

Four New Eulimid Gastropods Associated with Shallow-Water Diadematid Echinoids in the Western Pacific¹

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ABSTRACT: A new genus, *Pulicicochlea*, and a new subgenus, *Pseudoretusa*, have been erected to accommodate *Pu. (Pu.) astropyga* from the echinoid *Astropyga radiata*, *Pu. (Pu.) fusca* from *Diadema setosum*, *Pu. (Pu.) calamaris* (the type of the genus) from *Echinothrix calamaris*, and *Pu. (Ps.) faba* from *E. diadema*. The host specificity of these gastropods and their distributions in relation to those of relevant diadematids are shown and discussed. All are external parasites; the species of *Pulicicochlea* s.s. probably feed on the epithelium of the host's spines and *Pu. (Ps.) faba* on the host's body fluids. Anatomical information is given for *Pu. calamaris* and *Pu. (Ps.) faba* (the only two examined alive), and the relationships of *Pulicicochlea* with other genera in the family are discussed in this light. It is suggested that the Stiliferidae is not separable from the Eulimidae.

SPECIES OF THE DIADEMATIDAE have been collected by one of us (Gooding) throughout the Pacific Ocean and the Caribbean Sea in order to study their animal commensals. During this investigation, small ectoparasitic mollusks were found associated with some of the tropical diadematid species. In most cases, these proved to be the four eulimid species described below.

In general, Ponder is responsible for the taxonomic and anatomical work discussed and Gooding for the collecting information, host data, and observations on living material.

MATERIALS AND METHODS

Host urchins were usually collected by day by prizing them out and lifting them off the

bottom with a rod. Different species were placed in separate plastic buckets. Unless they were to be processed immediately, the water was poured off and the urchins kept damp and cool to prevent dehydration.

For general samples, the seawater was renewed, chloretone or menthol crystals were added, and the whole was allowed to stand (usually overnight). If the urchins continued to show signs of life, formalin was added to make a solution of about 5 percent and the sample left at least 10 min. Samples that could not be processed immediately were, after standing for about 12 hr, preserved or washed in 5 percent formalin.

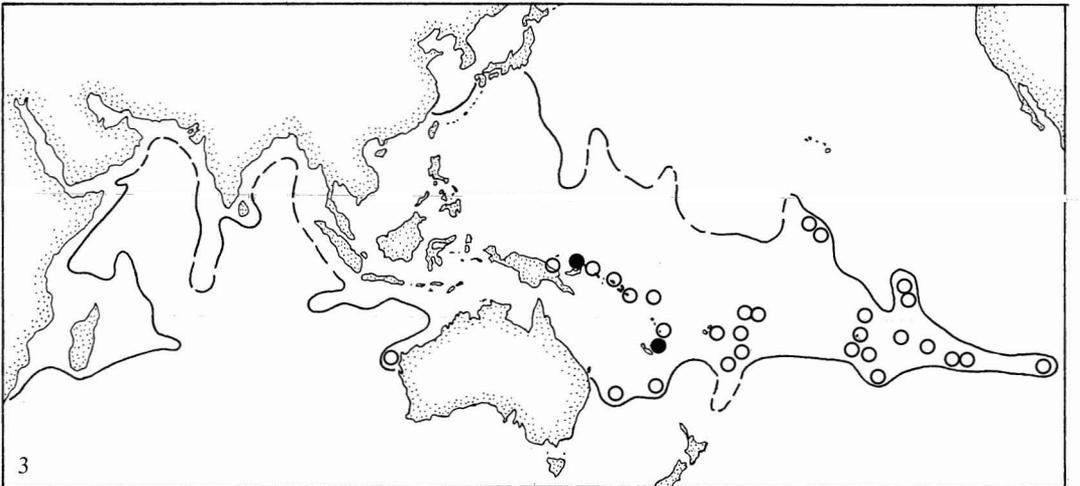
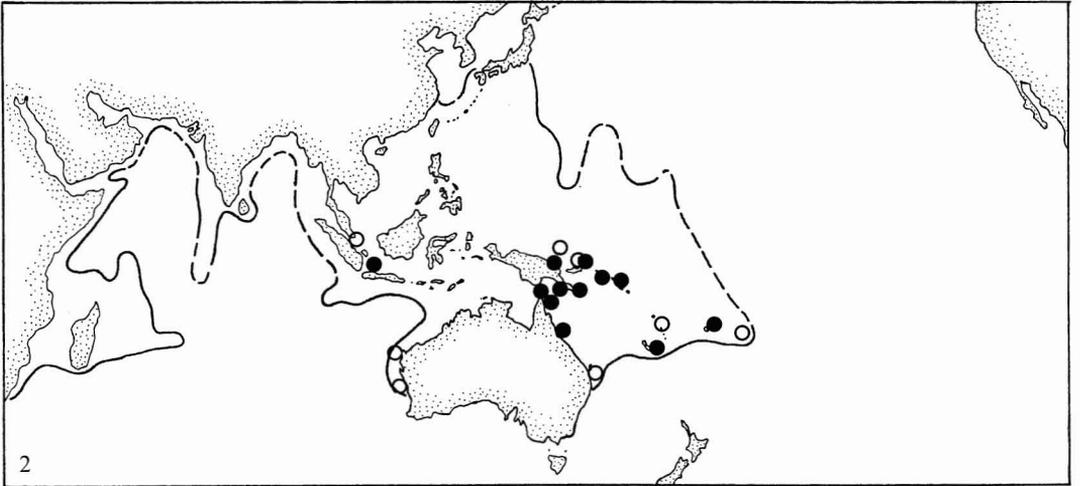
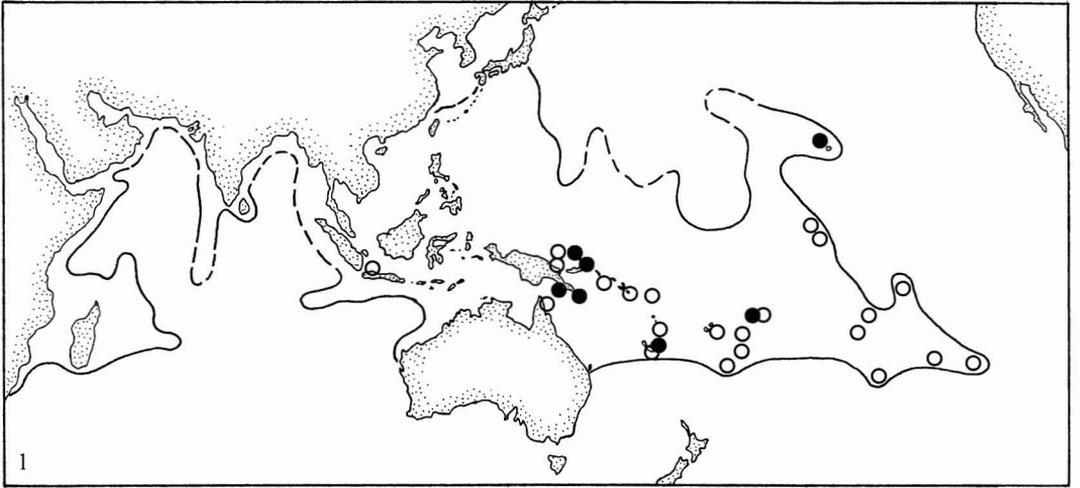
The urchins were then shaken with tongs, with long forceps, or by hand; removed and measured; and the fluid filtered through a 0.25-meter plankton net of 49.2 mesh/cm (125 mesh/inch). The residue was rinsed on the net with gentle water pressure (preferably seawater) and sorted within the day when possible. If the residue could not be sorted the same day, it was preserved in about 10 percent neutral seawater formalin, and rinsed in the same manner as the fresh residue before sorting.

