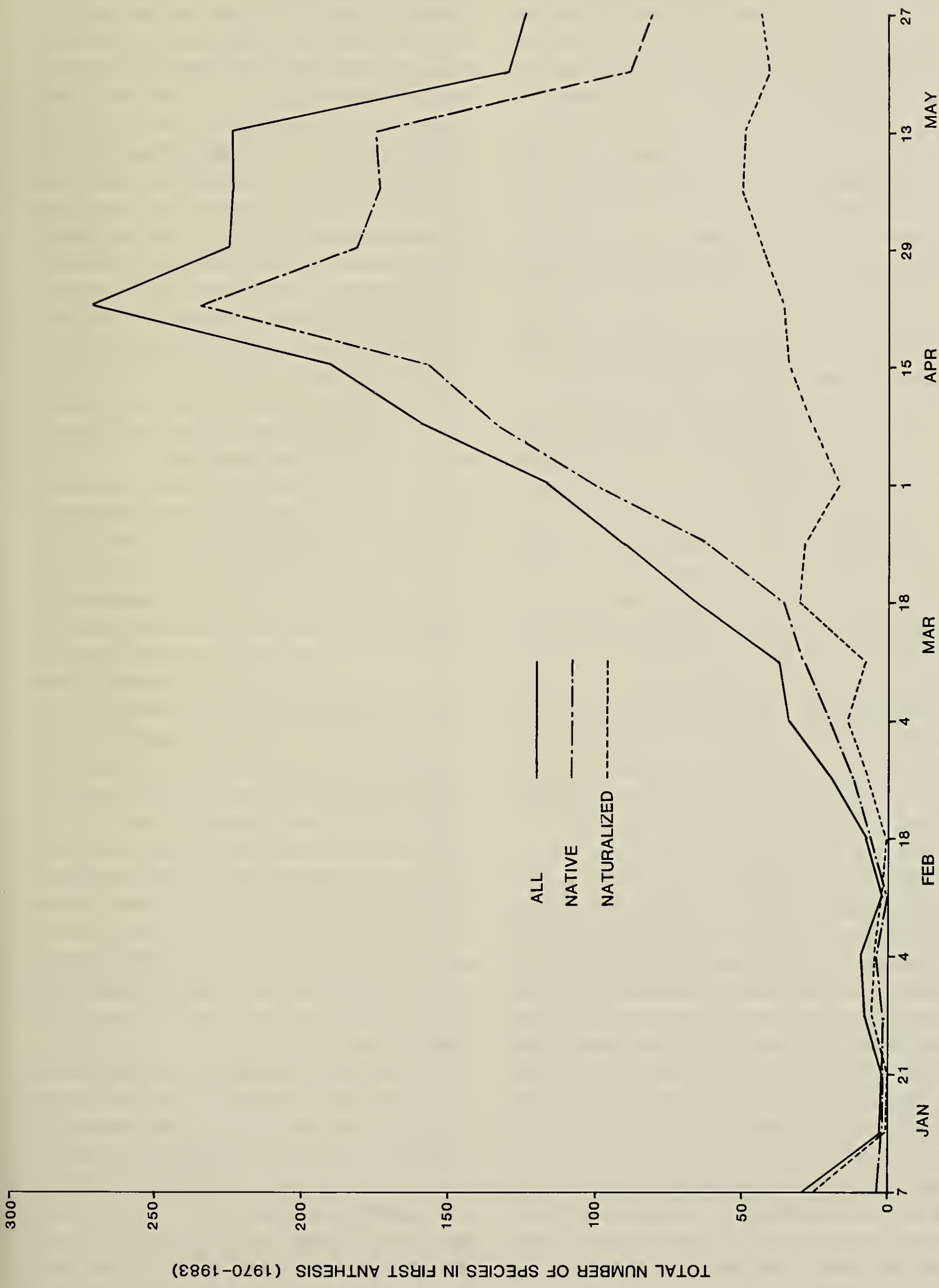

Fig. 4. Graphs of cumulative totals of species coming into flower week by week during the season, as in Fig. 3, but with the total broken down by "native" and "naturalized" instead of by life-forms.

mium amplexicaule), and speedwell (*Veronica agrestis*). Ward (1881) and Hitchcock and Standley (1919) noted that in our area several weedy species with inconspicuous flowers bloom quite early in the season or even during the winter months when the weather is warm or when they are growing in especially sunny or protected spots. Penfound (1956) observed that *Taraxacum officinale* flowers discontinuously throughout the year, even in December and January. It is obvious that some of our weedy species bloom in December as well as January. Variability in first-flowering dates of weedy species is discussed in more detail later.

Naturalized exotic species make up two-thirds of the species that start to flower between January 1st and mid-February. The number of naturalized exotic species coming into flower increases gradually through the course of the season. Looking at the season as a whole, exotic species account for approximately 25% of the plants observed.

Native species begin to bloom in late February. In mid- to late March, the number of native plants coming into bloom increases sharply. This rate continues to increase sharply until mid- to late April when the number of first-flowering plants reaches a peak. The level then drops at an equally sharp rate until late May when there is a slight resurgence (Fig. 4).

Initially we thought that the drop in first-flowerings in late May was caused by a lack of sustained interest on the part of our observers in recording first-flowering dates after the initial excitement of looking for spring wildflowers in bloom. However, other researchers have noted a similar peak and fall in the number of species coming into bloom. Anderson and Hubricht (1940) observed a drop in the number of species coming into bloom after the April peak. They attributed this peak to woodland plants whose blooms must be completed by the time the leaves of the canopy trees are fully expanded, when the available light that reaches the forest floor is greatly reduced. This same reasoning was used by Wolfe et al. (1949), Jackson (1966), Taylor (1974), and Heinrich (1976) to explain similar spring peaks in their data. Anderson and Hubricht (1940) noted that treeless habitats are not under the same pressure and do not experience a spring peak. Rather, the number of plants beginning to bloom rises slowly to reach a peak in midsummer. It is likely that the slight increase in the number of plants coming into flower that we observed in late May can be attributed to herbaceous species of open habitats, such as field bindweed (*Convolvulus arvensis*), ox-eye daisy (*Chrysanthemum leucanthemum*), yarrow (*Achillea millefolium*), chicory (*Cichorium intybus*), and yellow sweet clover (*Melilotus officinalis*), and to late-blooming woody species.

To analyze the controlling factors in flowering peaks, the species observed were divided into categories by life-form. This showed that woody plants accounted for 31% of the records. Sporadic blooming of woody plants has been recorded prior to mid-February. This was observed in silver maple (*Acer saccharinum*), common alder (*Alnus serrulata*), and American elm (*Ulmus americana*). The early blooming of *Acer* and *Ulmus* in our area was also noted by Hitchcock and Standley (1919). Generally, however, the woody plants in the D.C. region start their blooming period in late February. Flowering remains at a low level until late March, when the number of species coming into flower begins to climb. The number continues to climb steadily until it reaches a peak in late April. It then falls slightly and remains at a constant level through June 1st (Fig. 3).

The peak in blooming of woody plants can be partially explained by the fact that many of the woody plants studied are wind-pollinated. It is most advantageous for wind-pollination to occur before trees leaf out completely and their leaves impede air movement. This rationale has been proposed by Heinrich (1976) and Whitehead (1969). Our data tend to support this proposition. Most of the wind-pollinated woody species, e.g., oaks (*Quercus* spp.), hazelnuts (*Corylus* spp.), river birch (*Betula nigra*), common alder (*Alnus serrulata*), American beech (*Fagus grandifolia*), American elm (*Ulmus americana*), and white ash (*Fraxinus americana*) begin to bloom before April 20 on the average. However, some wind-pollinated trees were observed to begin blooming after May 1st on the average. These are paper-mulberry (*Broussonetia papyrifera*), hickories (*Carya* spp.), black walnut (*Juglans nigra*), and osage-orange (*Maclura pomifera*). Most of the woody species that were observed beginning to bloom after May 1st on the average are not wind-pollinated, e.g., multiflora rose (*Rosa multiflora*), Japanese honeysuckle (*Lonicera japonica*), northern dewberry (*Rubus flagellaris*), mountain laurel (*Kalmia latifolia*), tulip poplar (*Liriodendron tulipifera*), maple-leaved viburnum (*Viburnum acerifolium*), and deerberry and blueberries (*Vaccinium* spp.). Pollination information was obtained from Proctor and Yeo (1972) and Cronquist (1981).

The majority (53%) of the records are of perennial species. The perennial group, like the woody-plant group, begins blooming in late February. The rate of increase of species coming into flower, however, is much faster than among the woody plants observed. The number of first-flowering perennials reaches a peak in mid- to late April. This is slightly earlier than that for woody plants. The number of perennials coming into flower drops dramatically after this peak until late May when it shows a resurgence (Fig. 3).

Many of the perennials studied are woodland spring ephemerals, e.g., jack-in-the-pulpit (*Arisaema triphyllum*), spring beauty (*Claytonia virginica*), harbinger-of-spring (*Erigenia bulbosa*), cut-leaved toothwort (*Dentaria laciniata*), toadshade (*Trillium sessile*). As mentioned previously, these plants must complete a large part of their life-cycle before the trees have finished leafing out, cutting off their light supply. Thus, the woodland spring ephemerals are highly adapted to take advantage of the narrow "window" of time in early spring when temperature, moisture, and light conditions allow renewed growth but before the canopy closes over and greatly reduces the available light on the forest floor. This adaptive peak most likely is what explains the sharp spring peak in the blooming of perennials.

Annuals and biennials make up a relatively small portion of spring-flowering species recorded. Approximately 5% of the species recorded over the entire study period were biennials, and 11% were annuals. Once the first annuals and biennials begin to bloom the total numbers of these species coming into flower each one-week period remain relatively constant throughout the spring season and have little influence on the cumulative peak, in late April, for all plants coming into flower in a given week (Fig. 3, solid line).

The peaks in the cumulative flowering curves for all species recorded are formed mainly by native perennials and woody plants (cf. Figs. 3 and 4). Biennials, annuals, and all naturalized plants in this study come into flower at a relatively uniform rate throughout the season. Their flowering levels do not have a large impact on the overall peaks of flowering for all species.

The range of year-to-year first-flowering dates varies considerably from species to species (Fig. 2). It is to be expected that species whose flowering is primarily governed by day-length will show the least year-to-year variability in first-flowering date while those species whose flowering is governed more by climatic conditions will show the most year-to-year variability. Leopold and Jones (1947), Jacques and Hilleary (1945), and Moss (1960) suggested that the earliest blooming species are likely to show the most annual variation in the start of flowering. Our data support these suggestions. Table 1 shows that the average departure from the average first-flowering date decreases progressively through the spring

Table 1.—Average number of days of departure from average dates of first-flowering, tabulated in weekly intervals.

Week of average first flowering date	Average of departures from average first flowering date*
Jan 29–Feb 5	26
Feb 6–Feb 12	22
Feb 13–Feb 19	**
Feb 20–Feb 26	11
Feb 27–Mar 5	27
Mar 6–Mar 12	14
Mar 13–Mar 19	14
Mar 20–Mar 26	18
Mar 27–Apr 2	10
Apr 3–Apr 9	7
Apr 10–Apr 16	8
Apr 17–Apr 23	7
Apr 24–Apr 30	6
May 1–May 7	6
May 8–May 14	6
May 15–May 21	5
May 21–May 27	4

* Examples from the week of March 13–March 19 are used here to illustrate how the average departure from average first-flowering date was computed. Five species, *Veronica hederaefolia, Claytonia virginica, Hepatica americana, Phlox subulata,* and *Tussilago farfara,* have average first-flowering dates in this week. The absolute value of the departure of each first-flowering date (in days) from each species' own average first-flowering date was calculated for each year for which a first-flowering date was recorded. For example, *Claytonia virginica* has an average first-flowering date of March 15. In 1982 its first-flowering date was March 24, which was 9 days later than the average. In 1971 its first-flowering date was March 13, which was 2 days earlier than the average. The absolute values of the departure from the average for these two years were 9 and 2 days, respectively. All of the absolute differences for all five species were totalled and then averaged together to come up with the overall average absolute departure for this one-week period.

** None of the species analyzed has an average flowering date in this time period.

season. The blooming times of early-flowering species may be more directly related to climate than the blooming times of late-flowering species and, therefore, may be reflecting the greater variation in the climate early in the season by the greater variation in their first blooming dates.

Temperature as a controlling factor is suggested particularly by the year-to-year variation in the average day of first-flowering. When all first-flowering dates are expressed in number of days from January 1 and these dates are then averaged over all species that bloom after March 1 for each year, the average day of first-flowering is seen to vary from the 101st (1977) to the 115th day (1971, 1982) of the year. This is a maximum fluctuation of two weeks. This kind of variation certainly supports the common notion of "early" and "late" springs. On the other hand, the average day of first-flowering is exactly the same for as many as three years (1975, 1978, 1983). The observations were too uncontrolled to carry this analysis any further.

Of the species studied, those with the most pronounced variation in first-flowering dates (60+ days) tend to be the weedier species. Most of these are exotic annuals, e.g., henbit (*Lamium amplexicaule*), bird's-eye speedwell (*Veronica agrestis*), whitlow-grass (*Draba verna*), common groundsel (*Senecio vulgaris*), and shepherd's-purse (*Capsella bursa-pastoris*). A small number of exotic perennials, e.g., false strawberry (*Duchesnea indica*) and white clover (*Trifolium repens*), also show high variability. In the case of some plants the first-flowering period would look much less variable if one were to select the most discrete clump of five or so dates from among the total observations that may span a relatively wide period. These are species such as chickweed (*Stellaria media*) and poor-man's pepper (*Lepidium virginicum*) that begin their main flowering period in, say, April or May but often have scattered individuals or populations that begin flowering much earlier in sheltered locations or during a mild year. In reality the more discrete cluster of dates represents more accurately the typical range of first-flowering dates for the species. Sporadic early flowering, owing to habitat protection, mild weather, or genetic diversity among populations or individuals, is especially likely among weedy species whose success as weeds may be due in part to flowering times that are less synchronized than in other species. They certainly do not flower uniformly throughout the year, although they may bloom sporadically in different seasons. Budd and Campbell (1959) suggest that in the range weeds that they studied early flowering may be an adaptation to enable the species to set seed before competitive grass species commence their rapid growth. Sporadic blooming aside, these species do have a time when a large proportion of their plants come into bloom. This probably would become apparent after many observations.

The native perennials that display long flowering spans, viz., blunt-leaved hepatica (*Hepatica americana*) and mosspink (*Phlox subulata*), may have one or two very early records, while the rest of the records are in a relatively discrete cluster. These early records may be aberrant, either recorded in a very warm year or recorded from a peculiar individual of a population in which the bulk of the population may have come into flower at a more predictable time.

Clearly, the onset of flowering in the spring is affected by a number of environmental variables. The earliest species vary the most in their flower initiation, but many species bloom year after year in a reasonably predictable time frame. This discrete pattern of flowering onset suggests, as many other studies have shown, a relatively precise adaptation to photoperiod and/or temperature regime (especially cumulative degree-days).

Some questions arise when attempting to interpret the flowering times of those species in our records with apparently discrete first-flowering spans. Although some species may truly flower in a quite discrete time span, there are at least two other possible explanations. On the one hand, in those cases where relatively few dates were recorded during the 14-year period there is less chance to vary, as, for example, in the cases of knawel (*Scleranthus annuus*), 5 records; narrow-leaved plantain (*Plantago lanceolata*), 5 records; and *Mazus japonicus,* 4 records. For such weedy species one would expect a more variable first-flowering span, which more records probably would show. Likewise, some of the species recorded toward the end of the final month (i.e., May) of the annual observation period may also appear to have discrete flowering periods when in fact a longer period (i.e., beyond June 1st) of recording might have shown that in some years first-flowering did not begin until after June 1st.

Given the rather uncontrolled way in which this study was conducted, one would not be justified in drawing more definite conclusions. Basically, we are presenting here a large set of observations that we think are of interest in themselves, and we have tried not to carry our analysis beyond what is justified by the nature of the data. Additional studies of individual species with a rigorous experimental design would be needed to answer the questions raised.

Acknowledgments

We are indebted to the numerous persons—109 to be exact—who voluntarily recorded one or more flowering dates on our charts over the 14-year period. Deserving special mention are Aaron Goldberg and John Wurdack, who both recorded many species year after year and were by far the most important contributors to the data for cultivated species. Several high school students in the Co-curriculum Program of the Madeira School, Greenway, Virginia, helped compile the records from the charts and punch the data on cards for processing; Helen Bartlett and Eugenia Minonda, in particular, provided indispensable assistance in the compilation. The initial computer programming and processing were done by Thomas Kopler. Kenneth McCormick did the programming for the computer-generated graph. Finally, special thanks are due Laura Lehtonen for her many hours of work on the preparation of the data for analysis.

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Appendix 1.—Alphabetical list of spring-blooming native and naturalized species of plants of the Washington, D.C., area for which the date of first-flowering was recorded one or more times during the years 1970 to 1983.

Species	Range of dates	Average date	No. of years
Acer negundo	3/16–4/15	4/4	12
Acer rubrum	2/22–4/2	3/11	14
Acer saccharinum	1/18–3/20	2/22	14
Acer saccharum	4/4–4/20	4/12	5
Achillea millefolium	5/12–5/30	5/22	7
Acorus calamus	5/22–5/24	5/23	2
Actaea pachypoda	4/29–4/29	4/29	1
Ailanthus altissima	5/21–5/31	5/27	4
Ajuga reptans	4/1–5/9	4/16	8
Alliaria officinalis	3/31–4/29	4/15	13
Allium vineale	5/27–5/27	5/27	1
Alnus serrulata	2/4–4/12	3/10	10
Amelanchier arborea	3/28–4/16	4/5	8
Amelanchier canadensis	4/2–4/18	4/9	6
Amelanchier laevis	4/17–4/23	4/20	2
Anagallis arvensis	5/29–5/29	5/29	1
Anemone quinquefolia	4/10–4/25	4/20	8
Anemonella thalictroides	3/25–4/26	4/7	13
Antennaria neglecta	4/10–5/4	4/25	3
Antennaria neodioica	4/10–5/7	4/22	5
Antennaria parlinii	5/9–5/9	5/9	1
Antennaria plantaginifolia	3/31–5/1	4/16	6
Anthemis arvensis	4/29–5/26	5/13	3
Anthoxanthum odoratum	4/12–5/2	4/22	6
Aplectrum hyemale	5/14–5/22	5/17	4
Apocynum androsaemifolium	5/26–5/26	5/26	1
Apocynum cannabinum	5/16–5/30	5/25	4
Aquilegia canadensis	4/4–5/7	4/21	13
Arabidopsis thaliana	3/29–5/9	4/18	4
Arabis laevigata	3/25–4/16	4/3	10
Arabis lyrata	3/19–5/11	4/11	9
Arabis patens	4/20–5/11	4/29	3
Aralia nudicaulis	4/25–4/25	4/25	1
Arisaema dracontium	5/8–5/15	5/12	2
Arisaema triphyllum	4/14–4/29	4/22	13
Aronia arbutifolia	4/19–5/9	5/2	7
Aronia melanocarpa	4/24–5/10	5/1	3
Aronia prunifolia	5/4–5/12	5/8	2
Asarum canadense	3/28–4/25	4/14	13
Asimina triloba	4/12–5/3	4/25	11
Asparagus officinalis	5/11–5/16	5/14	2
Barbarea verna	4/7–4/7	4/7	1
Barbarea vulgaris	3/20–4/20	4/14	10
Betula nigra	4/7–4/29	4/20	3
Brassica campestris	4/7–4/25	4/15	4
Brassica nigra	5/24–5/24	5/24	1
Brassica rapa	4/16–4/16	4/16	1
Broussonetia papyrifera	5/6–5/21	5/15	4
Caltha palustris	4/17–4/30	4/23	4
Capsella bursa-pastoris	1/1–5/9	3/28	10
Cardamine bulbosa	3/17–5/7	4/17	7
Cardamine hirsuta	1/1–3/21	2/27	14
Cardamine pensylvanica	3/19–5/7	4/11	6
Carex pensylvanica	4/11–4/16	4/14	2
Carex platyphylla	5/6–5/6	5/6	1
Carpinus caroliniana	3/27–4/29	4/10	6
Carya glabra	5/1–5/1	5/1	1
Carya tomentosa	5/2–5/7	5/5	2
Caulophyllum thalictroides	4/7–4/29	4/19	6
Ceanothus americanus	5/30–5/30	5/30	2
Celastrus orbiculatus	5/8–5/8	5/8	1
Celastrus scandens	5/5–5/11	5/8	2
Celtis occidentalis	4/29–4/29	4/29	1
Centaurea maculosa	5/24–5/24	5/24	1
Cerastium arvense	4/14–5/10	4/25	10
Cercis canadensis	3/23–5/2	4/12	12
Chaerophyllum procumbens	4/12–5/1	4/19	11
Chamaelirium luteum	5/12–5/12	5/12	1
Chelidonium majus	4/19–5/5	4/27	6
Chionanthus virginicus	4/29–5/19	5/10	12
Chrysanthemum leucanthemum	5/7–5/22	5/16	7
Chrysogonum virginianum	4/20–5/11	5/3	9
Cichorium intybus	5/22–5/31	5/27	6
Claytonia virginica	2/19–4/1	3/15	13
Clematis viorna	5/19–5/19	5/19	1
Comandra umbellata	4/29–5/23	5/7	4
Commelina communis	5/31–5/31	5/31	1
Comptonia peregrina	4/2–4/11	4/6	4
Conium maculatum	5/29–5/29	5/29	1
Conopholis americana	4/4–5/17	5/5	7
Convolvulus arvensis	5/14–5/17	5/16	4
Convolvulus sepium	5/22–5/31	5/26	5
Cornus florida	4/6–5/12	4/21	14
Coronilla varia	5/29–5/29	5/29	1
Corydalis flavula	3/25–4/21	4/8	14
Corylus americana	3/1–3/17	3/8	4
Corylus cornuta	2/23–3/19	3/7	2
Crepis japonica	5/9–5/9	5/9	1
Cryptotaenia canadensis	5/31–5/31	5/31	2
Cymbalaria muralis	4/3–4/29	4/16	2
Cynodon dactylon	5/31–5/31	5/31	1
Cynoglossum virginianum	5/14–5/14	5/14	1
Cypripedium acaule	4/17–5/10	4/28	6
Cypripedium calceolus	4/29–5/10	5/4	6

Appendix 1.—Continued.