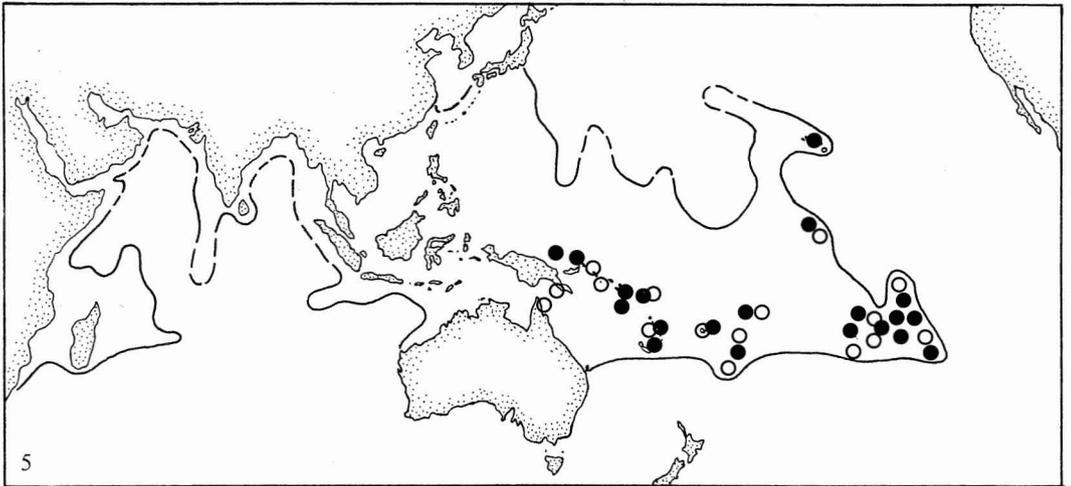
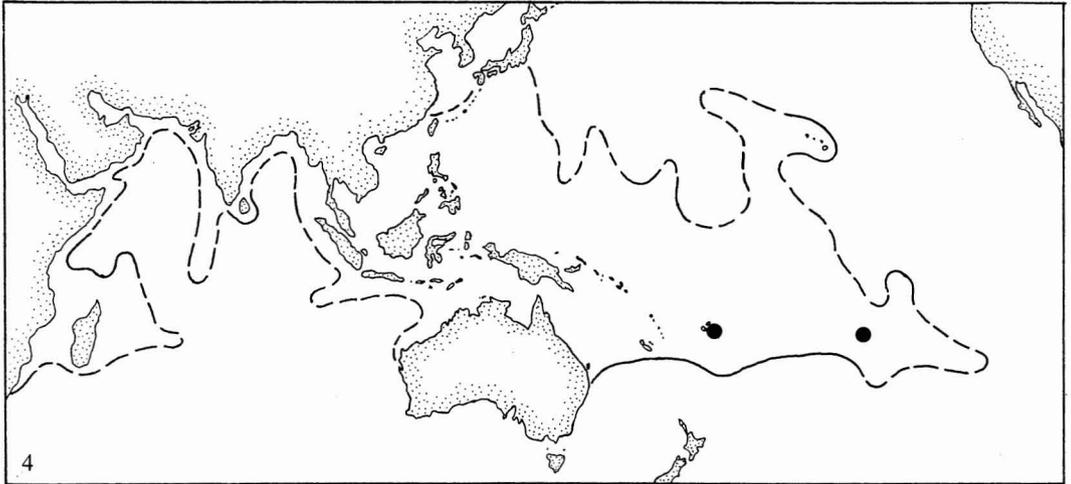
Residue samples were sorted under a dissecting microscope at 6 to 15 ×. Gastropods were temporarily stored in 10 percent neutral

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FIGURES 1–5. Distribution of *Pulicicochlea* species in relation to their host urchins. The circles represent collections made of the host urchins, but because of space limitations some indicate more than one collection. In each case, the solid circles show the collections that were positive for the parasite and the open circles collections that were negative for the parasite. A solid black line indicates the known distribution limits of the host urchins and a broken line the probable limits of the range. 1, *Pulicicochlea* (*Pu.*) *calamaris* and *Echinothrix calamaris*. 2, 3, *Pulicicochlea* (*Pu.*) *fusca* and *Diadema setosum* (Figure 2), and *D. savignyi* (Figure 3). 4, *Pulicicochlea* (*Pu.*) *astropyga* and *Astropyga radiata*. 5, *Pulicicochlea* (*Pseudoretusa*) *faba* and *Echinothrix diadema*.

seawater formalin. Most specimens are now stored in the Australian Museum in 5 percent neutral seawater formalin, but a few lots have been dried.

To obtain live specimens for observation and/or histological fixation, either 20 percent magnesium sulfate solution (in fresh water) diluted by half with seawater or ethyl alcohol diluted to about 10 percent in seawater was used. The first was satisfactory for *Pulici-*

cochlea calamaris sp. nov. but apparently not for *Pu. faba* sp. nov. The fluid was filtered at intervals and the residue washed into a white dish with seawater, where it was sorted by eye. The gastropods usually recovered quickly from this treatment, provided they had not been anaesthetized more than 2 hr. Only about half the specimens in a sample, however, could be collected within this time.

Live specimens were examined in seawater

under a stereoscopic microscope either in isolation or in relation to small hosts whose spines had been cut short. For later sectioning they were preserved by dropping directly into Bouin's fluid, either at room temperature or warmed to steaming. Fixation was for a minimum of 24 hr; the specimens were then decolorized and stored in 70 percent ethyl alcohol.

The histological material was prepared by dehydrating specimens in absolute alcohol, and these were embedded in Paraplast paraffin and sections cut serially at 6 μ m. Staining was with Harris's Haematoxylin-Eosin.

Dissection of formalin-fixed material was attempted but, because of the small size of these gastropods, the results were generally not as helpful as reconstruction from sections.

HOST SPECIES

The host urchins are all shallow-water, tropical, Indo-West Pacific, diadematid echinoids; large (about 7–20 cm horizontal test diameter), with relatively long, slender, sharp spines (up to $\frac{1}{3}$ meter in *Diadema*), and dark in color. The urchins tend to be gregarious and highly mobile (particularly *Astropyga* and *Diadema*). The known and presumed distributions of the urchins are shown in Figures 1–5.

Astropyga radiata (Leske, 1778) usually occurs at depths of more than 10 meters (in the present survey), although it has been reported to come into very shallow water occasionally. It is also often strongly localized; for example, in Tahiti, one of the local divers (Jack Bennett) knew it, but had seen it only in a single spot (which needed precise definition by shore marks).

The other three hosts [*Diadema setosum* (Leske, 1778), *Echinothrix calamaris* (Pallas, 1774), and *E. diadema* (Linnaeus, 1758)], together with the possible host *D. savignyi* Michelin, 1845, are typically coral reef forms. They are sometimes found in close inter-specific aggregations, although each tends to have its specific habitat, and often large areas are dominated by one species. On outer reefs, *E. diadema* is most commonly found almost in

the surf zone toward the outer side of the reef flat. *Diadema savignyi* is found a little more landward, where the waves rarely break but where currents are still strong. *Echinothrix calamaris* is found on the inner (= lagoon-al, if a lagoon occurs) side of the reef. *Diadema setosum* is found in quiet water and is usually the only one of the hosts found on sandy bottoms or even in quite turbid water. But it prefers—as the others (particularly *Echinothrix*) seem almost to require—firm support, such as rocks or coral. The species of *Echinothrix* tend to move under cover during the day, but at night all four species are normally in the open, feeding, mainly by rasping off algae growing on rock or coral.

There are no other species of *Echinothrix* known, but *Astropyga* and *Diadema* are circumtropical genera containing additional species.