Species	Range of dates	Average date	No. of years
Cytisus scoparius	4/28–5/8	5/2	3
Dactylis glomerata	4/19–5/4	4/29	4
Daucus carota	5/31–5/31	5/31	2
Dentaria heterophylla	3/20–4/24	4/5	11
Dentaria laciniata	3/10–4/11	3/25	14
Dicentra canadensis	4/1–4/29	4/12	10
Dicentra cucularia	3/19–4/16	4/3	14
Dioscorea quaternata	5/21–5/29	5/24	3
Dioscorea villosa	5/13–5/13	5/13	1
Diospyros virginiana	5/31–5/31	5/31	1
Dirca palustris	3/13–4/8	3/26	8
Dodecatheon meadia	4/17–4/25	4/22	3
Draba verna	1/13–3/29	3/8	11
Duchesnea indica	1/2–4/30	3/21	12
Epigaea repens	3/17–4/24	4/4	11
**Equisetum arvense*	4/19–4/19	4/19	2
Erigenia bulbosa	3/1–4/11	3/16	13
Erigeron annuus	5/15–5/15	5/15	1
Erigeron philadelphicus	5/5–5/11	5/8	3
Erigeron pulchellus	4/27–5/13	5/6	3
Erodium cicutarium	1/1–5/2	3/23	7
Erythronium albidum	4/7–4/19	4/15	9
Erythronium americanum	3/23–4/16	4/1	14
Euonymus americanus	5/11–5/29	5/19	7
Euphorbia commutata	4/20–4/20	4/20	1
Euphorbia cyparissias	4/19–5/7	4/30	3
Euphorbia supina	5/25–5/25	5/25	1
Fagus grandifolia	4/11–4/23	4/17	3
Festuca ovina	5/15–5/30	5/23	2
Floerkea proserpinacoides	4/9–4/25	4/18	9
Fragaria virginiana	4/4–5/9	4/17	10
Fraxinus americana	4/8–4/8	4/8	1
Galinsoga ciliata	5/20–5/22	5/21	2
Galium aparine	4/22–5/2	4/29	9
Gaylussacia baccata	4/30–5/26	5/13	4
Gaylussacia frondosa	5/12–5/20	5/16	2
Geranium carolinianum	4/5–5/28	5/8	6
Geranium maculatum	4/11–5/4	4/22	12
Geranium molle	5/15–5/15	5/15	1
Geum vernum	4/18–4/18	4/18	1
Gillenia trifoliata	5/23–5/23	5/23	1
Glechoma hederacea	3/7–4/16	3/31	13
Hepatica americana	1/9–4/11	3/16	13
Hesperis matronalis	4/25–5/8	4/30	4
Heuchera americana	5/15–5/21	5/17	3
Hieracium pratense	5/20–5/23	5/22	2
Hieracium venosum	5/5–5/23	5/13	4
Houstonia caerulea	2/22–4/25	4/4	14
Houstonia purpurea	5/23–5/23	5/23	1
Hybanthus concolor	5/5–5/11	5/7	3
Hydrophyllum virginianum	4/29–5/17	5/9	4

Appendix 1.—Continued.

Species	Range of dates	Average date	No. of years
Hypericum perforatum	5/30–5/30	5/30	1
Hypoxis hirsuta	4/28–5/23	5/11	5
Ilex opaca	5/8–5/22	5/14	9
Ilex verticillata	5/22–5/31	5/27	3
Impatiens capensis	5/28–5/28	5/28	1
Iris cristata	4/30–5/11	5/4	3
Iris verna	4/29–4/29	4/29	1
Iris versicolor	5/8–5/26	5/16	3
Isotria verticillata	4/29–5/16	5/5	3
Jeffersonia diphylla	3/25–4/16	4/6	10
Juglans nigra	5/4–5/20	5/13	4
**Juniperus virginiana*	3/13–3/28	3/23	3
Kalmia angustifolia	5/16–5/22	5/18	3
Kalmia latifolia	5/5–5/30	5/20	10
Krigia dandelion	4/29–5/5	5/1	4
Lamium amplexicaule	1/2–4/18	2/28	14
Lamium purpureum	2/5–4/9	3/19	13
Lathyrus venosus	5/9–5/9	5/9	1
Leonurus cardiaca	5/22–5/29	5/26	2
Lepidium campestre	4/3–5/11	4/30	5
Lepidium virginicum	1/2–5/23	4/22	6
Leucothoe racemosa	4/25–5/23	5/11	4
Linaria canadensis	5/22–5/30	5/25	3
Lindera benzoin	3/7–4/11	3/27	14
Linum usitatissimum	4/11–4/11	4/11	1
Linum virginianum	5/23–5/23	5/23	1
Liparis lilifolia	5/21–5/29	5/25	2
Liquidambar styraciflua	4/19–4/30	4/24	5
Liriodendron tulipifera	4/21–5/21	5/8	14
Lithospermum arvense	4/25–4/25	4/25	1
Lobelia spicata	5/30–5/30	5/30	1
Lolium perenne	5/14–5/30	5/23	3
Lonicera japonica	4/17–5/30	5/11	9
Lonicera morrowii	4/20–5/6	4/28	2
Lonicera sempervirens	5/20–5/25	5/23	2
Lotus corniculatus	5/2–5/2	5/2	1
Lupinus perennis	5/7–5/7	5/7	1
Luzula campestris	3/24–4/16	4/8	3
Lyonia ligustrina	5/23–5/23	5/23	1
Lysimachia nummularia	5/20–5/24	5/22	3
Lysimachia quadrifolia	5/26–5/26	5/26	1
Lythrum salicaria	5/30–5/30	5/30	1
Maclura pomifera	5/17–5/20	5/19	5
Magnolia virginiana	5/3–5/22	5/13	5
Maianthemum canadense	4/19–5/7	4/30	5
Marrubium vulgare	5/29–5/29	5/29	2
Mazus japonicus	4/26–5/16	5/8	4
Medeola virginiana	5/7–5/24	5/16	7
Medicago lupulina	5/5–5/5	5/5	1
Medicago sativa	5/15–5/30	5/23	2
Melilotus alba	5/22–5/31	5/27	5
Melilotus officinalis	5/3–5/23	5/13	7
Mertensia virginica	3/12–4/13	4/2	14

Appendix 1.—Continued.

Species	Range of dates	Average date	No. of years
Mitchella repens	5/26–5/31	5/29	3
Mitella diphylla	4/17–5/2	4/23	5
Morus alba	4/19–5/5	4/26	5
Morus rubra	4/23–4/23	4/23	1
Muscari botryoides	3/21–4/24	4/6	9
Nepeta cataria	4/16–4/16	4/16	1
Nuphar advena	5/20–5/20	5/20	1
Nymphaea odorata	5/16–5/16	5/16	1
Nyssa sylvatica	5/3–5/27	5/15	8
Obolaria virginica	4/12–4/30	4/20	4
Oenothera laciniata	5/26–5/26	5/26	1
Oenothera tetragona	5/30–5/30	5/30	1
Opuntia humifusa	5/30–5/30	5/30	1
Orchis spectabilis	4/21–5/14	5/2	5
Ornithogalum nutans	4/10–4/25	4/18	5
Ornithogalum umbellatum	4/18–5/6	4/30	6
Orobanche uniflora	4/30–5/15	5/8	7
Orontium aquaticum	4/22–5/11	4/30	3
Osmorhiza claytoni	4/16–5/2	4/24	9
Osmorhiza longistylis	4/16–5/7	4/25	9
**Osmunda cinnamomea*	4/29–4/29	4/29	1
**Osmunda claytoniana*	4/29–4/29	4/29	1
Ostrya virginiana	3/27–4/29	4/15	3
Oxalis corniculata	4/12–4/12	4/12	1
Oxalis europaea	4/27–4/30	4/29	2
Oxalis grandis	5/5–5/5	5/5	1
Oxalis stricta	5/2–5/15	5/8	4
Oxalis violacea	4/30–5/23	5/11	5
Panax trifolius	4/1–5/7	4/20	9
Paulownia tomentosa	4/9–5/9	5/2	12
Phacelia dubia	4/29–5/13	5/5	4
Phacelia ranunculacea	4/18–4/29	4/25	6
Phleum pratense	5/31–5/31	5/31	1
Phlox divaricata	3/12–4/24	4/11	13
Phlox subulata	1/1–4/10	3/16	14
Physocarpus opulifolius	5/15–5/28	5/19	4
Phytolacca americana	5/31–5/31	5/31	1
**Pinus strobus*	5/15–5/28	5/19	4
**Pinus virginiana*	5/2–5/9	5/7	4
Plantago lanceolata	4/25–5/16	5/3	7
Plantago rugelii	5/26–5/26	5/26	1
Plantago virginica	4/25–5/10	5/3	4
Platanus occidentalis	4/25–5/3	4/30	5
Poa annua	1/24–4/27	3/23	9
Poa cuspidata	3/31–4/28	4/12	5
Poa pratensis	4/12–5/8	4/29	4
Podophyllum peltatum	4/14–5/5	4/27	14
Polygonatum biflorum	5/3–5/28	5/10	6
Polygonatum canaliculatum	5/16–5/16	5/16	1
Polygonum aviculare	4/15–4/15	4/15	1
Polygonum hydropiperoides	5/28–5/28	5/28	1

Appendix 1.—Continued.

Species	Range of dates	Average date	No. of years
Polygonum persicaria	5/24–5/24	5/24	1
Populus deltoides	3/16–4/28	4/8	8
Populus grandidentata	3/29–3/29	3/29	1
Potentilla argentea	5/17–5/17	5/17	1
Potentilla canadensis	4/8–4/29	4/18	10
Potentilla norvegica	5/24–5/30	5/27	2
Potentilla recta	5/9–5/26	5/18	2
Potentilla simplex	4/20–5/9	4/28	5
Prunus americana	3/16–4/21	4/3	2
Prunus angustifolia	3/9–4/25	3/27	3
Prunus pensylvanica	4/19–4/30	4/23	4
Prunus serotina	4/12–5/17	5/5	13
Prunus virginiana	5/11–5/11	5/11	1
Ptelea trifoliata	5/16–5/29	5/23	2
Quercus alba	4/23–4/30	4/26	4
Quercus borealis	3/29–4/24	4/13	5
Quercus coccinea	4/24–4/29	4/27	2
Quercus palustris	3/30–5/1	4/17	4
Quercus phellos	4/19–5/4	4/27	4
Quercus prinus	4/29–4/29	4/29	1
Quercus stellata	4/29–5/3	5/1	4
Ranunculus abortivus	3/19–4/16	4/7	14
Ranunculus acris	4/18–4/18	4/18	1
Ranunculus bulbosus	3/27–5/9	4/21	10
Ranunculus ficaria	3/25–3/25	3/25	1
Ranunculus hispidus	4/7–5/6	4/23	3
Ranunculus micranthus	4/12–4/24	4/18	2
Ranunculus recurvatus	4/28–5/11	5/6	7
Ranunculus septentrionalis	4/5–4/24	4/13	11
Rhododendron nudiflorum	4/19–5/13	4/30	11
Rhododendron viscosum	5/26–5/26	5/26	1
Rhus aromatica	4/11–4/19	4/16	4
Rhus radicans	5/5–5/30	5/16	7
Rhus typhina	5/26–5/29	5/28	2
Rhus vernix	5/20–5/20	5/20	1
Robinia pseudo-acacia	4/19–5/15	5/7	12
Rosa carolina	5/23–5/23	5/23	1
Rosa multiflora	5/12–5/28	5/20	5
Rubus allegheniensis	4/23–5/24	5/7	3
Rubus argutus	5/16–5/16	5/16	1
Rubus enslenii	5/11–5/11	5/11	1
Rubus flagellaris	5/5–5/12	5/9	5
Rumex acetosella	4/2–5/22	4/27	8
Rumex crispus	5/4–5/30	5/20	5
Sagina decumbens	3/28–5/1	4/10	3
Sagittaria rigida	5/30–5/30	5/30	1
Salix alba	4/2–5/5	4/19	2
Salix humilis	3/20–3/28	3/25	3
Salix nigra	3/21–5/9	4/26	4
Salix sericea	3/27–4/5	3/31	3
Salvia lyrata	4/28–5/28	5/11	7
Sambucus canadensis	5/20–5/25	5/23	4

Appendix 1.—Continued.

Species	Range of dates	Average date	No. of years
Sanguinaria canadensis	3/13–4/4	3/26	13
Sanicula gregaria	5/7–5/22	5/15	2
Sarracenia purpurea	5/9–5/12	5/10	3
Sassafras albidum	3/25–4/24	4/11	13
Saxifraga pensylvanica	4/29–4/29	4/29	1
Saxifraga virginiensis	3/7–4/15	3/31	13
Scleranthus annuus	4/16–5/4	4/23	5
Scutellaria serrata	5/4–5/22	5/13	2
Sedum ternatum	4/25–5/10	5/2	11
Senecio aureus	3/10–5/7	4/12	12
Senecio crawfordii	5/12–5/12	5/12	1
Senecio smallii	5/9–5/9	5/9	2
Senecio vulgaris	1/7–4/27	3/11	4
Silene alba	5/5–5/10	5/8	2
Silene caroliniana	3/31–5/4	4/19	10
Silene vulgaris (cucubalus)	5/9–5/9	5/9	1
Sisymbrium officinale	5/20–5/31	5/26	2
Sisyrinchium spp.	4/30–5/30	5/13	7
Smilacina racemosa	4/30–5/21	5/9	11
Smilacina stellata	5/9–5/9	5/9	1
Smilax herbacea	5/23–5/28	5/25	4
Smilax rotundifolia	5/23–5/23	5/23	1
Solanum carolinense	5/28–5/31	5/29	3
Solanum dulcamara	4/26–5/21	5/10	8
Solidago juncea	5/26–5/26	5/26	1
Sonchus asper	5/22–5/22	5/22	1
Sonchus oleraceus	5/16–5/20	5/18	2
Sparganium eurycarpum	5/23–5/29	5/27	4
Staphylea trifolia	4/11–4/30	4/22	9
Stellaria graminea	5/30–5/31	5/31	2
Stellaria longifolia	5/5–5/5	5/5	1
Stellaria media	1/1–3/23	1/28	13
Stellaria pubera	3/20–4/18	4/8	12
Symplocarpus foetidus	1/1–3/14	2/9	12
Taenidia integerrima	5/22–5/22	5/22	1
Taraxacum officinale	1/1–3/21	2/1	14
Thalictrum dioicum	4/17–5/7	4/27	2
Thalictrum polygamum	5/23–5/23	5/23	1
Thaspium barbinode	5/7–5/11	5/9	2
Thlaspi arvense	5/17–5/17	5/17	1
Tiarella cordifolia	4/16–4/29	4/22	4
Tilia americana	5/31–5/31	5/31	2
Tradescantia virginiana	4/28–5/26	5/10	5
Tragopogon pratensis	5/12–5/16	5/14	2
Trifolium dubium	5/8–5/20	5/15	3
Trifolium hybridum	4/29–5/21	5/9	4
Trifolium pratense	4/25–5/10	5/4	8
Trifolium procumbens	5/23–5/23	5/23	1
Trifolium repens	1/2–5/19	4/10	6
Trillium sessile	4/2–4/16	4/8	12
Triodanis perfoliata	5/16–5/31	5/25	5
Triosteum angustifolium	5/9–5/9	5/9	1
**Tsuga canadensis*	4/24–4/30	4/26	3
Tussilago farfara	2/24–4/13	3/15	13
Typha angustifolia	5/29–5/29	5/29	1
Ulmus americana	2/1–3/22	3/2	14
Ulmus rubra	4/11–4/11	4/11	1
Urtica dioica	5/29–5/29	5/29	1
Uvularia perfoliata	4/21–5/10	5/2	8
Uvularia sessilifolia	4/8–5/1	4/19	9
Vaccinium angustifolium	4/22–4/24	4/23	2
Vaccinium atrococcum	4/7–5/9	4/26	3
Vaccinium corymbosum	4/10–5/13	4/23	6
Vaccinium stamineum	4/23–5/26	5/6	11
Vaccinium vacillans	4/20–5/9	4/26	7
Valeriana pauciflora	5/10–5/19	5/16	3
Veronica agrestis	1/2–4/12	2/28	9
Veronica arvensis	2/1–4/27	3/25	4
Veronica hederaefolia	2/23–4/11	3/18	14
Veronica officinalis	3/7–5/21	4/23	3
Veronica persica	3/3–4/30	3/31	7
Veronica serpyllifolia	5/15–5/15	5/15	1
Viburnum acerifolium	5/14–5/23	5/19	5
Viburnum dentatum	5/5–5/30	5/21	4
Viburnum prunifolium	4/11–5/4	4/25	12
Viburnum rafinesquianum	5/11–5/15	5/13	3
Viburnum recognitum	5/5–5/5	5/5	1
Vicia angustifolia	5/1–5/12	5/6	5
Vicia caroliniana	4/21–5/23	5/2	5
Vicia villosa	5/29–5/29	5/29	1
Viola affinis	4/1–4/27	4/17	5
Viola cucullata	4/4–4/13	4/10	3
Viola eriocarpa	3/18–5/2	4/12	13
Viola fimbriatula	4/12–5/9	4/24	3
Viola kitaibeliana	3/25–4/21	4/8	10
Viola papilionacea	3/14–4/16	4/3	14
Viola pedata	4/11–5/7	4/21	5
Viola primulifolia	4/21–5/9	5/4	4
Viola pubescens	4/12–4/16	4/14	2
Viola sagittata	5/9–5/23	5/16	4
Viola sororia	4/2–4/29	4/18	3
Viola striata	4/3–5/2	4/18	12
Viola triloba	4/29–5/10	5/3	3
Vitis labrusca	5/28–5/28	5/28	1
Vitis vulpina	5/23–5/25	5/24	2
Zizia aurea	3/25–5/19	4/15	9

* Non-flowering plants. Date of "first flowering" is date when spores are first released or when male cones begin to shed pollen.

Appendix 2.—Alphabetical list of spring-blooming cultivated species of plants of the Washington, D.C. area for which the date of first-flowering was recorded more than one time during the years 1970 to 1983.