DISTRIBUTION AND COLLECTION DATA

The geographical distribution of most collections, whether successful or not, is shown in relation to that of their host urchin in Figures 1–5. One of us (Gooding) has collected animal associates from other species of *Astropyga* and *Diadema* and from the warm-temperate species of *Centrostephanus*, but none have proved to host *Pulicicochlea* or similar gastropods. The latter comprise collections of *C. tenuispinus* Clark, 1914, from Western Australia; and *C. rodgersi* (A. Agassiz, 1863) from the Sydney region, Lord Howe Island, Norfolk Island, and New Zealand. The other species of *Astropyga* sampled were *A. pulvinata* (Lamarck, 1816) and *A. magnifica* A. H. Clark, 1934; and other species of *Diadema* were *D. paucispinum* A. Agassiz, 1863, *D. mexicanum* A. Agassiz, 1863, *D. antillarum* (Philippi, 1845), *D. palmeri* Baker, 1966, and *D. ascensionis* Mortensen, 1909.

In general, host distributions are based on Clark and Rowe (1971) or the references they quote, and on Mortensen (1940). The southeastern limit for *Diadema setosum* stems from Gooding's collecting [despite the statement in Mortensen (1940, p. 263) that this species occurs in Tahiti]. The occurrence of *Echi-*

nothrix calamaris in Western Australia is recorded from specimens in the Western Australian Museum (Point Cloates, N.W. Australia, W.A. Mus. Cat. No. 615-71).

TAXONOMY

Family Eulimidae (= Strombiformidae, Melanellidae, Stiliferidae)

Genera placed in the Eulimidae and in the Stiliferidae are normally parasitic on echinoderms and, as pointed out by Vaney (1913), there appears to be a transition between typical eulimids (such as species placed in *Eulima* Risso, 1826) and species of *Stilifer* Broderip, 1832. Species placed in *Mucronalia* A. Adams, 1860, are one such transitional group. Grusov (1965) has suggested that the family names Eulimidae (= Strombiformidae and Melanellidae) and Stiliferidae as well as the Pelseeneeriidae, Paedophoropodidae and Asterophilidae, can be united into a single broad family (the Eulimidae). The degree of parasitism, size of the pseudopallium, reduction (and sometimes disappearance) of the shell, foot and cephalic tentacles, attainment of hermaphroditism, and relative enlargement and nonretractability of the proboscis are all variable features, showing gradual transitions between genera. It is thus difficult to draw a meaningful line between the Stiliferidae and the Eulimidae, and for the purposes of this account they are considered to be one family.

Before a real assessment of the genera of the Eulimidae (*sensu lato*) is possible, a critical investigation of more species is called for. Simple shell features and the lack of a radula make anatomical information obligatory, and the taxonomy of this group will probably remain a problem until much more information is available.

Table 1 summarizes some of the main features separating the shelled eulimid genera that have been anatomically investigated. A survey of the available literature suggests that the features described below are common to the Eulimidae (*sensu lato*) and may serve as a family diagnosis.

Foot usually small in relation to rest of animal; sometimes very reduced and often without operculum. Two pedal glands usually present which occupy much of the anterior body cavity. Lateral pedal flaps sometimes developed. Pallial cavity usually with gill, osphradium, and hypobranchial gland. A pseudopallium (restricted here to a fold arising from the base of the proboscis) often present and sometimes large; in some parasitic forms reflected over shell. Proboscis present, sometimes nonretractable. Anterior alimentary canal lacking accessory glands [a "proboscis gland" present in *Robillardia* (Gooding and Lützen 1973)], no odontophore (or radula), but usually with a buccal cavity developed as a pump. Stomach absent or small; intestine short (or occasionally absent). Sexes separate or hermaphrodite; pallial genital ducts open grooves [except female tract in *Goodingia* (Lützen 1972a)]; penis usually present in male [absent in *Mucronalia nitidula* (Pease, 1860) (Hoskin and Cheng 1970)]; seminal receptacle in female but no true bursa copulatrix (Fretter 1955, Johansson 1953). Nervous system with large, condensed circumesophageal ganglia. Shell variable, usually smooth with pyriform aperture; sometimes very reduced or absent in adult.

Pulicicochlea gen. nov.

ETYMOLOGY: *Cochlea* (Latin) = snail; *pulex* (Latin) = flea. Gender feminine.

TYPE SPECIES: *Pulicicochlea calamaris* sp. nov.

The combination of characters that distinguishes the new genus is: the complex anterior esophagus and exceedingly narrow posterior esophagus; the relatively simple, retractable proboscis lacking an obvious pseudopallium; the retractable pedal flaps that can cover the shell and also extend ventrally; the lack of an operculum; and the medium-sized (for the family) to small foot. The presence of a fairly well-developed pharyngeal bulb and an hermaphroditic condition are additional features that some genera lack.