Species	Range of dates	Average date	No. of years
Acer campestre	5/2–5/3	5/3	2
Acer palmatum	4/1–4/27	4/16	5
Acer platanoides	3/25–4/25	4/9	10
Acer pseudo-platanus	4/5–5/10	4/27	10
Actinidia arguta	5/10–5/24	5/19	4
Adonis amurensis	2/20–3/15	3/7	3
Aegopodium podagraria	5/21–5/26	5/24	2
Aesculus glabra	4/25–5/10	5/2	4
Aesculus hippocastanum	4/19–5/15	5/2	9
Aesculus pavia	4/25–5/4	4/30	5
Akebia quinata	4/11–4/17	4/14	4
Alchemilla vulgaris	4/19–4/24	4/22	3
Allium christophii	5/15–5/15	5/15	2
Allium fistulosum	5/2–5/16	5/8	3
Allium giganteum	5/21–5/29	5/25	2
Allium schoenoprasum	5/15–5/20	5/18	2
Amsonia tabernaemontana	4/25–5/4	4/30	4
Anemone "De Caen"	4/9–4/10	4/10	2
Anemone blanda	2/21–5/23	3/28	7
Anemone pulsatilla	3/15–4/2	3/21	3
Angelica archangelica	5/14–5/15	5/15	2
Antirrhinum majus	5/21–5/30	5/26	2
Aquilegia ecalcarata	5/1–5/7	5/4	2
Aquilegia flabellata	4/22–4/24	4/23	3
Arabis caucasica	1/26–4/2	3/1	3
Arctostaphylos uva-ursi	4/11–4/19	4/16	4
Arenaria grandiflora	5/15–5/15	5/15	2
Arenaria montana	5/6–5/15	5/9	3
Arisaema sikokianum	4/22–4/26	4/25	4
Arisaema thunbergii	4/30–5/2	5/1	2
Arisaema vingens	4/30–5/2	5/1	2
Aristolochia durior	5/15–5/16	5/16	2
Armeria juncea	4/17–4/26	4/22	2
Armeria juniperifolia	4/5–4/13	4/9	2
Armeria maritima	5/6–5/10	5/9	3
Armoracia rusticana	5/3–5/7	5/5	2
Arum italicum spp. *pictum*	5/15–5/26	5/21	2
Asarum minus	5/1–5/2	5/2	2
Asarum naniflora	4/19–5/2	4/26	2
Asarum shuttleworthii	4/19–5/9	4/30	4
Asarum virginicum	4/2–4/19	4/11	2
Aucuba japonica	3/11–4/18	4/1	5
Baptisia australis	5/2–5/10	5/6	3
Berberis gagnepainii	4/7–4/8	4/8	2
Berberis julianae	3/27–4/20	4/9	4
Berberis thunbergii	3/17–4/29	4/11	6
Betula pendula	4/4–4/10	4/7	2
Betula platyphylla	4/4–4/12	4/9	4

Appendix 2.—Continued.

Species	Range of dates	Average date	No. of years
Betula populifolia	4/26–4/30	4/28	2
Bletilla striata	5/15–5/17	5/16	3
Borago officinalis	5/29–5/30	5/30	2
Brassica oleracea	3/17–4/10	3/29	2
Buxus semperiverens	3/6–4/13	3/26	6
Calendula officinalis	4/30–5/30	5/15	2
Calycanthus floridus	4/26–5/15	5/7	4
Camellia japonica	1/27–4/6	3/12	11
Campanula rotundifolia	5/9–5/30	5/16	3
Caragana arborescens	4/19–5/1	4/25	3
Carum carvi	4/25–5/29	5/7	4
Carya illinoensis	5/6–5/18	5/11	3
Catalpa speciosa	5/17–5/30	5/25	6
Centaurea montana	5/2–5/7	5/5	2
Centranthus ruber	5/2–5/15	5/8	3
*Cephalotaxus harringtonia	4/16–4/17	4/17	2
Cercidiphyllum japonicum	3/24–4/6	3/31	4
Cercis chinensis	4/17–5/1	4/24	2
Chaenomeles japonica	1/15–4/16	3/3	5
Chaenomeles lagenaria	1/12–4/11	3/9	4
Chaenomeles speciosa	3/17–3/19	3/18	2
Chaenomeles sp.	1/1–3/29	2/12	4
*Chamaecyparis pisifera	4/5–5/14	4/25	2
Cheiranthus cheiri	3/20–4/19	4/4	3
Chelidonium japonicum	4/13–4/26	4/21	3
Chimonanthus praecox	1/1–3/15	2/4	4
Chionanthus retusus	5/3–5/15	5/8	3
Chionodoxa luciliae	3/12–4/8	3/22	10
Chloranthus japonicus	4/5–4/17	4/14	4
Chrysanthemum coccineum	5/7–5/9	5/8	2
Chrysanthemum parthenium	5/29–5/29	5/29	2
Cladrastis lutea	5/5–5/10	5/8	2
Clematis addisonii	4/26–5/8	5/2	3
Clematis albicoma	4/26–5/2	4/28	3
Clematis coactilis	4/26–5/8	5/2	3
Clematis integrifolia	5/15–5/16	5/16	2
Clematis versicolor	5/16–5/27	5/22	2
Clematis viticaulis	5/13–5/22	5/17	3
Convallaria majalis	4/19–5/5	4/29	8
Coriandrum sativum	5/2–5/29	5/16	2
Coriaria japonica	5/23–5/26	5/25	2
Cornus kousa	5/16–5/27	5/22	5
Cornus mas	1/27–3/22	3/6	14
Corydalis ambigua	3/29–4/13	4/7	3
Corydalis lutea	4/2–4/18	4/12	3
Corydalis ochroleuca	4/17–4/20	4/19	2
Corylopsis pauciflora	3/14–4/5	3/25	5
Corylus avellana	1/2–4/4	3/2	8
Cotinus coggygria	5/22–5/23	5/23	2

Appendix 2.—Continued.

Species	Range of dates	Average date	No. of years
Crataegus mollis	3/23–4/13	4/6	11
Crataegus phaenopyrum	5/27–5/29	5/28	2
Crocus biflorus var. *weldenii*	2/27–3/20	3/10	2
Crocus chrysanthus	1/28–2/11	2/4	2
Crocus etruscus	3/13–3/20	3/17	2
Crocus flavus	1/10–3/13	2/14	5
Crocus fleischeri	2/27–3/20	3/10	2
Crocus sieberi	1/10–3/20	2/16	5
Crocus tomasinianus	3/17–3/25	3/21	3
Crocus vernus	3/10–3/15	3/13	2
Crocus spp.	2/4–3/14	2/18	9
Croton alabamensis	4/2–4/17	4/10	2
**Cryptomeria japonica*	3/13–3/15	3/14	2
**Cunninghamia lanceolata*	4/19–4/26	4/23	2
Cyclamen coum	2/22–3/9	3/2	2
Daphne genkwa	3/27–4/14	4/7	3
Daphne odora	3/12–3/27	3/21	4
Daphne retusa	4/2–4/17	4/12	4
Datura stramonium	5/22–5/24	5/23	2
Delphinium tricorne	5/4–5/8	5/6	3
Dentaria multifida	4/13–4/22	4/18	2
Dianthus barbatus	5/2–5/7	5/5	2
Dianthus caryophyllus	4/24–5/20	5/7	2
Dicentra eximia	4/12–5/9	4/24	4
Dicentra formosa	4/17–4/24	4/21	2
Dicentra formosa var. *oregana*	4/20–4/24	4/22	2
Dicentra spectabilis	4/20–5/10	4/29	4
Dictamnus albus	5/7–5/9	5/8	3
Digitalis grandiflora	5/22–5/29	5/26	2
Digitalis purpurea	5/10–5/24	5/18	4
Draba rigida	3/20–3/29	3/25	2
Dracocephalum calophyllum	5/23–5/27	5/25	2
Endymion non-scriptus	4/27–5/4	5/1	2
Enkianthus campanulatus	5/6–5/28	5/17	2
Epimedium grandiflorum	4/2–4/17	4/11	5
Epimedium perralderanum	4/10–4/17	4/14	3
Epimedium sagittatum	4/10–5/2	4/21	2
Epimedium sempervirens	4/13–4/16	4/15	2
Epimedium × rubrum	4/5–4/14	4/10	3
Epimedium × versicolor	4/10–4/13	4/12	2
Epimedium × warleyense	4/2–4/14	4/9	4
Eranthis hyemalis	1/27–3/22	2/27	13
Erica carnea	2/2–4/21	3/19	6
Erythronium rostratum	3/27–3/29	3/28	2

Appendix 2.—Continued.

Species	Range of dates	Average date	No. of years
Eschscholzia californica	5/3–5/24	5/18	4
Eunomia oppositifolia	3/5–3/27	3/17	3
Euonymus alata	4/28–5/23	5/7	5
Euphorbia epithymoides	4/26–5/1	4/29	2
Forsythia suspensa	3/12–3/19	3/15	4
Forsythia spp.	1/1–3/22	2/25	8
Fothergilla gardenii	4/19–4/30	4/24	3
Fraxinus excelsior	4/8–4/16	4/12	3
Fritillaria imperialis	4/4–4/10	4/7	2
Fritillaria meleagris	4/5–4/22	4/15	3
Gaillardia pulchella	5/17–5/24	5/21	3
Galanthus elwesii	2/14–3/10	2/22	9
Galanthus nivalis	1/1–3/15	2/17	14
Galax urceolata	5/22–5/29	5/26	3
Galium odoratum	4/23–5/3	4/27	3
Genista sagittalis	5/16–5/27	5/22	2
Geranium macrorrhizum	5/7–5/16	5/10	3
Geranium phaeum	5/2–5/13	5/8	2
Geum rivale	3/13–3/27	3/20	2
Geum urbanum	5/15–5/20	5/18	2
**Ginkgo biloba*	4/19–5/2	4/25	4
Glaucium flavum	5/15–5/20	5/18	2
Gleditsia triacanthos	5/9–5/17	5/11	5
Globularia cordifolia	4/26–5/7	5/1	3
Gymnocladus dioica	5/18–5/31	5/24	3
Gypsophila repens	5/2–5/30	5/15	3
Halesia carolina	4/19–5/2	4/25	5
Hamamelis mollis	1/31–3/22	2/22	6
Hamamelis vernalis	2/1–2/27	2/14	2
Helianthemum nummularium	5/1–5/30	5/16	2
Heliotropium arborescens	5/20–5/29	5/25	2
Helleborus niger	3/5–3/17	3/9	4
Helleborus orientalis	2/14–3/20	3/5	5
Hemerocallis minor	5/20–5/22	5/21	2
Hepatica nobilis	3/5–3/20	3/14	5
Heuchera sanguinea	4/26–5/7	5/2	4
Hyacinthus orientalis	3/11–4/1	3/19	11
Hydrangea anomala	5/16–5/22	5/20	3
Hypericum fragile	5/15–5/27	5/21	2
Iberis sempervirens	1/1–4/5	3/6	7
Ilex aquifolium	4/14–4/26	4/20	2
Ilex crenata	5/24–5/29	5/26	3
Ilex glabra	5/30–5/31	5/31	3
Illicium floridanum	4/2–5/2	4/15	4
Ipheion uniflorum	3/29–4/17	4/7	3
Iris bakerana	3/1–3/17	3/9	3
Iris danfordiae	2/18–4/1	3/4	9
Iris gracilipes	5/2–5/16	5/8	3
Iris histrioides	3/1–3/9	3/5	2
Iris pseudacorus	5/8–5/30	5/17	3

Appendix 2.—Continued.

Species	Range of dates	Average date	No. of years
Iris reticulata	2/22–3/15	3/5	9
Iris × germanica	1/12–5/20	4/11	7
Isatis tinctoria	4/19–4/30	4/24	3
Itea virginica	5/29–5/31	5/30	4
Jasminum nudiflorum	1/1–3/22	2/10	14
Jeffersonia dubia	3/29–4/17	4/7	3
Kerria japonica	4/18–4/20	4/19	2
Kolkwitzia amabilis	5/3–5/20	5/11	3
Laburnum anagyroides	4/20–5/10	5/3	4
**Larix decidua*	4/4–4/20	4/12	2
Lavandula pinnata	5/28–5/29	5/29	2
Leitneria floridana	4/8–4/16	4/11	5
Leucojum aestivum	4/17–4/20	4/18	3
Leucothoe fontanesiana	4/24–5/2	4/29	3
Limnanthes alba	5/14–5/15	5/15	2
Linaria annua	4/10–5/1	4/21	2
Linum perenne	4/24–4/30	4/27	2
Lonicera fragrantissima	1/2–3/22	2/20	14
Lonicera maackii	5/7–5/8	5/8	2
Loropetalum chinense	4/11–5/15	4/25	3
Lychnis coronaria	5/22–5/30	5/26	2
Lyonia mariana	5/17–5/30	5/24	2
Magnolia acuminata	5/2–5/10	5/6	2
Magnolia ashei	5/15–5/27	5/23	3
Magnolia grandiflora	5/11–5/30	5/23	12
Magnolia kobus	3/19–4/5	3/28	2
Magnolia macrophylla	5/18–5/30	5/23	4
Magnolia stellata	3/4–3/28	3/17	14
Magnolia tripetala	5/1–5/11	5/6	4
Magnolia × loebneri	3/5–3/27	3/16	2
Magnolia × soulangiana	3/5–4/8	3/22	14
Mahonia aquifolium	3/20–4/5	3/29	5
Mahonia bealei	1/1–3/14	2/12	4
Mahonia repens	4/5–4/5	4/5	2
Mahonia spp.	1/25–2/28	2/11	2
Malus angustifolia	4/29–5/7	5/3	2
Malus baccata	4/12–4/17	4/15	2
Malus halliana	4/2–4/17	4/10	2
Malus hupehensis	3/23–4/11	4/3	9
Malus sylvestris	4/5–4/25	4/15	2
Matricaria recutita	5/2–5/7	5/5	2
Muscari armeniacum	3/20–4/13	4/1	2
Myrica cerifera	5/4–5/8	5/6	3
Myrica pensylvanica	4/25–5/7	5/1	4
Narcissus "February Gold"	3/3–3/25	3/15	5
Narcissus "Jack Snipe"	3/30–3/31	3/30	3
Narcissus "King Alfred"	3/17–3/18	3/18	2
Narcissus "Tete-a-tete"	3/13–3/20	3/16	3

Appendix 2.—Continued.

Species	Range of dates	Average date	No. of years
Narcissus asturiensis	3/5–3/20	3/13	2
Narcissus bulbocodium	4/10–4/17	4/14	2
Narcissus bulbocodium var. *conspicuus*	3/15–3/20	3/18	2
Narcissus jonquilla	4/23–5/8	5/1	2
Narcissus pseudo-narcissus	3/1–3/24	3/11	12
Narcissus scaberulus	3/18–4/13	3/31	2
Narcissus triandrus	3/6–4/17	3/27	2
Nigella damascena	5/22–5/29	5/25	3
Nothoscordum bivalve	4/22–5/1	4/26	4
Pachysandra procumbens	4/5–4/13	4/8	4
Pachysandra terminalis	3/7–4/21	3/28	10
Papaver orientale	5/10–5/20	5/15	2
Penstemon hirsutus	5/15–5/17	5/16	3
Penstemon pinifolius	5/15–5/27	5/21	2
Petasites japonicus	3/13–3/29	3/23	3
Philadelphus spp.	4/20–5/20	5/9	3
Phlox bifida	4/5–4/17	4/13	3
Phlox stolonifera	4/15–4/24	4/20	3
Phlox × procumbens	4/20–4/22	4/21	2
Picrasma quassioides	5/7–5/8	5/8	2
Pieris "Forest flame"	3/23–3/29	3/26	3
Pieris floribunda	3/12–3/27	3/20	2
Pieris japonica	2/22–3/23	3/12	14
**Pinus banksiana*	4/19–5/4	4/29	3
**Pinus densiflora*	5/7–5/8	5/8	2
**Pinus nigra*	4/24–5/5	5/1	5
**Pinus wallichiana*	5/22–5/31	5/26	4
Plantago psyllium	5/7–5/15	5/10	3
Platycladus orientalis	3/5–3/27	3/16	3
Polemonium reptans	4/8–5/2	4/20	2
Polygonatum falcatum	5/14–5/16	5/15	3
Polygonatum odoratum	5/1–5/2	5/2	2
Poncirus trifoliata	4/4–4/23	4/15	3
Populus tremuloides	3/20–4/5	3/28	4
Potentilla aurea	4/17–5/2	4/25	2
Potentilla fruticosa	5/2–5/7	5/5	2
Potentilla nevadensis	3/29–4/13	4/5	3
Potentilla tridentata	5/4–5/22	5/11	3
Primula japonica	5/2–5/16	5/10	4
Prunus "Flowering Cherry"	1/3–3/26	2/25	4
Prunus cerasifera	3/17–4/10	3/29	2
Prunus laurocerasus	1/1–4/30	4/7	7
Prunus mume	3/5–3/16	3/12	3
Prunus persica	3/24–3/25	3/25	2
Prunus subhirtella	3/12–4/10	3/26	4
Prunus yedoensis	3/4–4/6	3/26	9
Prunus yedoenesis/serrulata	3/17–4/9	3/29	5
Psoralea subacaulis	5/7–5/8	5/8	2

Appendix 2.—Continued.

Species	Range of dates	Average date	No. of years
Pterocarya stenoptera	4/11–4/23	4/15	3
Pulmonaria angustifolia	4/10–4/17	4/14	2
Pulmonaria officinalis	3/20–3/27	3/24	2
Puschkinia scilloides	3/4–4/1	3/19	9
Pyracantha "Mohave"	4/19–5/14	5/2	2
Pyracantha spp.	5/14–5/22	5/18	2
Pyrus calleryana	3/12–4/12	3/30	9
Pyrus communis	3/22–4/27	4/10	7
Quercus acutissima	4/21–4/23	4/22	2
Quercus falcata	4/14–4/24	4/20	6
Rhododendron "Azalea"	3/18–4/12	3/29	4
Rhododendron "Pioneer"	3/14–3/18	3/16	2
Rhododendron catawbiense	5/14–5/26	5/20	2
Rhododendron chapmanii	5/7–5/13	5/9	3
Rhododendron keiskei	3/29–4/10	4/4	2
Rhododendron mucronulatum	1/1–3/22	2/22	9
Rhodotypos scandens	4/26–5/29	5/18	3
Robinia hispida	5/15–5/29	5/22	2
Rorippa indica	5/20–5/22	5/21	2
Rosa foetida	5/8–5/14	5/10	3
Rosa rugosa	5/7–5/8	5/8	2
Rosmarinus officinalis	4/10–4/17	4/13	3
Ruta graveolens	5/9–5/29	5/18	3
Salix aegyptiaca	3/5–3/27	3/16	2
Salix babylonica	3/25–4/13	4/5	5
Salix caprea	3/8–4/5	3/23	4
Salix discolor	2/24–4/2	3/15	2
Salix glaucophylloides	4/2–4/4	4/3	2
Salix gracilistyla	3/15–3/23	3/19	3
Salix purpurea	3/20–3/27	3/24	2
Salix × chrysocoma	3/27–4/2	3/30	2
Salix spp.	2/27–3/4	3/2	2
Salvia officinalis	5/14–5/15	5/15	2
Sanguinaria canadensis (cv.)	3/29–4/14	4/6	2
Sanguisorba minor	5/3–5/8	5/6	3
Saponaria × oliviana	5/7–5/15	5/11	2
Sarcococca hookerana	3/5–4/12	3/22	4
Saxifraga caroliniana	5/7–5/15	5/11	2
Schivereckia doerfleri	3/27–4/13	4/5	2
Scilla bifolia	3/5–3/20	3/12	5
Scilla siberica	2/22–3/27	3/12	13
Scilla tubergeniana	3/12–3/29	3/21	4
Scorzonera hispanica	5/22–5/29	5/26	2
Sedum pulchellum	5/7–5/17	5/13	3
Senecio haworthii	4/17–4/26	4/22	3
Shortia galacifolia	3/12–4/14	3/29	5
Skimmia japonica	4/5–4/8	4/7	2
Spiraea prunifolia	3/30–5/2	4/20	3

Appendix 2.—Continued.

Species	Range of dates	Average date	No. of years
Spiraea × vanhouttei	4/24–5/13	5/6	6
Styrax japonicus	5/14–5/26	5/21	3
Styrax obassia	5/9–5/16	5/12	3
Symphytum officinale	4/25–5/7	5/1	3
Symplocos paniculata	4/25–5/7	5/2	4
Syringa oblata	4/11–4/23	4/17	2
Syringa vulgaris	3/30–4/24	4/14	9
**Taxodium distichum*	3/29–4/2	3/31	3
**Taxus baccata*	3/13–3/29	3/22	3
**Taxus cusipidata*	3/5–3/18	3/14	5
**Thuja occidentalis*	3/15–3/29	3/22	2
Thymus praecox	5/14–5/22	5/18	2
Thymus vulgaris	5/15–5/15	5/15	2
Tilia × europaea	5/27–5/31	5/29	3
Torreya nucifera	4/25–5/7	5/2	4
Tradescantia hirsuticaulis	5/2–5/8	5/5	3
Tradescantia longipes	5/1–5/7	5/4	2
Trillium cuneatum	4/1–4/22	4/10	4
Trillium decipiens	4/1–4/13	4/7	4
Trillium decumbens	4/5–4/13	4/9	4
Trillium discolor	5/7–5/8	5/8	2
Trillium erectum	4/14–5/7	4/23	6
Trillium grandiflorum	4/14–4/29	4/19	5
Trillium maculatum	4/5–4/13	4/9	3
Trillium ovatum	4/2–4/17	4/11	3
Trillium pusillum var. *pusillum*	3/31–4/1	3/31	3
Trillium pusillum var. *virginianum*	3/27–4/2	3/30	4
Trillium tschonoskii	3/29–4/13	4/7	3
Trillium underwoodii	4/9–4/24	4/17	3
Trillium viride	4/26–5/8	5/4	2
Trochodendron aralioides	5/3–5/17	5/10	2
Trollius europaeus	4/25–5/8	5/3	3
Tulbaghia violacea	5/8–5/16	5/12	2
Tulipa "Gold Coin"	3/21–4/2	3/27	2
Tulipa batalinii	4/19–4/26	4/23	2
Tulipa kaufmanniana	3/25–4/8	4/1	4
Tulipa kolpakowskiana	4/17–4/17	4/17	2
Tulipa linifolia	4/26–5/1	4/29	2
Tulipa maximowiczii	4/20–5/1	4/26	2
Tulipa pulchella var. *violacea*	3/18–3/27	3/23	2
Tulipa spp.	3/27–4/4	3/30	5
Valeriana officinalis	5/8–5/14	5/10	3
Vancouveria hexandra	5/17–5/22	5/20	2
Viburnum alnifolium	4/26–5/4	4/30	2
Viburnum carlesii	2/19–4/17	4/1	10
Viburnum farreri	2/12–4/8	3/17	3
Viburnum plicatum	5/7–5/8	5/8	2

Appendix 2.—Continued.