Distinctive shell features are the thin, glossy texture, elongate aperture, and sinuate outer lip. Apertural side of body whorl tends

TABLE 1

COMPARISON OF THE MAIN CHARACTERS SEPARATING SOME OF THE GENERA OF THE EULIMIDAE (*sensu lato*)

GENERA	SHELL	FOOT/OPERCULUM	TENTACLES/EYES	PROBOSCIS/ PSEUDOPALLIUM	ESOPHAGUS, PHARYNGEAL BULB	SEXES SEPARATE OR HERMAPHRODITE
<i>Echineulima</i> Lützen & Nielsen, 1975	Ovate, medium spire, mammillate protoconch; animal can contract into shell	Foot with creeping sole; operculum present	Tentacles long; eyes present	Proboscis large, long; pseudopallium rudimentary	Buccal pump small; esophagus elongate, simple	Sexes separate, dimorphic
<i>Eulima</i> Risso, 1826, <i>Balcis</i> Leach, 1847*	Tall; animal can retract completely into shell	Usually not fixed; foot usually well developed; operculum present	Both well developed	Proboscis retractable, long; pseudopallium not well developed	Esophagus simple; pharyngeal bulb present	Sexes separate
<i>Goodingia</i> Lützen, 1972	Swollen, like <i>Stilifer</i> animal probably can retract	Foot reduced, nonfunctional; operculum present	Both well developed	Proboscis very large, nonretractable, with terminal sucker used for attachment to host and locomotion; a narrow skirt around proboscis may represent pseudopallium	Anterior gut with long glandular section (= buccal cavity) anterior to pharynx; no rectum or stomach	Hermaphrodite, gonads separate
<i>Megadenus</i> Rosén, 1910	Shining, globose, thin, finely striate; animal cannot completely retract	Fixed (internal in holothurian gut); foot moderately large; no operculum	Both present but reduced	Long, nonretractable proboscis; pseudopallium better developed in male than in female	Esophagus simple; pharyngeal bulb present	Sexes separate
<i>Mucronalia</i> A. Adams, 1860†	Cylindrical, porcellaneous; animal can usually retract completely	Usually fixed, foot reduced; operculum present; some with pedal flaps	Eyes present or absent; tentacles present	Proboscis nonretractable, long; pseudopallium usually well developed to absent	Esophagus simple; pharyngeal bulb absent	Sexes separate or hermaphrodite
<i>Paramegadenus</i> Humphreys & Lützen, 1972	Swollen, smooth, polished, thin	Foot reduced; no operculum (internal in asteroid skin)	Both reduced but present	No proboscis; pseudopallium large, more developed in male	Buccal cavity very simple	Sexes separate, male much smaller than female
<i>Pelseneeria</i> Köhler & Vaney, 1908, <i>Rosenia</i> Schepman, 1913 (= <i>Turtonia</i> Rosén, 1910)	Squat; animal cannot completely retract	Fixed, foot very small; operculum absent; pedal fold covers shell	Tentacles usually well developed; eyes usually present	Nonretractable proboscis	Esophagus narrow, simple; pharyngeal bulb present	Hermaphrodite, gonads separate

TABLE 1 (cont.)

COMPARISON OF THE MAIN CHARACTERS SEPARATING SOME OF THE GENERA OF THE EULIMIDAE (*sensu lato*)

GENERA	SHELL	FOOT/OPERCULUM	TENTACLES/EYES	PROBOSCIS/ PSEUDOPALLIUM	ESOPHAGUS, PHARYNGEAL BULB	SEXES SEPARATE OR HERMAPHRODITE
<i>Pisolamia</i> Bouchet & Lützen, 1976	Ovate, depressed, mammillate protoconch	Foot reduced(?); no operculum	Tentacles long; no eyes	Proboscis proximal end disklike, remainder narrow, very long; no pseudopallium	Esophagus simple; no rectum or anus	Simultaneous hermaphrodite, one gonad
<i>Pulicicochlea</i> gen. nov.	Spire absent to medium; animal can completely retract	Capable of free movement; foot moderately well developed to small; operculum absent; pedal flaps cover shell	Both well developed	Proboscis retractable, moderately long; pseudopallium not well developed	Esophagus complex; pharyngeal bulb present	Hermaphrodite, gonads separate
<i>Robillardia</i> E. A. Smith, 1889	Depressed spire, inflated body whorl, mammillate protoconch; animal cannot completely retract	Foot with well-developed functional sole; pedal fold covers much of shell and produced into siphon; no operculum (internal, in echinoid rectum)	Both well developed	Very long proboscis with unpaired "proboscis gland"; no pseudopallium	Esophagus long, simple; pharyngeal bulb present	Consecutive hermaphrodite(?); males live in female's brood pouch
<i>Stilifer</i> Broderip, 1832	Thin, hyaline mucronate apex; animal cannot completely retract	Fixed; foot usually reduced; no operculum	Tentacles sometimes present; eyes usually reduced	Large, retractable proboscis; pseudopallium covers shell	Esophagus simple; pharyngeal bulb absent	Consecutive hermaphrodite

NOTE: The information was largely obtained from Vaney (1913), but some also came from Bouchet and Lützen (1976), Fretter (1955), Gooding and Lützen (1973), Hirase (1932), Hoskin and Cheng (1970), Humphreys and Lützen (1972), Koehler and Vaney (1908, 1912), Lützen (1972a, 1972b), Lützen and Nielsen (1975), Risbec (1954), and Schepman and Nierstrasz (1909).

*This is a tentative generic grouping where much further subdivision may be necessary due to the wide range of anatomical features apparently exhibited between species.

[†]It is likely that when the type species of *Mucronalia* is described anatomically it will be found to have little or no relationship with the species presently included in that genus for which details of the anatomy are already known (J. Lützen, *in lit.*).

to be concave; protoconch squat, rounded, almost colorless, of few whorls. There is also an unusual tendency for the spire to become asymmetrically immersed in the last whorl. Color is uniform dark red-brown or dark brown.

The new genus differs in its combination of characters from other eulimid genera for which anatomical information is available. A comparison of the main anatomical features can be seen by reference to Table 1.

It is difficult to contrast shell features at the generic level in the Eulimidae, but the long aperture, minute size, and dark coloration are very characteristic of *Pulicicochlea* and are a combination of characters not found in the genera so far described.

Pulicicochlea sensu stricto

DIAGNOSIS: Foot medium size for family; cephalic tentacles long. Proboscis rather short, emerges between tentacle bases in midline of animal. Esophagus with muscular

esophageal bulb, short glandular region and lacks a crop. Digestive gland with wide lumina.

Shell with short to tall spire, showing a tendency for asymmetrical immersion in later whorls, apertural side of body whorl only slightly concave, flat, or convex.

Pseudoretusa subgen. nov.

ETYMOLOGY: *Pseudo* (Greek) = false; *Retusa* is the opisthobranch (cephalispidean) genus. Gender feminine.

TYPE SPECIES: *Pulicicochlea (Pseudoretusa) faba* sp. nov.

DIAGNOSIS: Foot relatively small; cephalic tentacles short. Proboscis large, emerges on left side of foot. Esophagus with nonmuscular esophageal bulb, long glandular area, and a croplike expansion. Digestive gland with very narrow lumina.

Shell bean-shaped, with completely sunken spire and long body whorl which is distinctly concave on its apertural side.

KEY TO SPECIES OF THE GENUS *Pulicicochlea*

- 1. Spire extends beyond aperture2
 Spire does not extend beyond aperture *Pulicicochlea (Pseudoretusa) faba* sp. nov.
- 2. Spire narrow, with about two visible teleoconch whorls above the body whorl
 *Pulicicochlea (Pu.) calamaris* sp. nov.
 Spire moderately broad to swollen, with less than one visible teleoconch whorl above the body whorl3
- 3. Shell more or less regularly ovate, color dark brown
 *Pulicicochlea (Pu.) fusca* sp. nov.
 Shell subcylindrical, color red-brown *Pulicicochlea (Pu.) astropyga* sp. nov.

Pulicicochlea (Pulicicochlea) calamaris sp. nov.

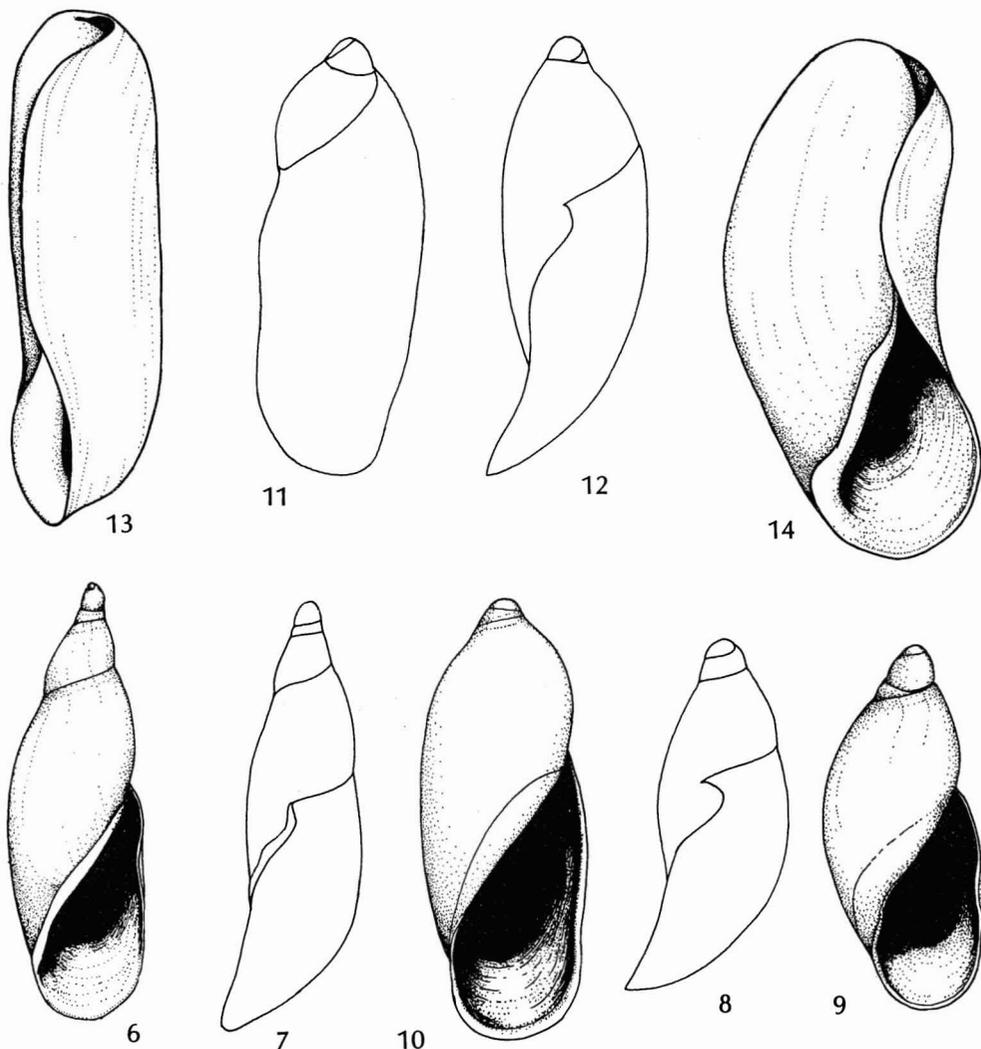
Figures 1, 6, 7, 15-17, 20-26.