Species	Range of dates	Average date	No. of years
Viburnum rhytidophyllum	4/13–5/2	4/25	3
Vinca minor	1/1–4/7	3/13	14
Viola canadensis	4/17–4/30	4/25	3
Viola labradorica	4/10–4/15	4/13	2
Viola odorata	3/13–4/12	3/25	4
Viola tricolor	1/1–4/11	2/6	8
Waldsteinia lobata	4/17–4/17	4/17	2
Weigelia florida	5/13–5/14	5/14	2
Weigelia japonica	5/8–5/11	5/10	2

Appendix 2.—Continued.

Species	Range of dates	Average date	No. of years
Wisteria floribunda	4/16–4/27	4/21	3
Wisteria sinensis	3/30–5/6	4/20	5
Wisteria spp.	4/17–5/2	4/25	4
Xanthorhiza simplicissima	4/11–4/12	4/12	2
Zelkova serrata	4/20–4/26	4/23	2

* Non-flowering plants. Date of "first flowering" is date when spores are first released or when male cones begin to shed pollen.

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HYPOCONCHA PARASITICA (LINNAEUS, 1763), A SENIOR SYNONYM OF *HYPOCONCHA SABULOSA* (HERBST, 1799) (CRUSTACEA: DECAPODA: BRACHYURA)

L. B. Holthuis and Raymond B. Manning

Abstract.—*Hypoconcha parasitica* (Linnaeus, 1763) is the oldest available name for the species now known as *Hypoconcha sabulosa* (Herbst, 1799).

The identity of *Cancer parasiticus* Linnaeus, 1763, almost always indicated by its invalid junior synonym *Cancer pinnophylax* Linnaeus, 1767, has puzzled several authors. Especially in the 18th and the first third of the 19th centuries efforts were made to place the species in the system of the Brachyura. It was considered to be either a dorippid or a pinnotherid, but in almost all cases its identity was considered dubious. After 1830 the name virtually disappeared from the carcinological literature. In 1837 H. Milne Edwards cited *Cancer pinnophylax* Linnaeus, 1767, in the synonymy of *Dorippe astuta* Fabricius, 1798, ignoring its priority. Schmitt, McCain, and Davidson (1973:53, 56), in their review of the pinnotherid literature, dealt with the species under *Pinnotheres maculatus* Say, 1818, but came to the conclusion that Linnaeus' species was unidentifiable.

In a recent review of the subfamily Dorippinae, family Dorippidae (Holthuis and Manning, in preparation), we encountered the problem of *Cancer parasiticus* versus *Cancer pinnophylax*. A study of the literature led us to believe that we have found its correct solution.

The original description of *Cancer parasiticus*, based on material from America, was published by Linnaeus (1763:415) in the thesis of his pupil Boas Johansson. The text is as follows:

"CANCER *parasiticus* brachyurus, thorace inaequali orbiculato ciliato, pedibus dorsalibus quatuor.

"*Habitat in* America *intra Camam lazarum D. D. Jaquin.* Testa *magnitudine dimidii imperalis.* Thorax *orbiculatus, integerrimus, convexus, cinereus, laevis, subinaequalis tuberculis paucis minutissimis. In Dorso pedes 4 minores; ungvibus duobus aduncis.* Pedes *subtus 4 praeter manus. Cauda inflexa brevis.*"

Four years later, Linnaeus (1767:1039) gave the species a new name, *Cancer pinnophylax,* and described it as follows:

"Pinnophylax. 5. C[ancer] brachyurus, thorace orbiculato inaequali ciliato, pedibus dorsalibus quatuor. *Amoen.acad.* 6. p. 415.n.93. *Rumph. mus.* 35. Pinnotheres. *Habitat in America intra* Chamam Lazarum, *D. Jacquin,* cujus *Pinnotheres & custos est.*"

That the name *Cancer pinnophylax* was intended by Linnaeus (1767) to replace *Cancer parasiticus* is evident from the fact that he referred to the description in *Amoenitates Academicae.* Furthermore, the 1767 description is an abbreviated version of that given in 1763, supplemented by the addition of the reference to Rumphius. However, the account of *Pinnoteres* (not *Pinnotheres*) in Rumphius (1705:25 [not 35]) deals with pontoniid shrimps and pinnotherid crabs from Amboina, Moluccas.

Most subsequent authors of the 18th century (Houttuyn 1769:317; Fabricius 1775:

402; 1781:498; 1787:317; 1793:444; Statius Müller 1775:1100; Gmelin 1789:2964; Olivier 1791:156) copied or translated Linnaeus' description without adding anything new and evidently without having seen any additional material. All used the name *Cancer pinnophylax* for the species, and although most did refer to the paper in the *Amoenitates Academicae,* the name *parasiticus* was not accepted. Like Linnaeus (1767), these authors, under *Cancer pinnophylax,* also gave references to the descriptions of true pinnotherids by pre-Linnaean authors. Herbst (1783:104, pl. 2, fig. 27) in the synonymy of *Cancer pinnophylax* cited not only the above authors but also references to other descriptions of pinnotherids and of dorippids, at the same time remarking that he was not certain that not more than one species was involved. His own illustration was clearly that of a pinnotherid. Fabricius (1798:361), however, cited *Cancer pinnophylax* Linnaeus in the synonymy of his own *Dorippe astuta,* not adopting Linnaeus' name. Bosc (1802:243, pl. 6, fig. 3) placed the species in the Pinnotheridae as *Pinnotheres pinnophylax,* and his figure is a copy of that published by Herbst. Latreille (1803:84) did not agree with Bosc and suggested that Linnaeus' species was "plus voisin des dorippes." As already mentioned above, H. Milne Edwards (1837: 157) followed Fabricius in considering *Cancer pinnophylax* a synonym of *Dorippe astuta.* This was practically the last that was heard of Linnaeus' species until Schmitt, McCain, and Davidson (1973) again discussed it. Rathbun (1918:66) meanwhile had assigned Bosc's (1802) material of *Pinnotheres pinnophylax,* but not the material of Linnaeus, with considerable doubt to *Pinnotheres ostreum* Say, 1817.

It seems clear that authors like Herbst and Bosc, who identified *Cancer pinnophylax* with a pinnotherid, were led to this conclusion by Linnaeus' description of the carapace as circular, smooth and convex, and the fact that the animals were said to live in bivalve shells. However, the dorsal position of the last two pairs of legs and the fact that these legs end in two hook-shaped claws is evidence against the pinnotherid nature of the species. The position of the last two pairs of legs evidently suggested to Fabricius, Latreille, and H. Milne Edwards that the species was closer to the dorippids, although these do not have circular, smooth, convex bodies and do not live in shells, although some species certainly do carry them around.

In our opinion, the only genus that fits Linnaeus' description is the dromiid *Hypoconcha.* In *Hypoconcha* the outline of the body is circular (orbiculato); the front of the carapace is semicircularly rounded and although the lateral margins may be straight or even concave, they are covered by the last two pairs of legs in such a way that the whole is more or less circular. The dorsal surface of the carapace is smooth (laevis), uneven (subinaequalis or inaequalis) and convex; the lateral margin has no teeth (integerrimus), only a few widely placed tubercles (tuberculis paucis minutissimus). Also the margin of the carapace is conspicuously ciliated, bearing a fringe of long hairs (ciliato). The last two pairs of legs of *Hypoconcha* are turned dorsally and are shorter than the other legs (in dorso pedes 4 minores); they each end in two sharp, hook-shaped claws (unguibus duobus aduncis). This leaves on the ventral side two pairs of long pereiopods next to the cheliped (pedes subtus 4 praeter manus). *Hypoconcha* holds with its last legs the shell of a bivalve into which it can retract itself. Although no species of *Hypoconcha* has been reported to carry a shell of *Chama,* the shape of these shells is such that to find *Hypoconcha* using a valve of *Chama* is a real possibility. The bivalve mentioned by Linnaeus, *Chama lazarus* Linnaeus, is an Indo-West Pacific species, and it is therefore more likely that the shell in which *Cancer parasiticus* was found is the American *Chama macerophylla* Gmelin, as already pointed out by

Rathbun (1918:66) and Schmitt, McCain, and Davidson (1973:56); also, there is the possibility that Linnaeus (or Jacquin) misidentified the genus.

The size of the carapace (testa) of *Cancer parasiticus* was given by Linnaeus as "magnitudine dimidii imperalis." The word "imperalis" probably is a typographical error for "imperialis," and undoubtedly refers to the Russian gold coin, the imperial, which was first issued in 1745 during the reign of Empress Elisabeth Petrovna, daughter of Peter the Great, who was born in 1709 and reigned from 1741 to 1762. The value of the gold imperial is 10 rubles, that of the half-imperial being 5 rubles. The dutch translation of Linnaeus' description by Houttuyn (1769:312) indicates its size as follows: "De Schaal heeft de grootte van een halve Ryksdaalder" (The shell has the size of a half rijksdaalder) (the latter is sometimes translated as rix dollar). The German translation by Statius Müller (1775:1100) runs as follows: "Das ganze rauhhaarige Schild ist nicht grösser als ein Achtgroschenstück."

We are indebted to the coin dealer from Amsterdam, Messrs. Jacques Schulman, for the information that the diameter of a half imperial (a gold five ruble piece, first coined in 1753) is 26 mm.

The type of *Cancer parasiticus* was collected in America by "D. D. Jaquin." Jaquin is, without any doubt, Nicolas Joseph Jacquin (born Leiden, The Netherlands, 16 February 1727—died Vienna, Austria, 24 October 1817), who was appointed imperial botanist at the Austrian court in 1752, and who between 1754 and 1759 made a botanical expedition to America, in the course of which evidently he obtained the specimen of *Cancer parasiticus* that he sent to Linnaeus.

Although there can be little doubt that Linnaeus' species is a *Hypoconcha,* it is more difficult to determine which species he had before him. As Jacquin collected mainly or exclusively in the West Indies, his specimens can belong only to one of the three western Atlantic species: *Hypoconcha sabulosa* (Herbst, 1799), *H. arcuata* Stimpson, 1858, or *H. spinosissima* Rathbun, 1933. This latter species is conspicuously spinous and lives in deeper water than the others so it is less likely to have been found by Jacquin. The best known of the three western Atlantic species is *H. sabulosa*; it has long been known from the West Indies. Rathbun (1937:44) cited the description and illustration of it made by P. Nicolson based on a specimen from Santo Domingo and published in 1776. *Hypoconcha sabulosa* is characterized by the presence of "three large granulated tubercles on either side of ventral surface of carapace" (Rathbun 1937: 44).

Of interest here is the fact that Herbst (1783:104), when describing *Cancer pinnophylax* Linnaeus ("Der *Linnéische* Pinnewächter"), ended the German translation of Linnaeus' description with the words "die Scheeren sind grade, und haben an der Seite drey Punkte" (the chelae are straight and have laterally three points), which might very well refer to the three granualated tubercles characteristic of *Hypoconcha sabulosa.* We have not been able to find these characters mentioned in any of Linnaeus' descriptions of *Cancer parasiticus* or *C. pinnophylax* and we do not know where Herbst got his information. If the observation is correct, there can be little doubt that *Cancer parasiticus* is conspecific with *Hypoconcha sabulosa.*

There is another piece of circumstantial evidence supporting this supposition. Herbst (1799:57), when describing his *Cancer sabulosus,* mentioned that he had found his specimen in the Imperial collection of Austria in Vienna. It is not unlikely that Jacquin, before sending a specimen of *Hypoconcha sabulosa* to Linnaeus, placed material of the same species first in the Imperial collection of Austria, and that Herbst had seen one of those specimens.

In summary we can say that there is not

the slightest doubt that *Cancer parasiticus* (and thus *C. pinnophylax*) is a species of *Hypoconcha,* as Linnaeus' description does not fit any other genus. Furthermore it is most likely that it is a senior synonym of *Cancer sabulosus* Herbst as (1) that species was known to collectors in the 18th century and evidently could be obtained without any special equipment, (2) Linnaeus' description fits the species, even to size, and, if Herbst's observation that the type has three points near the chelae is correct, there can be no doubt of its conspecificity with *C. sabulosus,* and (3) there seems to be a good possibility that the types of *Cancer parasiticus* and *C. sabulosus* came from a single lot, collected by N. J. Jacquin for the Imperial Austrian collection in Vienna.

In order to settle the identity of *Cancer parasiticus,* we here select a male specimen (carapace length 23.2 mm, carapace width, 22.4 mm; larger of 2 males in lot) taken in the channel between White Shoal and Loggerhead Key, Tortugas, Florida, 9.5 fms (=17 m), 21 June 1931, leg. Waldo L. Schmitt to be the neotype of *Cancer parasiticus* Linnaeus, 1763 and of *Cancer pinnophylax* Linnaeus, 1767. The specimen agrees completely with M. J. Rathbun's description (1937:45) of *Hypoconcha sabulosa* (Herbst, 1799); it was figured by her (1937) on pl. 8, figs. 3, 4. It is housed in the collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., under catalogue number USNM 66796.

This is contribution number 197 from the Smithsonian Marine Station at Link Port, Fort Pierce, Florida.

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OBSERVATIONS ON THREE KNOWN FREE-LIVING MARINE NEMATODES OF THE FAMILY IRONIDAE (NEMATODA: ENOPLIDA) AND A DESCRIPTION OF *THALASSIRONUS LYNNAE* N. SP. FROM NORTHWEST FLORIDA

Edwin J. Keppner

Abstract.—Two known species of free-living marine nematodes, *Thalassironus britannicus* and *Thalassironus americanus,* are described from sediments vegetated with manatee grass (*Syringodium filiformis*) and shoal grass (*Halodule wrightii*) and non-vegetated sediments from St. Andrew Bay, Bay County, Florida. Differences between specimens from the two habitats are discussed. *Thalassironus lynnae* n. sp. is described from vegetated sediments in St. Andrew Bay. It differs from the other species in the genus by having a long, flagellate tail, shorter more posteriorly located double cervical setae, and by the presence of a segmented, pre-anal papilla in males. A key to the species of the genus *Thalassironus* is given. *Ironella prismatolaima* is described from non-vegetated sediments from the Gulf of Mexico off Sea Horse Key, Levy County, Florida.

Chitwood (1960) discussed the genera of the family Ironidae De Man, 1876, and provided a key to their identity. Lorenzen (1981) discussed the taxonomic characters of the members of the Ironidae and listed the genera within the subfamily Thalassironinae Andrassy, 1976. Species belonging to two of the genera of the Thalassironinae, *Thalassironus* De Man, 1889, and *Ironella* Cobb, 1920, were recently recovered from sediments in St. Andrew Bay, Bay County, Florida and the Gulf of Mexico off Levy County, Florida. The specimens of *Thalassironus* described herein were recovered from subtidal, non-vegetated sediments or subtidal sediments vegetated with either manatee grass (*Syringodium filiformis*) or shoal grass (*Halodule wrightii*) in St. Andrew Bay by the writer. The specimens of *Ironella prismatolaima* Cobb, 1920, were loaned by Dr. Armen C. Tarjan from the University of Florida Nematode Collection. The specimens of *I. prismatolaima* were recovered from subtidal, non-vegetated sediment from the Gulf of Mexico.

Materials and Methods

Specimens of *Thalassironus* were collected with a core sampler 4.5 cm in diameter and 10 cm in length and were extracted from the sediment by repeated washing and decanting. Nematodes were removed alive, fixed in hot alcohol-formalin-acetic acid, cleared in glycerine and mounted in anhydrous glycerine on Cobb slides. The borrowed specimens of *Ironella* had been fixed in formalin and mounted in anhydrous glycerine on Cobb slides. Nematodes were measured with a calibrated ocular micrometer. All measurements are given in μm unless otherwise stated, and the mean is followed by the range in parentheses. Spicular lengths are given as the chord of the arc.

Ironidae De Man, 1876
Thalassironinae Andrassy, 1976
Thalassironus De Man, 1889

The genus *Thalassironus* contains those members of the family Ironidae in which the cephalic sensillae are setiform; there are two subventral and a single, double, dorsal tooth; spicules are equal in length and caudal glands are present. The genus contains the following species: *Thalassironus britannicus* De Man, 1889, *Thalassironus bipartitus* (Wieser, 1953) Chitwood, 1960, *Thalassironus jungi* Inglis, 1964, *Thalassironus bisetosus* Vitiello, 1970, and *Thalassironus americanus* Keppner, 1986. The sixth species of the genus is described herein. In addition, specimens of *T. britannicus* collected from two habitats in St. Andrew Bay are described and additional observations are provided for *T. americanus* from vegetated sediments.

Thalassironus lynnae, new species
Figs. 1–6, 29, 30

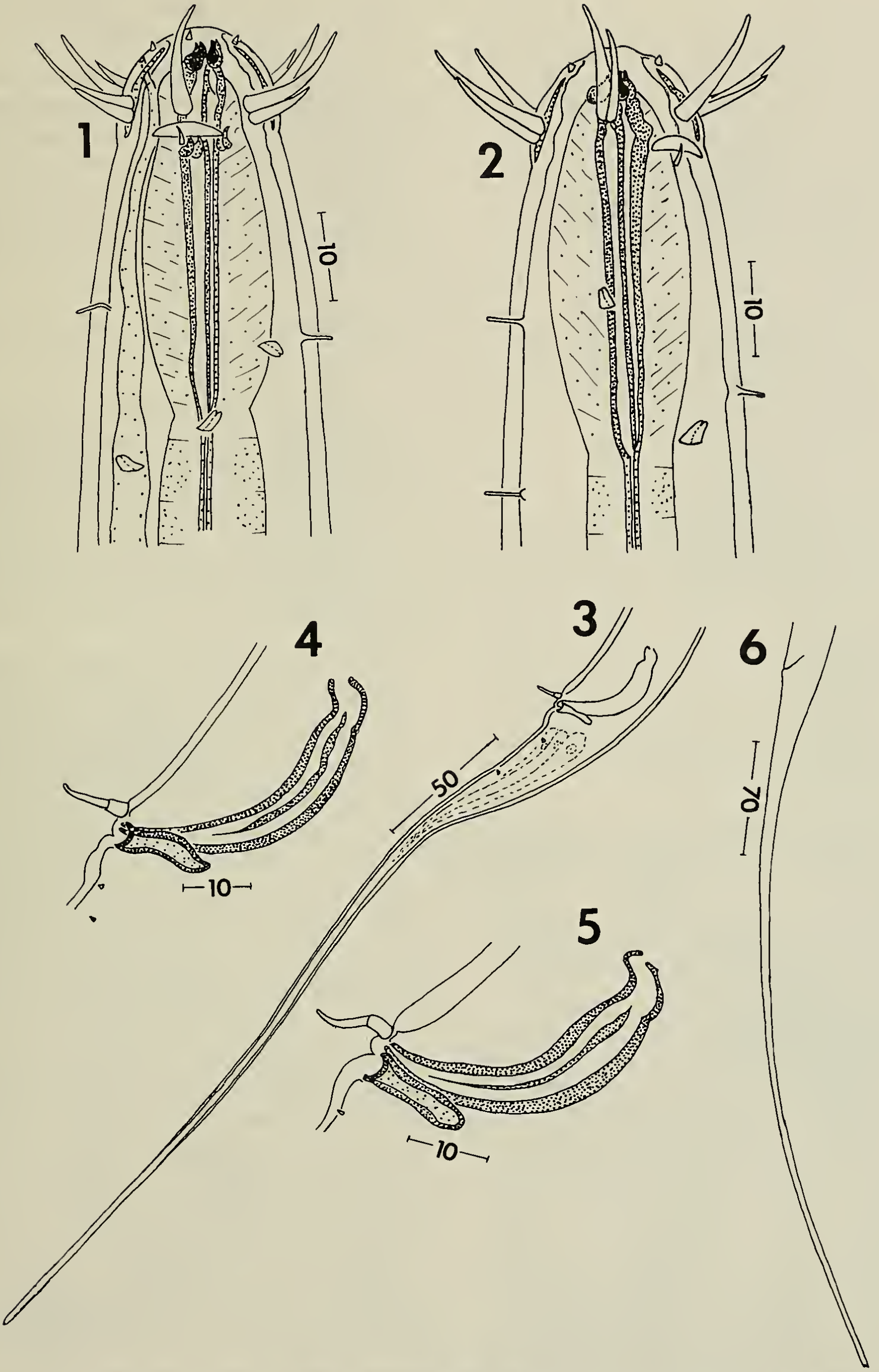
Diagnosis.—Two males and one female. Body slender, cuticle smooth; distinct longitudinal and transverse striations absent. Head with 6 small, labial papillae. Cephalic setae arranged as anterior circle of 6 long setae and circle of 4 short submedian setae immediately posterior to circle of 6; posterior circle of 4 setae about 0.7 length of anterior 6 setae. Stoma long, narrow, with cuticularized walls and 3 prominent, anteriorly directed teeth (2 subventral and 1 double dorsal) at anterior end. One male with additional 3 teeth at level of amphid. Amphids just posterior to lateral cephalic setae; each amphid with short seta just posterior to middle of posterior margin. Short cervical setae arranged on each side as 1 subdorsal, 1 dorsoventral, 1 lateral, 1 ventrolateral and 1 subventral; each appears double with wide base, separated only at tip. Excretory pore anterior to cephalic setae. Somatic setae not observed, caudal setae sparse or absent. Esophagus surrounding buccal cavity and attaching to cephalic cuticle anteriorly, peribuccal portion expanded, then narrowed to nerve ring and expanded to junction with intestine. Tail conical then cylindrical; caudal glands present; presence or absence of spinneret could not be determined with certainty with light microscope.