Shell fragile, semitransparent, glossy, uniform reddish-brown, with rather elongate spire. Spire slightly bent to apertural side. Protoconch usually same color as teleoconch, of two whorls, the last narrow, the first large, slightly swollen, and making up most of the visible protoconch. Teleoconch with three slightly convex whorls, the last very long, about four-fifths of length of shell. Aperture

large, slightly over half total length of shell. Outer lip with a deep sinus posteriorly; anterior end broadly rounded, slightly expanded, and dished forward; middle part slightly curved forward. Inner lip a thin glaze, clearly marked off in mature shells. Columella short, with a very weak fold at anterior end; this hardly visible in face view. There is no sculpture.

DIMENSIONS OF HOLOTYPE: Height 2.56 mm; diameter 0.80 mm.

TYPE LOCALITY: On 11 *Echinothrix calamaris*, on rocky coral flat off east end of



FIGURES 6–14. Holotypes: 6, 7, *Pulicicochlea (Pulicicochlea) calamaris* sp. nov. 8, 9, *Pulicicochlea (Pulicicochlea) fusca* sp. nov. 10–12, *Pulicicochlea (Pulicicochlea) astropyga* sp. nov. 13, 14, *Pulicicochlea (Pseudoretusa) faba* sp. nov.

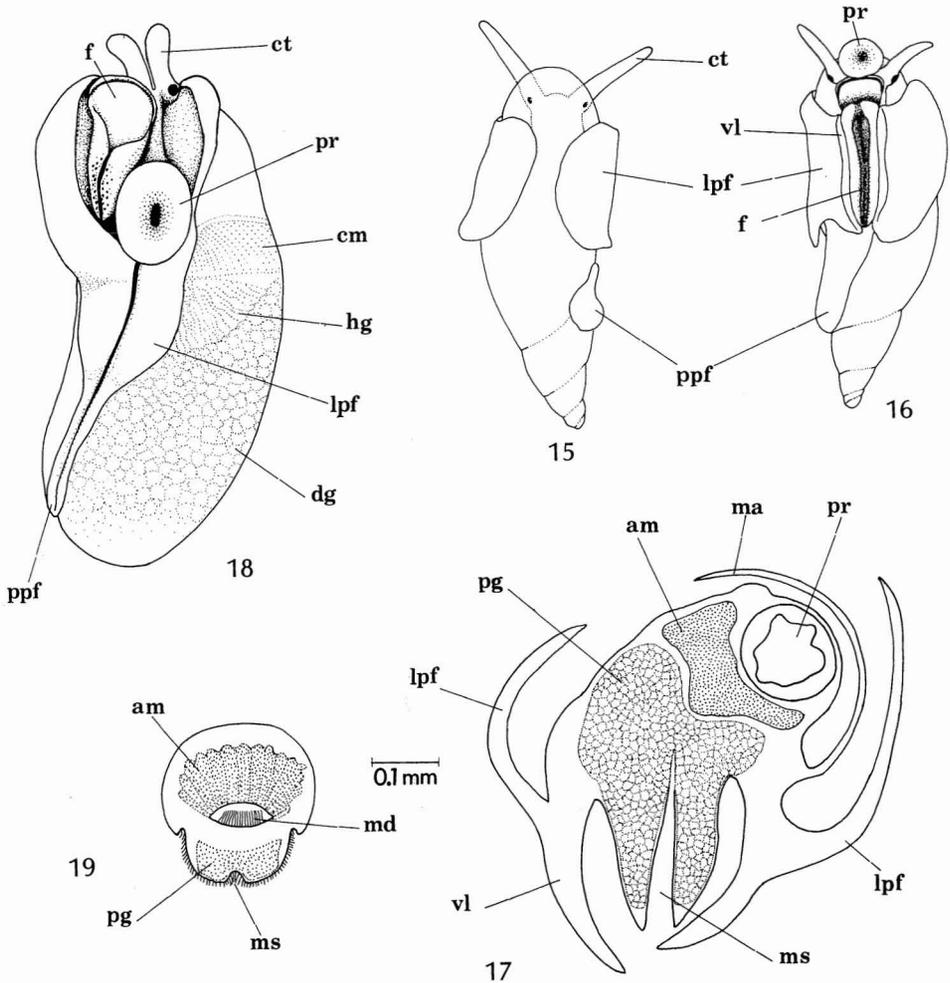
Waikiki Beach, south coast of Oahu Island, Hawaii, 21°15.7' N, 157°50.5' W, in 46 meters, 28 May 1971, collected by Gooding and D. Devaney. Holotype (C.102042) and 21 paratypes (C.102043, Australian Museum, Sydney).

On 10 *E. calamaris* at same location, but 21°15.9' N, 157°50.5' W, in 11 meters, 27 May

1971, collected by Gooding and W. Milisen, 20/10w paratypes⁴ (C.102288, Australian Museum, Sydney).