Males (n = 2): Length 3.13 mm (3.06–3.19), width at midbody 31 (30–32). Head diameter 18 (18–18) at level of cephalic setae; cephalic setae 15 (14–16) and 10.5 (10–11) long. Amphids 5.5 (5–6) wide. Stoma 40.5 (39–42) long and 6 (6–6) wide at base of teeth. Esophagus 355 (347–363) long; nerve ring 120 (115–125) from anterior end. Tail 300 long in holotype specimen and 245 long in paratype specimen but appears broken. Width at anus 26.5 (26–27). Tail with small setae on conical portion. Single large, segmented, midventral, pre-anal papilla present. Spicules 37.5 (35–40) long, broad, slightly curved. Gubernaculum 15 (14–16) long; elongate with blunt tip. a = 100.9 (99.7–102.0); b = 8.81 (8.43–9.19); c = 10.2 (holotype), 13.0 (paratype).

Female (n = 1): Length 3.84 mm, width at midbody 38. Head diameter at level of cephalic setae 19; cephalic setae 14 and 11 long. Amphids 6 wide. Stoma 42 long and 6 wide at base of teeth. Esophagus 389 long; nerve ring 120 from anterior end. Tail appearing broken, 506 long and 27 wide at anus; caudal setae not observed. Reproductive system amphidelphic, ovaries reflexed; vulva 1.85 mm from anterior end. Walls of vagina thin, not heavily cuticularized. a = 101.1; b = 9.87; c = 7.59; V = 48%.

Remarks.—*Thalassironus lynnae* belongs to that group of species in which the longer cephalic setae are about equal to the corresponding head diameter and the cervical setae are double or appear double. *Thalassironus lynnae* differs from the species in the group (*T. britannicus, T. jungi,* and *T. americanus*) in the presence of a long narrow tail; in the shorter, more posteriorly located double, cervical setae; presence of a small post-amphidial seta; and the presence of the segmented, pre-anal papilla in males. The first pair of cervical setae in the other three species is long and located just posterior to the amphids.

Type specimens.—Holotype male, USNM



Figs. 1–6. *Thalassironus lynnae*: 1, Paratype male, head, lateral view; 2, Holotype male, head, sublateral view; 3, Male, posterior end, lateral view; 4, Holotype male, left spicule and gubernaculum, lateral view; 5, Male paratype, left spicule and gubernaculum, lateral view; 6, Female, posterior end, lateral view. Scales in μm.

Table 1.—Selected measurements of males of the genus *Thalassironus**

Species	Length cephalic setae	Length stoma	Length spicules	Length gubernaculum	Pairs cervical setae	Length tail	Demanian ratios a	b	c
T. bisetosus Vitiello (1970)	7	39–42	82–84	28	0	151–154	67–86	15.8–16.5	39.0–41.7
T. bipatitus (Wieser, 1953)	7.5 & 6.5	42–46	52	—	0	4.5–5.0 AD†	30–38	5.1–5.6	10.2–10.9
T. jungi Inglis (1964)	26–27 & 14–16	97–101	58–60	28–30	1	186–204	63.3–66.3	7.3–7.6	26.9–28.2
T. lynnae n. sp.	14–16 & 10–11	39–42	35–40	14–16	5	245–300	99.7–102.0	8.43–9.19	10.2–13.0
T. britannicus Warwick (1977)	26–28 & 11–12	67–77	62–72	30–38	4	190–225	—	—	—
T. britannicus Yoshimura (1980)	21–24 & —	—	68–72	26–28	4	145–166	66.4–69.4	10.5–11.2	41.2–43.7
T. britannicus non-vegetated	24 & 10	72	56	29	4	147	41.2	6.62	21.8
T. britannicus vegetated	22–24 & 6–7	48–49	32–35	16–18	4	100–110	82.7–91.6	8.58–8.74	30.6–30.8
T. americanus non-vegetated	18–20 & 4–6	58–60	55–56	15–17	1	123–126	78.4–88.5	8.58–8.93	31.9–33.7
T. americanus vegetated	18–20 & 5–6	53–56	42–46	11–14	4	107–118	101.6–128.3	9.03–10.7	35.2–40.2

* = measurements in microns; † = anal diameters.

77101; paratype male, USNM 77102; allotype female, USNM 77103.

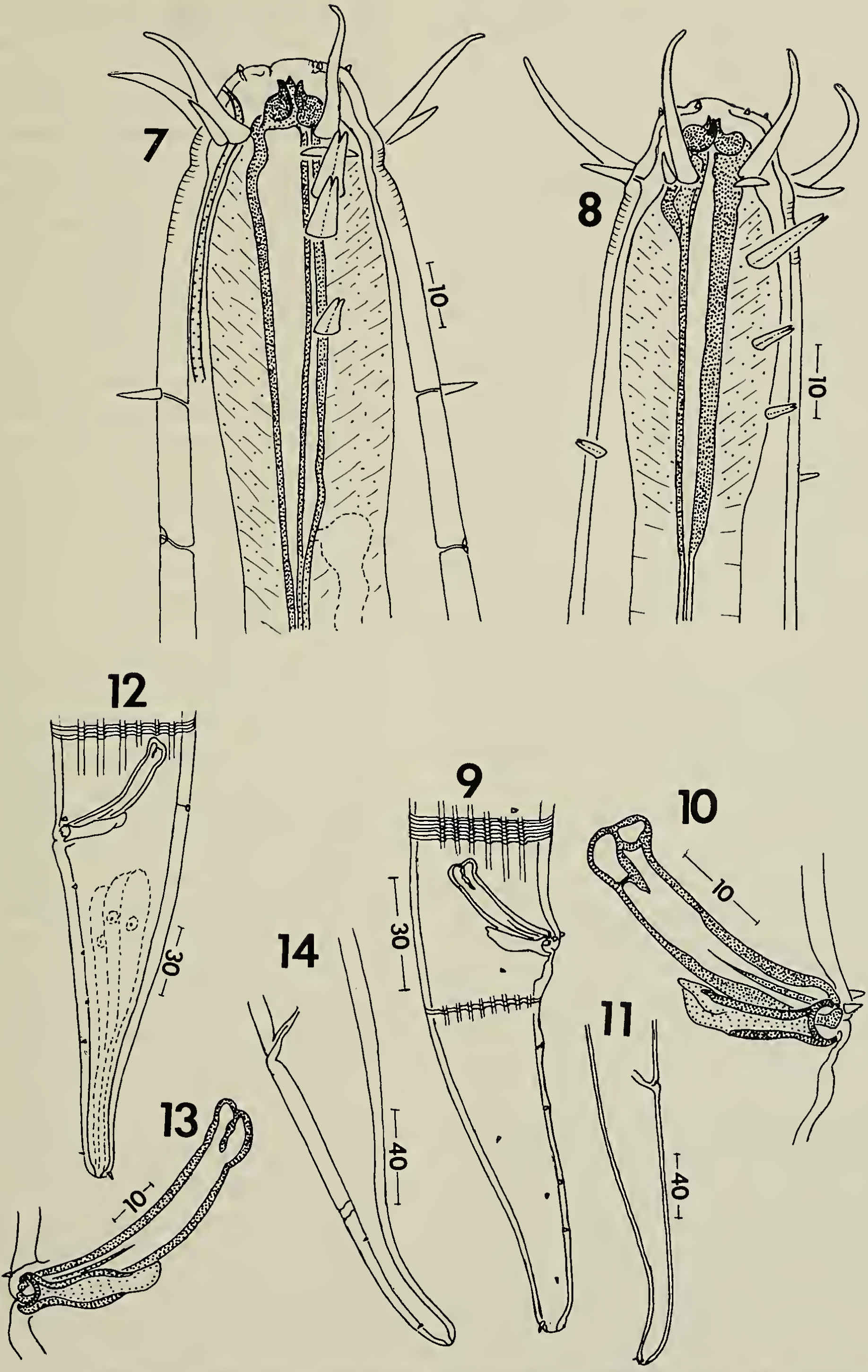
Type locality.—Subtidal sediment vegetated with manatee grass from mouth of Freshwater Bayou, St. Andrew Bay, Bay County, Florida (85°39′00″W, 30°07′30″N).

Etymology.—Named for my wife Lynn, in appreciation for her help with and generous support of my studies on nematodes.

Thalassironus britannicus De Man, 1889
Figs. 7–14, 31, 32

Diagnosis.—Two males and one female were recovered from vegetated sediments, and one male and two juvenile females were recovered from non-vegetated sediments in St. Andrew Bay. Although obviously the same species, the specimens from the two sites differed appreciably in some characters (Table 1).

Body long, slender or broad. Cuticle with delicate transverse striations beginning just posterior to cephalic setae, extending length of body; broad longitudinal striations present for length of body. Head with 3 lips, 6 small labial papillae and single circle of 10 (6 + 4) cephalic setae; 4 submedian setae about 0.3–0.4 length of other 6. Stoma long, narrow with cuticularized walls and 3 prominent teeth (2 subventral and 1 double dorsal) at anterior end. Amphids just posterior to lateral cephalic setae. Cervical setae double, separated only at tips; arranged as 3 setae in longitudinal row on each lateral surface and 1 seta on dorsal and ventral surfaces. Lateral cervical setae decreasing in length from anterior to posterior. Somatic setae not observed in specimen from non-vegetated sediment, present posteriorly in specimens from vegetated sediments. Small papilla-like structures present in cervical and caudal region in specimens from non-vegetated sediment; not observed in specimens from vegetated sediments. Caudal setae present. Excretory pore anterior to cephalic setae. Esophagus surrounding buccal cavity and attaching to cephalic cuticle, peribuccal portion expanded, then narrowed to nerve



Figs. 7–14. *Thalassironus britannicus*: 7, Male, head, sublateral view, from non-vegetated sediment; 8, Male, head, sublateral view, from vegetated sediment; 9, Male, posterior end, lateral view, from vegetated sediment; 10, Male, right spicule and gubernaculum, lateral view, from vegetated sediment; 11, Female, tail, lateral view, from vegetated sediment; 12, Male, posterior end, lateral view, from non-vegetated sediment; 13, Male, left spicule and gubernaculum, lateral view, from non-vegetated sediment; 14, Female, tail, lateral view, from non-vegetated sediment. Scales in μm.

ring and expanded to junction with intestine. Tail short, conical; spinneret and caudal glands present.

Males (n = 3): Table 1 gives the measurements for the males from non-vegetated and vegetated sediments separately. The following represents the totals of specimens from both sites. Length 3.26 mm (3.06–3.39), width at midbody 50.7 (37–78). Head diameter 24.3 (22–29) at level of cephalic setae; cephalic setae 23 (22–24) and 7.7 (6–10) long. Stoma 56 (48–72) long and 10.3 (8–13) wide at base of teeth. Amphid 7.7 (6–11) wide. Lateral, double, cervical setae located 21.7 (19–24), 29 (26–32), and 44.7 (42–48) from anterior end. Esophagus 410 (350–485) long; nerve ring 97 (83–115) from anterior end. Tail 119 (100–147) long and 40 (37–46) wide at anus. Tail with single pair small, pre-anal, subventral setae, 4–5 pairs subventral post-anal setae and single pair at tail tip. Spicules 41 (32–56) long; almost straight, broad. Gubernaculum 20.7 (16–29) long, elongate with blunt, cup-shaped distal end. a = 71.8 (41.2–91.6); b = 7.98 (6.62–8.74); c = 27.7 (21.8–30.8).

Mature female (n = 1): Specimen from vegetated sediment. Length 3.75 mm, width at midbody 42. Head diameter 22 at level of cephalic setae; cephalic setae 18 and 6 long. Amphids 6 wide. Stoma 48 long and 10 wide at base of teeth. Lateral cervical setae located 21, 27, and 43 from anterior end. Esophagus 411 long; nerve ring 147 from anterior end. Tail 131 long and 29 wide at anus. Caudal setae restricted to single pair at tail tip. Reproductive system amphidelphic, ovaries reflexed; vulva 2.31 mm from anterior end. Vagina with heavily cuticularized walls, brown in color. a = 89.3; b = 9.12; c = 28.6; V = 62%.

Juvenile females (n = 2): Specimens from non-vegetated sediments. Length 3.07 mm (3.01–3.12), width at midbody 85 (80–90). Head diameter 29.5 (29–30) at level of cephalic setae; cephalic setae 21.5 (21–22) and 9.5 (9–10) long. Amphid 9.5 (9–10) wide. Stoma 74.5 (69–80) long and 11 (11–11) wide at base of teeth. Lateral cervical setae located 21.5 (21–22), 32 (27–37) and 49.5 (43–56) from anterior end. Tail 153 (149–157) long and 50.5 (50–51) wide at anus. Caudal setae sparse, located posteriorly on tail. Reproductive system amphidelphic, ovaries reflexed; vulva 1.84 mm (1.81–1.86) from anterior end. Vagina with heavily cuticularized walls, brown in color. a = 36.2 (34.7–37.6); b = 6.04 (5.91–6.17); c = 20.1 (19.9–20.2); V = 60% (60–60).

Remarks.—The male and juvenile females from non-vegetated sediments agree with the descriptions of *T. britannicus* given by Warwick (1977) and Yoshimura (1980) except for the shorter body length and somewhat shorter spicules. However, the specimens from vegetated sediments differ appreciably from the above descriptions in the shorter length of the stoma, in the larger "a" value and in the thinner cuticle. In addition, the males from vegetated sediments differ from the above males in the shorter length of the spicules and gubernaculum.

Specimens.—Three males, USNM 77104, 77105, 77106; one female, USNM 77107; two juvenile females, USNM 77108, 77109.

Locality.—Non-vegetated, subtidal sediment in St. Andrew Bay at the National Marine Fisheries Service Laboratory, Panama City, Bay County, Florida (85°42′43″W, 30°08′33″N). Subtidal sediments vegetated with manatee grass or shoal grass in Freshwater Bayou, St. Andrew Bay, Bay County, Florida (85°39′00″W, 30°07′30″N).

Thalassironus americanus Keppner, 1986
Figs. 15–21, 33, 34

Diagnosis.—Five males and three females were recovered from vegetated sediments (manatee grass or shoal grass). The original description of *T. americanus* was based on specimens from non-vegetated sediments. Table 1 gives the measurements of the type material for comparison with that given below for those from vegetated sediments.

Body long, slender; cuticle smooth. Head with 3 lips, 6 small, labial papillae and single circle of 10 (6 + 4) cephalic setae; lateral and 4 submedian setae about ¼ length of longer 4 submedian setae. Four double cervical setae in longitudinal row on each lateral surface. First lateral cervical seta much longer than others, not separated at tip; 3 posterior laterals short with elongate base, separated at tip. Single normal seta present dorsally and ventrally just posterior to last double, lateral seta. Somatic setae not observed, caudal setae present. Stoma long, narrow, with cuticularized walls and 3 prominent teeth (2 subventral and 1 double dorsal) at anterior end. Anterior points of subventral teeth between 2 points of dorsal tooth resulting in points being in straight, transverse series at oral aperture. En face views of *T. americanus* at various levels similar in structure to that described for *Thalassironus jungi* by Van der Heiden (1975). Amphids just posterior to lateral cephalic setae. Excretory pore anterior to cephalic setae. Esophagus surrounding buccal cavity and attaching anteriorly to cephalic cuticle, peribuccal portion expanded, then narrowing to nerve ring and expanding to junction with intestine. Male tail short, conical; female tail conical then expands to tip. Caudal glands and spinneret present.

Males (n = 5): Length 4.15 mm (3.86–4.62), width at midbody 36.4 (34–40). Head diameter 22.2 (21–24) at level of cephalic setae; cephalic setae 19 (18–20) and 5.2 (5–6) long. Amphids 9 (8–10) wide. Stoma 53.8 (53–56) long and 8.8 (8–10) wide at base of teeth. Lateral double cervical setae located 24.2 (22–27), 50.2 (45–58), 64.2 (58–69) and 85.4 (83–88) from anterior end. Esophagus 428 (411–438) long; nerve ring 149 (141–155) from anterior end. Tail 112 (107–118) long and 34.4 (34–35) wide at anus. Tail with 5 midventral, post-anal supplement-like structures; caudal setae sparse, 1 pair at tail tip. Spicules 44.4 (42–46) long, broad, arcuate with blunt tips. Gubernaculum short, broad, 11.6 (11–14) long. a = 114.3 (101.6–128.3); b = 9.7 (9.03–10.7); c = 37.1 (35.2–40.2).

Females (n = 4): Length 4.33 mm (4.17–4.51), width at midbody 36.8 (35–38). Head diameter 22.5 (21–24) at level of cephalic setae; cephalic setae 18.5 (18–19) and 4.5 (4–5) long. Amphids 9 (8–10) wide. Stoma 54 (53–56) long and 8.8 (8–10) wide at base of teeth. Lateral, double, cervical setae located 24 (22–26), 44.3 (43–45), 59.7 (53–64) and 81 (78–83) from anterior end. Esophagus 421 (400–442) long; nerve ring 145 (141–149) from anterior end. Tail 133 (128–136) long and 28.2 (27–30) wide at anus. Caudal setae sparse. Reproductive system amphidelphic, ovaries reflexed; vulva 3.14 mm (2.99–3.19) from anterior end. Vagina with heavily cuticularized walls, brown in color. a = 118.0 (112.7–124.0); b = 10.3 (9.40–10.8); c = 32.6 (30.7–33.7); V = 72.8% (70–76).

Remarks.—The specimens from non-vegetated sediments differ from those from vegetated sediments in that the cuticle is thicker, the spicules and gubernaculum are longer, the three posterior pairs of double cervical setae appear absent and the "a" value is smaller.

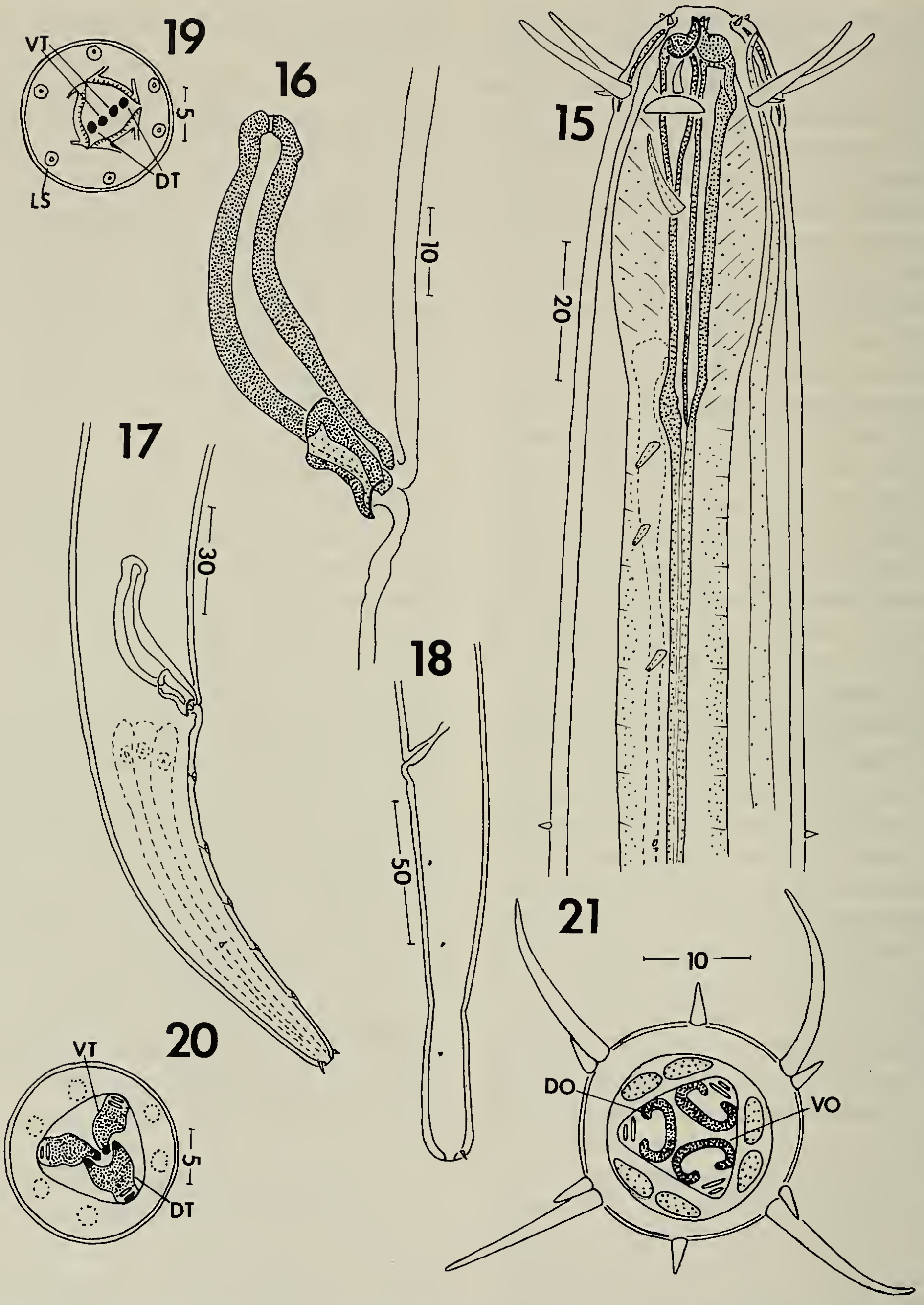
Specimens.—Three males, USNM 76391, 77110, 77111; 5 females, USNM 76390, 76392, 77112, 77113, 77114.

Locality.—Sediments vegetated with manatee grass or shoal grass in Freshwater Bayou, St. Andrew Bay, Bay County, Florida (85°39′00″W, 30°07′30″N).

Key to the Species of the Genus *Thalassironus* De Man, 1889

Vitiello (1970) provided a key to the species of *Thalassironus.* Warwick (1977) corrected the character used in the key for *T. britannicus.* The following key incorporates the species added since 1970.

1. Longer cephalic setae less than ½ corresponding diameter; double cervical setae absent 2
– Longer cephalic setae greater than ½



Figs. 15–21. *Thalassironus americanus* from vegetated sediment: 15, Male, anterior end, lateral view; 16, Male, right spicule and gubernaculum, lateral view; 17, Male, posterior end, lateral view; 18, Female, tail, lateral view; 19, Male, en face view, extreme anterior end; 20, Male, en face view, level of base of teeth; 21, Male, en face view, level of cephalic setae. (Abbreviations for Figs. 19–21: LS = labial seta, DT = dorsal tooth, VT = subventral tooth, DO = dorsal odontophore, VO = subventral odontophore.) Scales in μm.

corresponding diameter; double cervical setae present 3

2. Cuticle transversely striated. Tail 2.1–2.2 anal diameters long, conical with narrow, cylindrical, distal part. Spicules 82–84 long .... *T. bisetosus* Vitiello, 1970
- Cuticle smooth. Tail 4.5–5 anal diameters long, conical. Spicules 52 long . . *T. bipartitus* (Wieser, 1953) Chitwood, 1960

3. Tail long, flagellate; males with segmented, pre-anal papilla .... *T. lynnae* n. sp.
- Tail short, conical, not flagellate; males without segmented, pre-anal papilla 4

4. Head with 6 long and 4 short cephalic setae. Double cervical setae located in stomatal region only ... . *T. britannicus* De Man, 1889
- Head with 4 long and 6 short cephalic setae. Double cervical setae in stomatal region and posterior to stoma 5

5. Single pair double cervical setae just posterior to amphid. Spicules almost straight; gubernaculum elongate. Female tail conical .... *T. jungi* Inglis, 1964
- Four pairs lateral, double cervical setae; first posterior to amphid, remainder posterior to stoma. Spicules arcuate; gubernaculum short, broad. Female tail tip clavate ....*T. americanus* Keppner, 1986

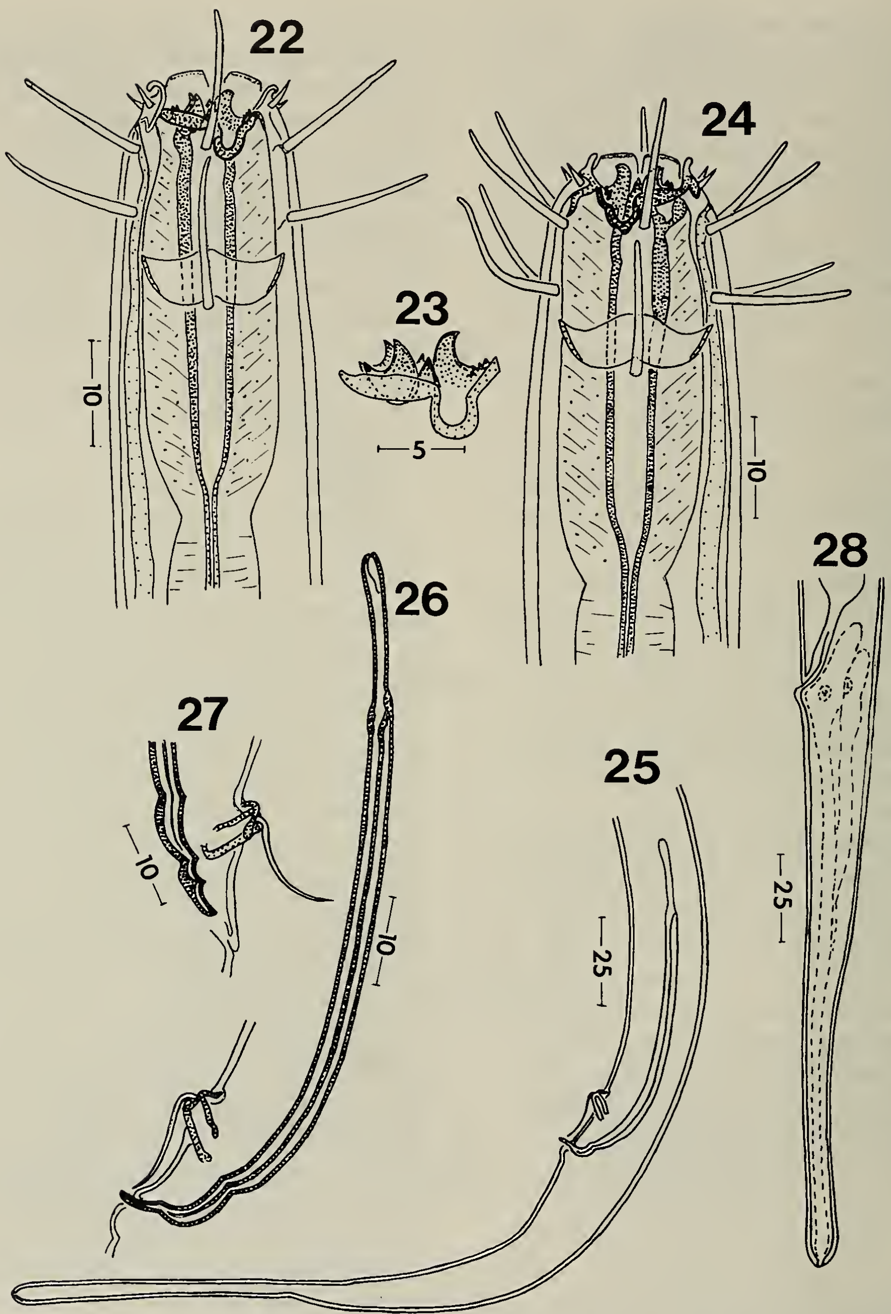
Ironella Cobb, 1920
Ironella prismatolaima Cobb, 1920
Figs. 22–28, 35–37

Diagnosis.—Body short, slender; cuticle thin, smooth. Head with 6 lips each with short seta; cephalic setae arranged as anterior circle of 6 and posterior circle of 4; all of equal length. Stomatal wall thickened at level of base of teeth. Amphid large, located about midlevel of stoma. Single long, postamphidial seta on each lateral surface. Stomatal walls cuticularized with anteriorly directed teeth arranged as 3 large (1 dorsal and 2 subventral) and 2 smaller laterals. Subventrals with large median point and smaller distal point; denticles present at base of dorsal tooth. Cervical, somatic and caudal setae not observed. Esophagus surrounding buccal cavity and attaching to cephalic cuticle. Excretory pore anterior to first circle cephalic setae. Tail long, conical then cylindrical. Caudal glands and spinneret present.

Males (n = 4): Length 1.61 mm (1.48–1.73), width at midbody 23 (22–24). Head diameter 20 (19–21) at level of amphid. Cephalic setae 12.5 (11–13) and 12.8 (11–14) long. Amphid 13.5 (11–15) wide. Stoma 35.3 (32–37) long and 5.5 (5–6) wide at base of teeth. Esophagus 334.2 (310–352) long; nerve ring 137 (122–146) from anterior end. Tail 154 (133–166) long and 21.8 (21–22) wide at anus. Single, tubular, pre-anal supplement 15 (14–16) from anus, aperture directed almost anteriorly with 1 long seta projecting from it. Spicules 87.8 (80–94) long, equal, curved; capitulum narrower than remainder of spicule. Gugernaculum, if present, a thin plate. a = 70.1 (65.0–75.9); b = 4.81 (4.68–4.91); c = 10.5 (9.94–11.1).

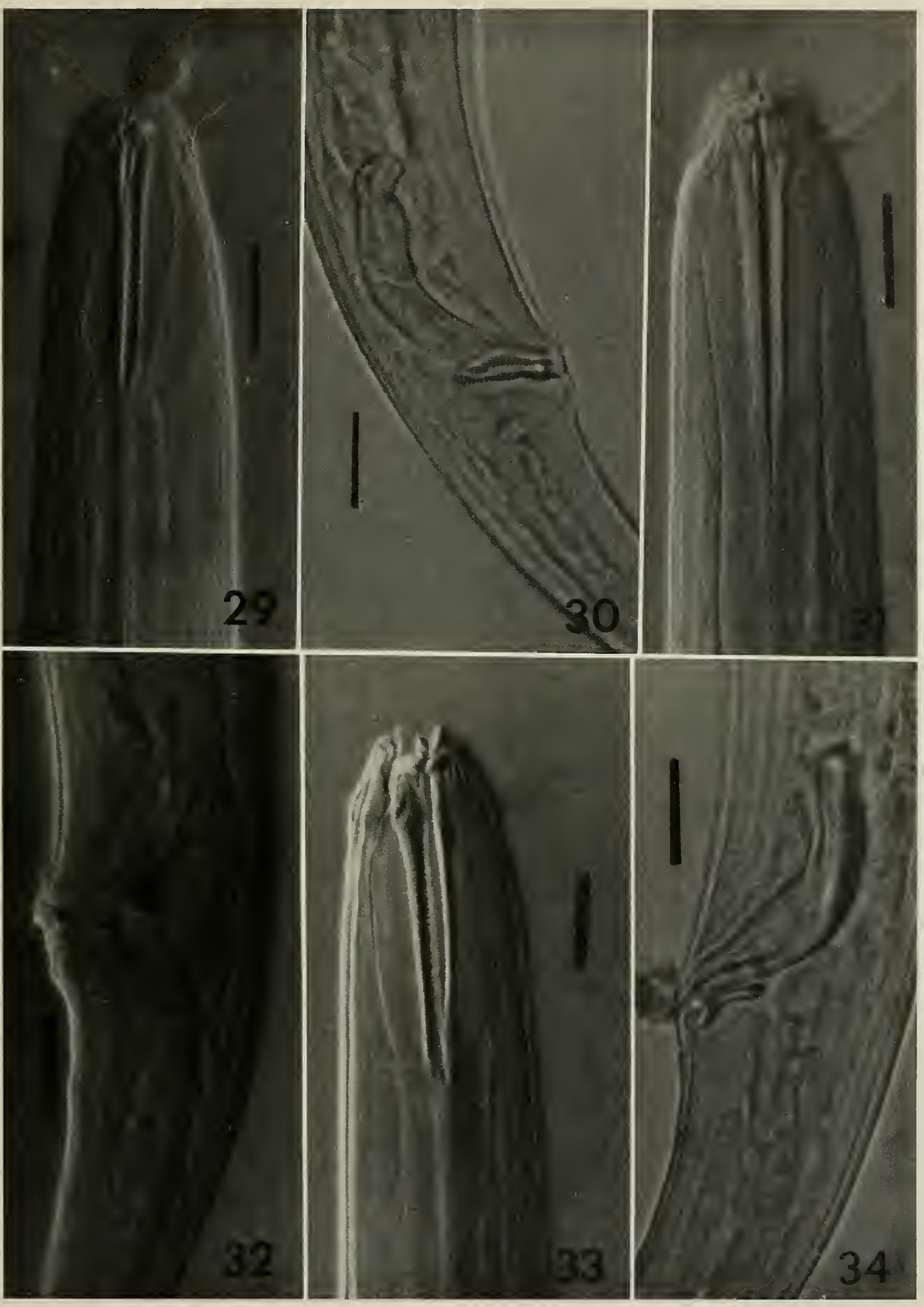
Female (n = 1): Length 1.61 mm, width at midbody 43. Head diameter 26 at level of amphid. Cephalic setae broken or absent. Amphid 13 wide. Stoma 42 long and 6 wide at base of teeth. Esophagus 325 long; nerve ring 131 from anterior end. Tail 168 long and 22 wide at anus. Reproductive system amphidelphic, ovaries reflexed; vulva 806 from anterior end. a = 37.4; b = 4.95; c = 9.58; V = 50%.

Remarks.—The genus *Ironella* contains two species, *I. prismatolaima* Cobb, 1920, and *I. cobbi* Timm, 1952. Cobb (1920) did not provide a drawing of the male genital apparatus of *I. prismatolaima.* Riemann (1966) described *I. prismatolaima* from European waters, and mentioned that this male

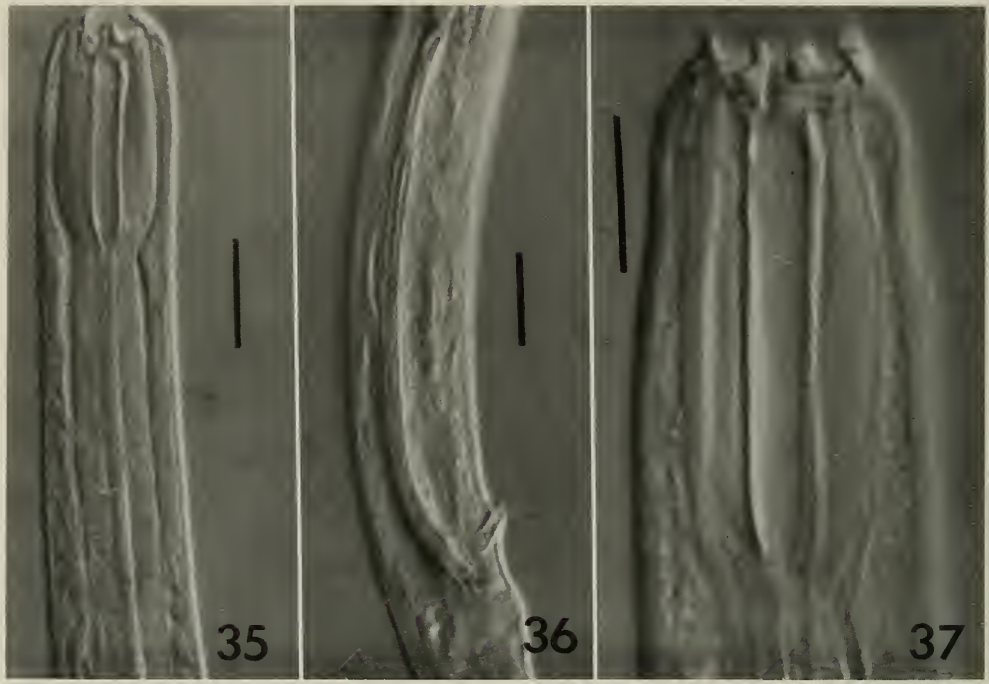


Figs. 22–28. *Ironella prismatolaima*: 22, Male, head, left lateral view; 23, Male, teeth, left lateral view; 24, Male, head, right lateral view; 25, Male, posterior end, lateral view; 26, Male, left spicule and supplement, lateral view; 27, Male, tip of right spicule and supplement, lateral view; 28, Female, tail, lateral view. Scales in μm.

specimen differed from the original description in the body length, relative length of cephalic setae and the length of the tail. The specimens described herein are very similar to the original description and to that of Riemann (1966). They differ from that of Riemann (1966) in the length of the spicules (80–94 vs. 53.5) and in the demanian "a"



Figs. 29–34. *Thalassironus lynnae*: 29, Male, head, lateral view; 30, Male, spicule and gubernaculum, lateral view. Scale bars = 15 μm. *Thalassironus britannicus*: 31, Male, head, lateral view; 32, Male, spicule and gubernaculum, lateral view. Scales bars = 15 μm. *Thalassironus americanus*: 33, Male, head, lateral view; 34, Male, spicules and gubernaculum, lateral view. Scale bars = 15 μm.



Figs. 35–37. *Ironella prismatolaima*: 35, Male, anterior end, lateral view; 36, Male, spicule and gubernaculum, lateral view. Scale bars = 15 μm. 37, Male, head, lateral view. Scale bar = 20 μm.

value (65.0–75.9 vs. 51). Timm (1952) described *I. cobbi* on the basis of a single female and mentions six long labial and six long cephalic setae but does not mention or figure additional cephalic setae. Therefore, the four cephalic setae of the posterior circle appear missing in *I. cobbi*. *Ironella* according to Cobb (1920) and Chitwood (1960) has ten cephalic setae in two circles of six and four. The single circle of six cephalic setae in *I. cobbi* would be unique for the genus. Therefore, *I. cobbi* should be regarded as a *species inquirenda* until the type specimen can be examined or other material becomes available.

Specimens.—Florida Nematode Collection, University of Florida, Gainesville, Florida, 1 female A-141 and 1 male A-142; and 2 males, USNM 77115, 77116 and 1 juvenile 77117.

Locality.—Six to eight miles off Sea Horse Key, Gulf of Mexico, off Levy County, Florida.

Acknowledgments

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HARRIETA, A NEW GENUS FOR *CYMODOCE FAXONI* (RICHARDSON) (CRUSTACEA: ISOPODA: SPHAEROMATIDAE)

Brian Kensley

Abstract.—A new genus, *Harrieta,* is diagnosed for *Cymodoce faxoni* (Richardson), a common shallow-water isopod of the Florida Keys and the eastern Gulf of Mexico. The new genus is characterized by the possession of three pairs of oostegites with five pairs of internal pouches and metamorphosed mouthparts in the female, and by a uropodal exopod twice the length of the endopod in the male.

That the isopod family Sphaeromatidae is in need of a generic revision based on phylogenetic principles, is no secret. Between 70 and 80 generic names are in current use, with generic diagnoses often blurred and overlapping. It comes as no surprise that when new criteria are used in an attempt to stabilize a taxonomy, earlier taxonomic placements become questionable. Thus with Harrison's work on the structure of the brood pouch of sphaeromatids (1984), following on from Hansen (1905), it was inevitable that the generic status of some species would need to be re-examined.

The use of such major morphological features as oostegites, internal pouches, and anterior and posterior pockets in ovigerous females, has the potential to give a degree of stability to the classification of the Sphaeromatidae. These female reproductive structures are here regarded as being of such crucial importance as to allow generic placement based on these features only. Which structures or combination of structures are apomorphic, and which plesiomorphic, however, remains to be worked out. This lack of determined apomorphic features lends some uncertainty, but still allows for comparison of genera based on major reproductive morphological features.

Examination of material of *Cymodoce faxoni* (Richardson), and comparison with the diagnosis of *Cymodoce* Leach, 1814 (see Harrison 1984:377) necessitates placing this species in a new genus.

Subfamily Sphaeromatinae
Harrieta, new genus

Diagnosis.—Sexual dimorphism marked by posterior margin of pleotelson more strongly trilobed, and elongation of uropodal exopods, in male.

Female: mouthparts metamorphosed. Mandible fused with cephalosome, incisor, lacinia, and molar not distinguishable. Maxilla 1 of 2 simple rounded lobes; maxilla 2 of 3 simple rounded lobes. Maxilliped with palp articles lacking setae; endite distally broadly truncate, unarmed. Brood pouch consisting of 3 pairs of oostegites on pereonites 2–4 overlapping in midline, plus 5 pairs of internal pouches. Uropodal rami subequal in length.

Male: Adult lacking dorsal processes. Pleopod 2, copulatory stylet articulating basally on endopod, curved, barely reaching beyond apex of ramus, with distal hook. Penes basally fused, rami slender, elongate, tapering to acute apices. Uropodal exopod twice length of endopod, slender, oval in cross section, tapering to narrowly acute apex.

Type species.—*Exosphaeroma faxoni* Richardson, 1905, Gender: feminine.

Etymology.—The generic name is in honor of Harriet Richardson, the original describer of the type species, and a prolific isopod researcher around the turn of the century.

Remarks.—Based on Harrison (1984: 377), the presence of three, rather than four, pairs of oostegites excludes *faxoni* from the genus *Cymodoce.* Harrison's tables 1 and 2 (1984:394–397) conveniently summarize the brood pouch and mouthparts information for most genera of sphaeromatids. From these tables it can be seen that the combination of three pairs of overlapping oostegites, five pairs of internal pouches, and metamorphosed mouthparts in the female fit none of the known sphaeromatine genera. The present separation of *faxoni* from *Cymodoce* draws attention to these differences and emphasizes the importance of brood pouch characters in the taxonomy of this group.

Harrieta faxoni (Richardson, 1905)
Fig. 1

Exosphaeroma faxoni Richardson, 1905: 292, figs. 307, 308.
Exosphaeroma faxoni: Pearse and Wharton, 1938:640.
Cymodoce faxoni: Menzies and Miller, 1955: 293, figs. 1,2.—Rouse, 1969:134.—Schultz, 1969:127, fig. 182.—Lyons et al., 1971:28.—Clark and Robertson, 1982:47, 49, 54, fig. 18.—Menzies and Kruczynski, 1983:50, fig. 14.—Harrison and Holdich, 1984:383.

Material examined.—National Museum of Natural History, Smithsonian Institution: USNM 41882, 2 ♂, 2 ovig. ♀, 7 immature, Key West, Florida, Jul 1874.—USNM 41883, 1 ♂, 1 ovig. ♀, Cedar Key, Florida, 1874.—USNM 86833, 2 ♂, 3 ovig. ♀, 1 immature, Jupiter Is., Florida, 16 Feb 1940.—USNM 86834, 2 immature, Apalachicola, Florida, 19 Jan 1936.—USNM 86835, 1 ♂, Apalachicola, Florida, 6 Jun 1935.—USNM 86836, 2 ♂, 1 ovig. ♀, 2 immature, Big Lake, Alabama, 28 Jan 1938.—USNM 86837, 2 ovig. ♀, Bottlepoint Key, Florida, 20 Nov 1939.—USNM 184382, 1 ♂, 8 ovig. ♀, 2 immature, Everglades National Park, Florida, 11 Nov 1965.—USNM 211432, 14 ♂, 4 ovig. ♀, 30 immature, Godfrey Creek, Lemon Bay, Florida, 23 Jan 1938.—USNM 211433, 4 ♂, 1 ovig ♀, 7 immature, Key West, Florida, 1968.—USNM 211434, 1 ♂, 3 immature, Fleming Key, Florida, 24 Mar 1968.

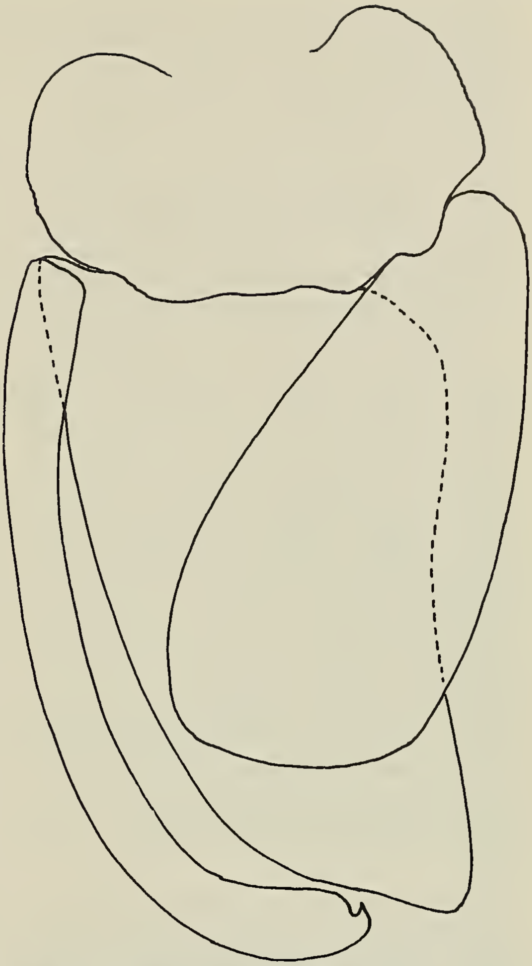

Fig. 1. *Harrieta faxoni,* male pleopod 2.

Indian River Coastal Zone Museum (all material from Florida): Sta 101c, 15 ♂, 22 ovig. ♀, 140 immature, Banana River, Brevard Co., intertidal, 27 Feb 1975.—1 ♂, 1 ovig. ♀, 1 immature, Haulover Canal, Brevard Co., Intertidal, 12 Dec 1978.—1 ♂, 1 ovig. ♀, 2 immature, Key Largo, *Thalassia* seagrass flat, 9 Mar 1982.—Sta 129, 19 ♂, 11 ovig. ♀, 39 immature, Indian River, St. Lucie Co., intertidal, 29 Oct 1975.—Sta 88b, 1 ♂, Indian River, Martin Co., intertidal, 17 Dec 1974.—Sta 116d, 1 immature, Indian River, Brevard Co., intertidal, 29 May 1975.—Sta 79c, 1 ♂, 7 ovig. ♀, 6 immature, Haulover Canal, Brevard Co., 14 Nov 1974.

Diagnosis.—Female: Frontal lamina with broad, slightly convex anterior margin. Cephalon with rounded ridge bearing 2 barely discernible submedian tubercles near posterior margin. Anterior fused pleonites with 2 low rounded submedian tubercles on posterior margin. Pleotelson with 2 strong broadly conical tubercles on inflated midregion; posterior margin faintly trilobed. Uropodal rami subequal in length, endopod distally oblique-truncate; exopod apically acute.

Male: Pleotelson as in female, but with trilobed apex more defined. Uropodal endopod distally oblique-truncate; exopod twice length of endopod, tapering to narrowly acute apex. Penes separate, slender, tapering to acute apex. Pleopod 2, copulatory stylet articulating basally on endopod, curved, barely reaching beyond apex of ramus, with distal hook.

Color.—The majority of freshly preserved specimens examined showed a scattering of red-brown chromatophores on the cephalon, pereon, pleon, antennular and antennal flagella, and uropodal rami. The sternites of ovigerous females are always fairly densely pigmented with a reticulate pattern. A few specimens were seen having the entire dorsum densely pigmented, while yet fewer specimens have the cephalon and pleon densely pigmented with no connecting pigment or a faint to fairly strong connecting middorsal band of pigment.

Distribution.—Florida to Texas, intertidal to shallow infratidal.

Remarks.—Menzies and Kruczynski (1983:50) place both *Exosphaeroma antillense* Richardson, 1912, and *Exosphaeroma barrerae* Boone, 1918, in the synonymy of *Cymodoce faxoni.* Examination of the holotype of *Exosphaeroma antillense* shows this to be a different species: the frontal lamina is not as broad as that of *Harrieta faxoni,* and both uropodal rami are distally rounded. The holotype of *Exosphaeroma barrerae* is more than twice the size of adult *Harrieta faxoni,* and shows several obvious differences, including the shape of the frontal lamina, pleotelson, and uropodal rami. *Exosphaeroma antillense* does possess three pairs of overlapping oostegites, the condition of the holotype does not allow further comment on the brood pouch structure, while the holotype of *E. barrerae* is a nonovigerous female. Until fresh ovigerous material of these species becomes available, and brood pouch structure can be elucidated, both are excluded from the genus *Harrieta.*

Cymodoce brasiliensis Richardson, 1906, was compared with the present species, in an attempt to discover a possible congener. Examination of the syntypic material (USNM 32246, 32626) showed the ovigerous female to have four pairs of oostegites on pereonites 1–4. The species redescribed as *C. brasiliensis* by Loyola e Silva (1960: 68, figs. 10, 11; 1963:2, unnumbered fig.) was said to have three pairs of oostegites, and is thus not Richardson's species. No mention was made of brood pouches. The male described by Loyola e Silva (1960) has subequal uropodal rami, and is clearly not *Harrieta faxoni.* The difference in the uropodal exopod would suggest that Loyola e Silva's species is not a congener of *Harrieta.*

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A NEW TROGLOBITIC CRAYFISH FROM NORTHWESTERN ARKANSAS (DECAPODA: CAMBARIDAE)

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Abstract.—A new troglobitic crayfish, *Cambarus* (*Jugicambarus*) *aculabrum*, is described from two cave streams in Benton County, Arkansas. Its closest affinities are with three other troglobitic species occurring in the Ozark region: *C.* (*J.*) *zophonastes* from Arkansas, *C.* (*J.*) *setosus* from Missouri, and *C.* (*J.*) *tartarus* from Oklahoma.

The crayfish described herein from Benton County, Arkansas, is the second troglobitic decapod to be reported from the state. Only the rare *Cambarus* (*Jugicambarus*) *zophonastes* Hobbs and Bedinger (1964:11), known from a single locality (Hell Creek Cave) in Stone County, has been found previously. Two additional closely related albinistic species, however, occur in the Ozark region: *C.* (*J.*) *setosus* Faxon (1889:237) in southern Missouri, and *C.* (*J.*) *tartarus* Hobbs and Cooper (1972:51) in eastern Oklahoma. The more distantly related troglobitic *C.* (*J.*) *cryptodytes* Hobbs (1941:110) frequents subterranean waters of the panhandle of Florida and southwestern Georgia. (For a review of what is known about these crayfishes, see Hobbs, Hobbs, and Daniel 1977.) Features that will aid in distinguishing between them are pointed out in the appended key and are illustrated in Fig. 2.

Cambarus (*Jugicambarus*) *aculabrum*, new species

Figs. 1a–l, 2a–c, e, j, n

Diagnosis.—Body and eyes without pigment, latter reduced. Body and chelipeds studded with conspicuous stiff setae. Rostrum usually with small marginal spines, occasionally tapering to apex without setting off distinct angle at base of acumen. Areola 17.5 to 54.5 times as long as wide, comprising 43.2 to 47.2 percent of entire length of carapace (50.3 to 55.3 percent of postorbital length), and with 1 or 2 punctations in narrowest part. Cervical spines minute; suborbital angle lacking; postorbital ridges reduced but sometimes with very small, corneous apical tubercles. Antennal scale 1.7 to 1.8 times as long as wide, broadest distinctly distal to midlength. Chela with subrectangular palm bearing irregular mesial arrangement of 20 to 25 tubercles; longitudinal ridges of fingers well developed. Hooks on ischia of third pereiopods of male distinctly compressed, not reaching basioischial articulation, and not opposed by tubercle on basis. First pleopod of first form male with rather long, strongly recurved, scythe-like central projection bearing distinct subapical notch; mesial process appearing somewhat degenerate, not inflated, with basal part of distal (morphological cephalic) margin shallowly concave, and disposed at about 120 degrees to shaft of appendage; proximolateral lobe not set off from shaft by groove. Annulus ventralis subsymmetrical in outline, caudal part slightly movable; cephalic half traversed by deep submedian longitudinal trough; sinus originating on caudolateral (either right or left) side of trough from which coursing caudomesially and, crossing median line, continuing to fossa, and from latter turning

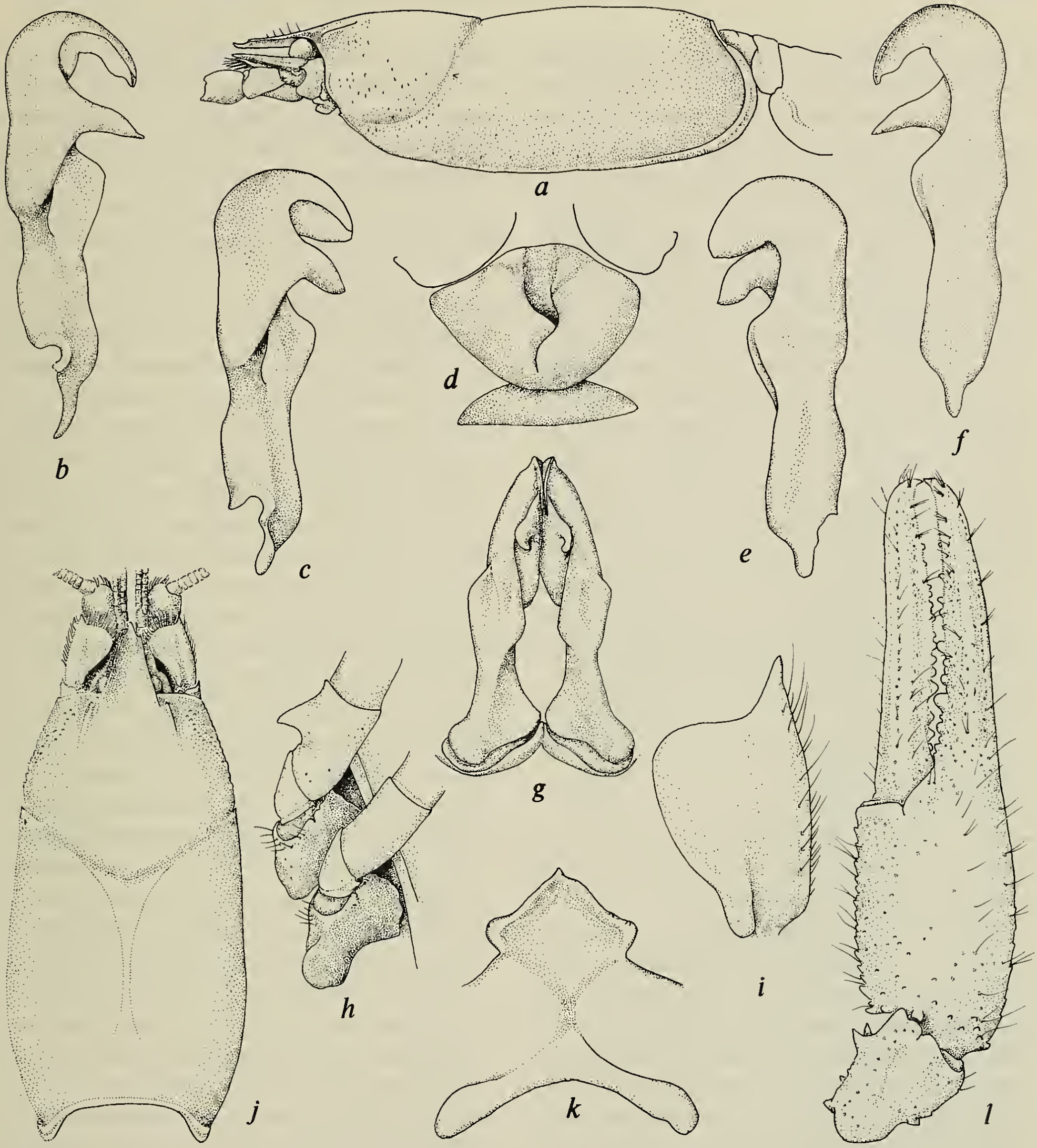

Fig. 1. *Cambarus* (*J.*) *aculabrum* (a, b, f–l from holotype; c, e from morphotype, and d from allotype): a, Lateral view of cephalothorax; b, c, Mesial view of first pleopod; d, Annulus ventralis; e, f, Lateral view of first pleopod; g, Caudal view of first pleopods; h, Ventral view of basal podomeres of third and fourth pereiopods; i, Right antennal scale; j, Dorsal view of carapace; k, Epistome; l, Dorsal view of distal podomeres of cheliped.

gently to median line where, after following it for short distance, ending on caudal wall of annulus. First pleopod of female represented by minute tuberculiform papilla.

Holotypic male, form I: Body subovate, strongly depressed (Figs. 1a, j). Abdomen narrower than thorax (9.1 and 11.6 mm). Areola narrow, 36.7 times as long as wide, with 1 punctation in narrowest part; length of areola 45.8 percent of entire length of carapace (53.9 percent of postorbital length). Rostrum with weakly thickened, elevated, strongly convergent borders bearing minute corneous tubercles at base of acumen; latter with upturned corneous tip overreaching base of ultimate podomere of antennular peduncle; upper surface of rostrum shallowly concave and bearing setiferous punctations, those on mesial flank of both borders deep. Subrostral ridge well developed and evident in dorsal aspect along basal half of rostrum. Postorbital ridges weak, deeply grooved dorsally, and dextral member with small corneous tubercle on cephalic extremity. Suborbital angle absent; branchiostegal spine small. Cervical spine also small but with acute, corneous tip. Carapace conspicuously punctate dorsally; hepatic, mandibular, and anteroventral branchiostegal regions tuberculate, most of branchiostegites granular; majority of punctations and granules supporting setae, many of which erect.

Abdomen and carapace subequal in length (24.1 and 24.0 mm); pleura rather short and rounded ventrally. Cephalic section of telson with two spines in each caudolateral corner, more mesial one movable. Proximal podomere of uropod with acute spine on mesial lobe; mesial ramus with moderately well developed median keel terminating distally in small premarginal spine; spine also present on distolateral angle.

Cephalic lobe of epistome (Fig. 1k) subtriangular with acute anteromedian angle, anterolateral margins elevated (ventrally), dextral one bearing 2 small tubercles; main body of epistome with longitudinal median trough lacking well-defined fovea, but distinct oblique ridge (not illustrated) extending anterolaterally from lateral extremity of arched zygoma. Basal segment of antennule with well developed spines lightly mesial to median line at base of distal third of podomere. Antennal flagellum broken. Antennal scale (Fig. 1i) decidedly wide, broadest distal to midlength; thickened lateral part terminating distally in acute, corneous-tipped spine overreaching tip of acumen and almost attaining distal extremity of antennular peduncle.

Right chela (Fig. 1l) little more than 3.5 times as long as wide, slightly depressed, and with subrectangular palm; mesial margin of palm with about 24 tubercles arranged roughly in 2 staggered rows and many with long, stiff setae extending from their distal bases; base of palm with irregular row of 9 or 10 tubercles extending transversely from ventrolateral condyle across lateral and dorsal surfaces to level of dorsomesial condyle; ventrodistal surface of palm with 3 submedian tubercles: 2 on proximal flank of oblique ridge and 1 proximal to them; lateral margin with row of low tubercles along proximal half and setiferous punctations distally; almost all punctations and tubercles on palm and fingers supporting long stiff setae. Opposable margin of fixed finger with 2 rows of tubercles: dorsal row consisting of 9 on proximal half and 2 minute ones (too small to include in illustration) in distal third; ventral row of 5 beginning just proximal to midlength of finger and extending to base of distal fourth; tubercles of both rows with corneous tips; single row of minute denticles extending almost entire length of finger between dorsal and ventral rows of tubercles. Opposable margin of dactyl with single row of 16 tubercles along proximal four-fifths of finger interspersed among single row of minute denticles; all tubercles, except for abraded ones, with corneous tips. Dorsal and ventral surfaces of both fingers with well developed longitudinal ridges; mesial margin of dactyl with conspicuous setiferous punctations.

Carpus of cheliped longer than broad (5.6 and 4.2 mm) with shallow, oblique furrow dorsally; mesial surface with 2 large spike-like tubercles situated distal to 3 much smaller ones; ventral surface with 3 tubercles on distal border, middle one smaller than others, mesial one largest; lateral surface with oblique row of several small tubercles and few others more proximally situated, 2 somewhat dorsally and 1 ventrally; podomere otherwise bearing setiferous punctations.

Dorsal surface of merus with single row of tubercles basally, but tubercles forming distally broadening band beyond midlength; ventral surface with mesial and lateral rows of 15 tubercles each, those in distal half of both rows spikelike. Mesial and lateral surfaces punctate, and distolateral extremity with single spikelike tubercle. Ischium with ventromesial row of 4 small tubercles distal to fracture suture.

Hook present on ischium of third pereiopod only (Fig. 1h); hook strongly compressed and not reaching basioischial articulation and not opposed by tubercle on basis. Coxa of fourth pereiopod with rounded, somewhat compressed caudomesial boss. Coxa of fifth pereiopod without prominences. For measurements see Table 1.

First pleopods (Figs. 1b, f, g) reaching coxae of third pereiopods when abdomen flexed. See "Diagnosis" for description.

Allotypic female: Differing from holotype in other than secondary sexual features in following respects: acumen almost reaching distal margin of penultimate podomere of antennular penduncle; postorbital ridges with minute, corneous apical tubercle; right cervical spine reduced to small tubercle; abdomen longer than carapace, and pleura more flared; both anterolateral margins of cephalic lobe of epistome with 2 tubercles, dextral with rudimentary third one, and most anterior one situated adjacent to rounded apex of lobe; oblique lateral ridge of main body of epistome with small spine at lateral extremity; antennal flagellum also broken but reaching fifth abdominal tergum; mesial margin of palm of right chela with 18 tubercles (left with 20) arranged in 2 rows; ventrodistal surface of palm with 1 (right) or 2 (left) tubercles; opposable margin of fixed finger of right cheliped with 6 tubercles (8 on left) in dorsal row and 3 (4 on left) in ventral row; opposable margin of dactyl with row of 10 (9 on left); mesial surface of right carpus with 1 spikelike tubercle and 6 smaller ones (left with 1 and 4); merus of right cheliped with ventrolateral row of 11 tubercles and ventromesial one of 16 (most spikelike); ischium of both chelipeds with ventromesial row of 3 small tubercles distal to fracture suture.

Table 1.—Measurements (mm) of *Cambarus* (*J.*) *aculabrum*.

	Holotype ♂ I	Allotype, ♀	Morphotype, ♂ II	Topotype ♂ I
Carapace:				
Entire length	24.0	23.8	19.7	23.1
Postorbital length	20.4	20.8	17.7	19.7
Width	11.6	11.8	9.9	11.6
Height	7.7	7.3	7.1	8.4
Areola:				
Width	0.3	0.2	0.2	0.3
Length	11.0	10.9	8.9	10.9
Rostrum:				
Width	2.7	2.8	2.5	2.6
Length	3.9	3.6	3.3	3.3
Chela:				
Length, palm mesial margin	8.9	8.9	7.5	7.9
Palm width	6.7	7.5	6.1	6.5
Length, lateral margin	24.7	23.5	20.0	22.4
Dactyl length	14.3	13.1	11.2	13.0
Abdomen:				
Width	9.1	10.3	7.9	9.3
Length	24.1	25.6	22.0	25.1

Annulus ventralis (Fig. 1d; see also Fig. 2n) as described in "Diagnosis."

Morphotypic male, form II: Differing from holotype in following respects: acumen falling short of midlength of ultimate podomere of antennular peduncle; postorbital ridges very poorly developed and neither with tubercle at cephalic extremity; abdomen longer than carapace; antennal scale with distolateral margins more concave, and left basal angle with small tubercle, distolateral spine reaching distal extremity of antennular peduncle; ventrodistal surface of palm of right chela with single tubercle on proximal flank of oblique ridge, left as in holotype; opposable margin of fixed finger of right chela with 6 tubercles in dorsal row and 3 in ventral (left chela with 6 and 2); opposable margin of dactyl with row of 10 tubercles on right chela and 13 on left; ventral surface of merus of right cheliped with 11 tubercles in lateral row and 13 in mesial (14 in each row on left); tubercles in ventromesial row of ischium very small. Typically, hook on ischium of third pereiopod smaller but otherwise similar to that in holotype. First pleopod (Fig. 1c, e) with terminal elements more robust but disposed almost as in holotype, although mesial process more strongly reflexed.

Type locality.—Logan Cave, about 11 km east of Shiloam Springs, Benton County, Arkansas (Gallatin Quadrangle T. 18N, R. 32W, Sec. 33; 36°11′50″N, 94°22′50″W). This Ozarkian solution channel, located in the Mississippian cherty-limestone Boone Formation of the Springfield Plateau, is approximately 2000 m long. Water flows (about 19,000 m^3/day) through the entire length of the cave and forms a brook where it surfaces at an elevation of about 323 m. A conical sink hole (10 m diameter × 10 m deep) provides a second access to the passageway about 300 m upstream from that at the spring opening. Collapse of the cave roof formed the sink and dammed the stream, creating an underground lake about 200 m long, 2–6 m wide, and 2–3 m deep. Most of the *Cambarus* (*J.*) *aculabrum* have been seen in this pool, but they also occur in other reaches of the stream. They are usually found along the side walls of the pool or at the margin of the stream. As many as six have been seen during one survey, but more often not one is in evidence. The cave contains a diverse array of other species including among the aquatic forms, an epigean crayfish, *Orconectes neglectus neglectus* (Faxon); Ozark cavefish, *Amblyopsis rosae* (Eigenmann); isopods, *Caecidotea stiladactyla* Mackin and Hubricht; amphipods, *Stygobromus ozarkensis* (Holsinger); sculpins, *Cottus carolinae* Gill, and salamanders, *Typhlotriton spelaeus* (Stejneger), *Eurycea lucifuga* Rafinesque, *E. longicauda* (Green), and *E. multiplicata* (Cope). Terrestrial cave inhabitants include a large population of gray bats, *Myotis grisecens* Howell, other bats, e.g., *Pipistrellis subflavus* Cuvier, collembolans, beetles, dipterans, millipedes, and pseudoscorpions.

Disposition of types.—The holotype, allotype, and morphotype are deposited in the National Museum of Natural History (Smithsonian Institution), numbers 219149, 219150, 219151, respectively. Paratypes, consisting of 1 ♂ I from Logan Cave, and 3 ♂ I, 3 ♂ II, and 1 ♀ from Bear Hollow Cave (see "Range"), are also in the Smithsonian Institution.

Size.—The largest specimen available is a female from Bear Hollow Cave possessing a carapace length of 28.2 mm (postorbital carapace length, 24.0 mm). The largest (the holotype) and smallest first form males have corresponding lengths of 24.0 (20.4) mm and 16.2 (13.7) mm, respectively.

Range.—This crayfish is known from only two localities, both in Benton County, Arkansas; the type locality and Bear Hollow Cave which is situated about 38 km NNW of Logan Cave (T. 21N, R. 30W, Sec. 18; 36°29′50″N, 94°13′25″W). The latter cave is also a solution tunnel in the Boone Formation, but the opening on the hillside is at an elevation of 1160 feet (354 m) and the small stream in it no longer discharges at the surface. There is less habitat available in the much smaller stream (about 200 m long and 0.2 m deep) in Bear Hollow Cave than in the type locality, but as many as nine crayfish have been seen during a single survey. The cave fauna is much less diverse than that in Logan Cave, probably reflecting

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Fig. 2. Epistome and secondary sexual features of troglobitic members of subgenus *Jugicambarus* (a, epistome; b, i–m, mesial view of first pleopod of first form male; c, lateral view of same; d–h, caudal view of same; n, annulus ventralis): a–c, n, Paratypes of *C.* (*J.*) *aculabrum* from Bear Hollow Cave; d, i, Holotype of *C.* (*J.*) *zophonastes*; e, j, Holotype of *C.* (*J.*) *aculabrum*; f, k, *C.* (*J.*) *setosus* from Smallins Cave; g, l, Holotype of *C.* (*J.*) *tartarus*; h, m, Holotype of *C.* (*J.*) *cryptodytes*.


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the lower energy source resulting from the absence of a large colony of bats.

Seasonal data.—First form males were obtained on 31 December 1985, 16 January 1986, 20 February 1986, 8 October 1986, and 25 February 1987. Females carrying eggs or young have not been observed.

Variations.—The most striking variations noted are in the shape and degree of development of the marginal tubercles of the rostrum, the ornamentation of the anteromedian lobe of the epistome, and in the relative width of the areola. The rostral margins may converge almost from the level of the orbit to the base of the acumen, or they may be subparallel or even slightly convex laterally. Moderately well developed marginal tubercles may mark the base of the acumen, but they may be minute, and occasionally are absent (perhaps resulting from injury in an earlier instar) and the angle missing at the base of the acumen. The anteromedian lobe of the epistome is basically in the form of an isosceles triangle with a relatively broad base; however, the anterolateral sides may be slightly concave, unevenly and asymmetrically crenate, and in at least one specimen the anterolateral angles are produced anteriorly (Fig. 2a); in all of the specimens examined, however, there exists an anteromedian, subacute angle. As pointed out above, the width of the areola is decidedly variable, ranging from 17.5 to more than 50 times as long as broad. Other variations occur in the numbers of tubercles on the several podomeres of the cheliped, but they scarcely extend the range of numbers noted in the descriptions of the primary types. Compare Figure 1b, f with 2b, c.

The populations in the two caves seem consistently to differ in two respects: specimens from the type locality exhibit rostra with more strongly convergent lateral margins than do those from Bear Hollow Cave; also, the areola is proportionately narrower (36.3 to 54.5, avg. 43.0 times as long as wide, n = 4) than that in specimens from the latter (17.5 to 35.3, avg. 26.8, n = 7).

Relationships.—There is every reason to believe that the four troglobitic crayfishes of the Ozark Region are more closely allied to one another than any one is to other troglobitic or epigean species. They resemble each other so closely, and the ranges of variation are so similar that one is almost forced to conclude that, unlike the troglobitic *Procambarus* in Florida in which at least three separate origins from epigean ancestors were postulated by Hobbs and Franz (1986), they appear to have been derived from a single stock that gained access to an early subterranean channel in the Ozark uplift. In this stock, a mien that was to become characteristic of all of the troglobitic *Jugicambarus* now known to inhabit the subterranean waters of the Ozark region was soon acquired. The features contributing to the existing similarities are apparently so much in accord with the similar environments in which subsequent isolated populations have become established that few consistently unique qualities, except in secondary sexual characters of the males, can be found in any of them.

The only local clues as to the nature of the ancestral epigean stock that entered the Ozark region must be sought in the very poorly known *C.* (*J.*) *causeyi* (Reimer 1966: 9). But, like its troglobitic relatives, this relict has become so highly adapted (burrowing in seepage areas and in the substrate of small headwater streams) that surely its physiognomy is unlikely to reflect many ancestral qualities of the early epigean Ozarkian *Jugicambarus* stock any better than do those of the troglobites. For example, its strongly compressed body is unique in the subgenus, and few other members of *Cambarus* appear to be so slender. Likely a better appreciation of the visage of the most recent epigean antecedent of the troglobites might be gained by turning to the stream-dwelling *Jugicambarus* frequenting the Cumberland

Plateau and Highland Rim of Tennessee and Kentucky. Perhaps surprising is the observation that marginal spines or tubercles on the rostrum, considered generally to be a primitive feature in crayfish lineages, are lacking in all *Jugicambarus* except the Ozarkian troglobites! Does their presence in these cave dwellers represent a primitive retention or an atavistic recurrence?

Two features seem consistently to set *C. (J.) aculabrum* apart from its close relatives. The anteromedian lobe of the epistome is produced anteriorly in an acute or subacute apex, hence the name accorded the species, and the first pleopod, which lacks even a trace of a groove at the base of the proximolateral lobe, exhibits a strongly reflexed, distally tapering central projection that bears a shallow subapical notch. The following key should aid in the identification of the first form males of the five troglobitic members of the subgenus *Jugicambarus.*

Key to the Troglobitic Members of the Subgenus *Jugicambarus* (Based on first pleopods of first form males)

1. Central projection directed at right angle to shaft of appendage (Fig. 2h, m) .... *C. (J.) cryptodytes*
– Central projection bent more than at right angle to shaft of appendage (Fig. 2i–l) 2
2. Proximolateral lobe of first pleopod set off from shaft by shallow or deep transverse groove (Fig. 2f, g) 3
– Proximolateral lobe of shaft of first pleopod not set off from shaft by transverse groove (Figs. 2d, e) 4
3. Central projection short, not tapering, truncate apically (Fig. 2g, l) .. .. *C. (J.) tartarus*
– Central projection moderately long, and tapering to rounded apex (Fig. 2f, k) .... *C. (J.) setosus*
4. Central projection short and lacking subapical notch (Fig. 2d, i) .... *C. (J.) zophonastes*
– Central projection moderately long and with shallow subapical notch (Fig. 2e, j) ....*C. (J.) aculabrum*

Acknowledgments

We extend our thanks to C. Stanley Todd for the interest, enthusiasm, and assistance provided during the course of a study, by one of us (AVB), of the Ozark caves and their faunas. His help in obtaining the series of specimens on which this report is based was invaluable. We are also grateful to the Arkansas Nongame Preservation Committee for a grant that made the cave study possible. For their comments and criticisms of the manuscript, appreciation is extended to Thomas E. Bowman of the Smithsonian Institution, J. F. Fitzpatrick, Jr., of the University of South Alabama, and H. H. Hobbs, III of Wittenberg University. We also appreciate the assistance of Mark E. Gordon with various aspects of the study.

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PROC. BIOL. SOC. WASH.
100(4), 1987, pp. 1049–1050

ON THE STATUS OF THE PHYLUM-NAME, AND OTHER NAMES, OF THE VESTIMENTIFERAN TUBE WORMS

Meredith L. Jones

Abstract.—Two phylum-names have been proposed for the same group of animals, the vestimentiferan tube worms of hydrothermal vents and elsewhere. Priority for the phylum-name Vestimentifera Jones, as well as for the classes Axonobranchia Jones and Basibranchia Jones and the orders Riftiida Jones and Lamellibrachiida Jones, is established; these are the senior synonyms for these taxa.

It has come to my attention that there exists a possibility of confusion concerning the valid name of the phylum containing tube worms of the genera *Lamellibrachia, Riftia, Escarpia, Tevnia, Oasisia* and *Ridgeia.*

The phylum Vestimentifera was proposed in a publication dated 30 December 1985 and was available for distribution on that date (Jones 1985). The phylum includes: the class Axonobranchia with the single order Riftiida and the single family Riftiidae, containing the genus *Riftia,* only; and the class Basibranchia with two orders, Lamellibrachiida (with two families, Lamellibrachiidae and Escarpiidae, each monogeneric, with *Lamellibrachia* and *Escarpia,* respectively), and Tevniida (with two families, Tevniidae, with the genera *Tevnia* and *Oasisia,* and Ridgeiidae, with the single genus *Ridgeia*).

The phylum Mesoneurophora was proposed in a publication that bears the date "1985" (Mañé-Garzón and Montero "1985"). The phylum includes a single class, Vestimentifera, with two orders, Lamellibrachida (with the single genus *Lamellibrachia,* with the family Lamellibrachiidae implied) and Ptyllida (with the single genus *Riftia,* with the family Riftiidae implied). This was something of a surprise to me since I had discussed my intent to propose a new phylum for these tube worms during "... un franco y positivo intercambio de ideas" (Mañé-Garzón and Montero "1985":27), when one of the authors visited me in my laboratory on 24 August 1985, my paper being "in press" (Jones 1985).

The two dates involved here suggest that there is a question of priority concerning the validity of the two sets of names of phylum, class, and order, for the date of the phylum Vestimentifera is quite late in the year.

On the back cover of the paper proposing the phylum Mesoneurophora there is printed "INZAURRALDE Prensa" and "Depósito Legal 215257/86." The final two figures of the number suggest that the paper may have been printed in 1986, in spite of the date inscribed, 1985.

Inquiries, by telephone, to INZAURRALDE Press, Montevideo, indicated that the paper was printed and available for distribution on or about 12 June 1986; a request for written confirmation of this date has not been answered as yet.

The number associated with "Depósito Legal," above, is assigned by the Biblioteca Nacional, Montevideo, to publications produced in Uruguay. In response to a request for details concerning the date of publication of the paper and of its availability, the Director of the Department of Public Service of the National Library stated, in a letter, that the date of issue of this number was 19 March 1986 and that their records showed that the paper was available to readers at the Library in July 1986.

A letter to the Editor of the Revista de Biología del Uruguay, dated 6 October 1986, concerning the date of publication of the article in question, has gone unanswered; a similar letter to the authors of the paper, dated 26 February 1987, likewise, has gone unanswered.

It is evident from the comments from the National Library, Montevideo, that there is a priority of date for the publication of 30 December 1985 proposing the phylum Vestimentifera, along the classes and orders proposed with it.

Although it is acknowledged that the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1985) does not apply to taxa above the familial level (Article 1 (b) (4)), some guidance is available for the present case; application of Article 21 (c) of the Code indicates that the earliest date of publication of the Uruguayan paper considered here must be 31 December 1985.

In either case, then, the phylum Vestimentifera Jones, the classes Axonobranchia Jones and Basibranchia Jones and the orders Riftiida Jones and Lamellibrachiida Jones have priority, on the basis of date, and the phylum Mesoneurophora Mañé-Garzón & Montero, the class Vestimentifera Mañé-Garzón & Montero and the orders Ptyllida Mañé-Garzón & Montero and Lamellibrachida Mañé-Garzón & Montero are their respective junior synonyms.

I thank F. M. Bayer of this department for comment on and discussion of the manuscript and V. Solís-Weiss, Universidad Nacional Autónoma de México, for help with translations and in making telephone calls to Uruguay.

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PROC. BIOL. SOC. WASH.
100(4), 1987, p. 1051

PUBLICATION OF THE *OFFICIAL LISTS AND INDEXES OF NAMES AND WORKS IN ZOOLOGY*

The 1987 edition of the "Official Lists and Indexes . . ." has been published by the International Trust for Zoological Nomenclature. This publication records for the first time in a single volume all the animal names and the titles of works on which the International Commission has ruled since it was set up in 1895. The volume comprises 366 pages and includes 9900 entries. References are arranged alphabetically in four sections: family-group names, generic names, specific names, and titles of works.

In North America, copies may be ordered from the American Association for Zoological Nomenclature (AAZN, % NHB Stop 163, Smithsonian Institution, Washington, DC 20560). The cost is $110.00 ($100.00 to AAZN members).

PROC. BIOL. SOC. WASH.
100(4), 1987, p. 1052

BIOLOGICAL SOCIETY OF WASHINGTON PROCEEDINGS

114th Annual Meeting, 27 May 1987

The meeting was called to order by Austin Williams at 1:00 p.m. in the Waldo Schmitt Room, National Museum of Natural History.

Don Wilson, Treasurer, reported that income from dues, subscriptions, and page charges were higher in 1986 than they had been in 1985, but that income from the sale of past issues of the Proceedings was, inexplicably, down. Total income for 1896 was $101,725.00. The estimated income for 1987 is $91,300.00, and the estimated expenditures are $67,500.00—leaving about $23,000.00 available to subsidize page charges. Austin noted that the report had been approved by the Council, and no questions were asked.

Brian Kensley, Editor, then reported on Volume 99 of the Proceedings. Ninety papers, totaling 770 pages, were published in 1986 and the number of papers related to botany seems to be increasing. It was noted that papers submitted by individuals unable to pay page-charges were currently subject to publication delays of up to a year. Unpaid papers now account for about 50 pages per issue, and Brian hopes that additional funds will be available to increase this to 60 pages per issue. There were no comments on this report.

Austin announced that the Nominations Committee, consisting of Richard P. Vari, Stanley M. Weitzman, and Donald B. Whitehead, will circulate an election ballot later in the year.

Bruce Collette moved that the meeting be adjourned; Ted Bayer seconded the motion; the meeting was adjourned at 1:30 p.m.

Respectively submitted,
C. W. Hart, Jr.
Secretary

INFORMATION FOR CONTRIBUTORS

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

Submission of manuscripts.—Submit manuscripts to the Editor, Proceedings of the Biological Society of Washington, National Museum of Natural History NHB-163, Smithsonian Institution, Washington, D.C. 20560.

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

Proofs.—First proofs are submitted to authors for correction and approval. Reprint orders are taken with returned proofs.

Publication charges.—Authors are asked to assume publication costs of page-charges, tabular material, and figures, at the lowest possible rates. Authors are required to pay the charges for figures, tables, changes at proof stage, and reprints. Payment of full costs will facilitate speedy publication.

Costs: Printed page @ $60.00, figures @ $10.00, tabular material $3.00 per printed inch. One ms. page = approx. 0.4 printed page.

Presentation.—Manuscripts should be typed **double-spaced throughout** (including tables, legends, and footnotes) on one side of 8½ × 11 inch sheets, with at least one inch of margin all around. Manuscripts in dot-matrix will not be accepted. Submit two facsimiles (including illustrations) with the original, and retain an author's copy. Pages must be numbered consecutively. Underline singly scientific names of genera and lower categories; leave other indications to the editor.

The sequence of material should be: Title, Author(s), Abstract, Text, Acknowledgments, Literature Cited, Author's(s') Address(es), Appendix, Figure Legends, Figures (each numbered and identified), Tables (**double-spaced throughout**, each table numbered with an Arabic numeral and with heading provided).

Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is required for descriptions and diagnoses. Literature citations in the text should be in abbreviated style (author, date, page), except in botanical synonymies, with unabbreviated citations of journals and books in the Literature Cited sections. Direct quotations in the text must be accompanied by author, date, **and pagination.** The establishment of new taxa must conform with the requirements of the appropriate international codes of nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Examples of journal and book citations:

Eigenmann, C. H. 1915. The Cheirodontidae, a subfamily of minute characid fishes of South America.—Memoirs of the Carnegie Museum 7(1):1–99.

Ridgely, R. S. 1976. A guide to the birds of Panama. Princeton, New Jersey, Princeton University Press, 354 pp.

Olson, S. L. 1973. The fossil record of birds. Pp. 79–238 *in* D. Farner, J. King, and K. Parkes, eds., Avian biology, volume 8. Academic Press, New York.

Figures and tables with their legends and headings should be self-explanatory, not requiring reference to the text. Indicate figure and table placement in pencil in the margin of the manuscript. Plan illustrations in proportions that will efficiently use space on the type bed of the Proceedings. **Original illustrations should not exceed 15 × 24 inches.** Figures requiring solid black backgrounds should be indicated as such when the manuscript is submitted, but should not be masked.

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