On 31 *E. calamaris* off west end of Waikiki Beach, 21°15.8' N, 157°51.5' W, among rocks and coral on tongue of outer edge of reef, in 9 meters, 25 June 1971, collected by Gooding and W. Milisen, 26/30w paratypes (C.102287, Australian Museum, Sydney). Two paratypes each held by Bernice P. Bishop Museum, Honolulu; U.S. National Museum, Washington; National Science Museum, Tokyo;

⁴Where both wet and dry paratypes are held, the number of dry paratypes is given first, followed by the number of wet paratypes with the letter w.



FIGURES 15-19. 15-17, *Pulicicochlea (Pu.) calamaris*: 15, 16, dorsal and ventral views of animal. 15, dorsal view of living animal with proboscis retracted. 16, ventral view of preserved specimen with extended proboscis. 17, transverse section through anterior end of animal. 18-19, *Pulicicochlea (Pseudoretusa) faba*: 18, ventral view of preserved specimen with shell removed to show external structures. 19, transverse section of anterior end of foot.

ABBREVIATIONS: *am*, anterior pedal gland; *cm*, columellar muscle; *ct*, cephalic tentacle; *dg*, digestive gland; *f*, foot; *hg*, hypobranchial gland; *lpf*, lateral pedal flap; *ma*, roof of mantle cavity; *md*, pedal gland duct; *ms*, mucous slit; *pg*, pedal gland; *ppf*, posterior pedal flap; *pr*, proboscis; *vl*, ventral lobe.

Western Australian Museum, Perth; National Museum of Victoria, Melbourne; and National Museum of New Zealand, Wellington.

ADDITIONAL MATERIAL: The number of *E. calamaris* sampled, followed by the number of specimens of *Pu. calamaris* collected, is given in parentheses after each locality listed below. All material was collected by Gooding.

Papua: east side of Basilisk Passage, off Port Moresby, 1 meter, 3 August 1969 (16/

"many"). Samarai, under main wharf, 0-3 meters, 12 August 1969 (10/"many"). *New Ireland*: Kavieng, on small reef at shore, 1 meter, 11 September 1969 (5/4). *New Britain*: south end, east side of Atliklikun Bay, Gazelle Peninsula, on outer edge of coral reef, 1/2 meter, 2 October 1969 (5/7). Waterhouse Cove, off Burukuk, east side of northeast tip of Duke of York Island, near edge of fringing reef, 1-2 meters, 15 October 1969 (2/20). Off Burukuk, west of northeast tip of Duke of

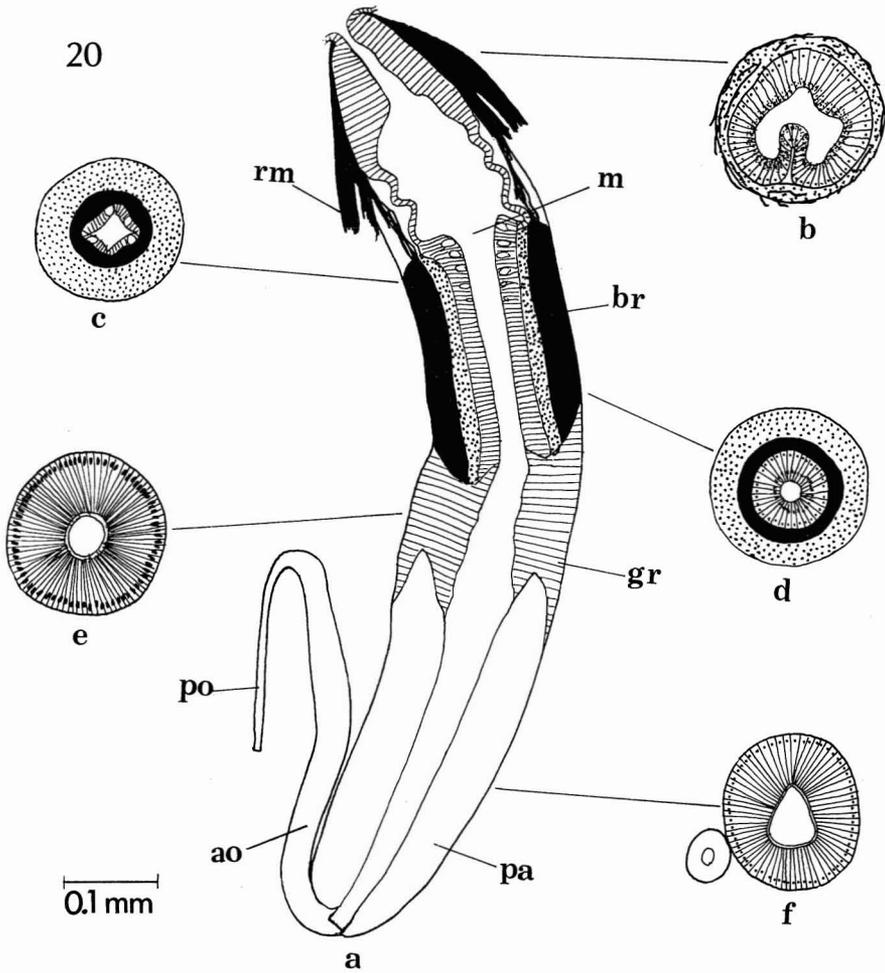


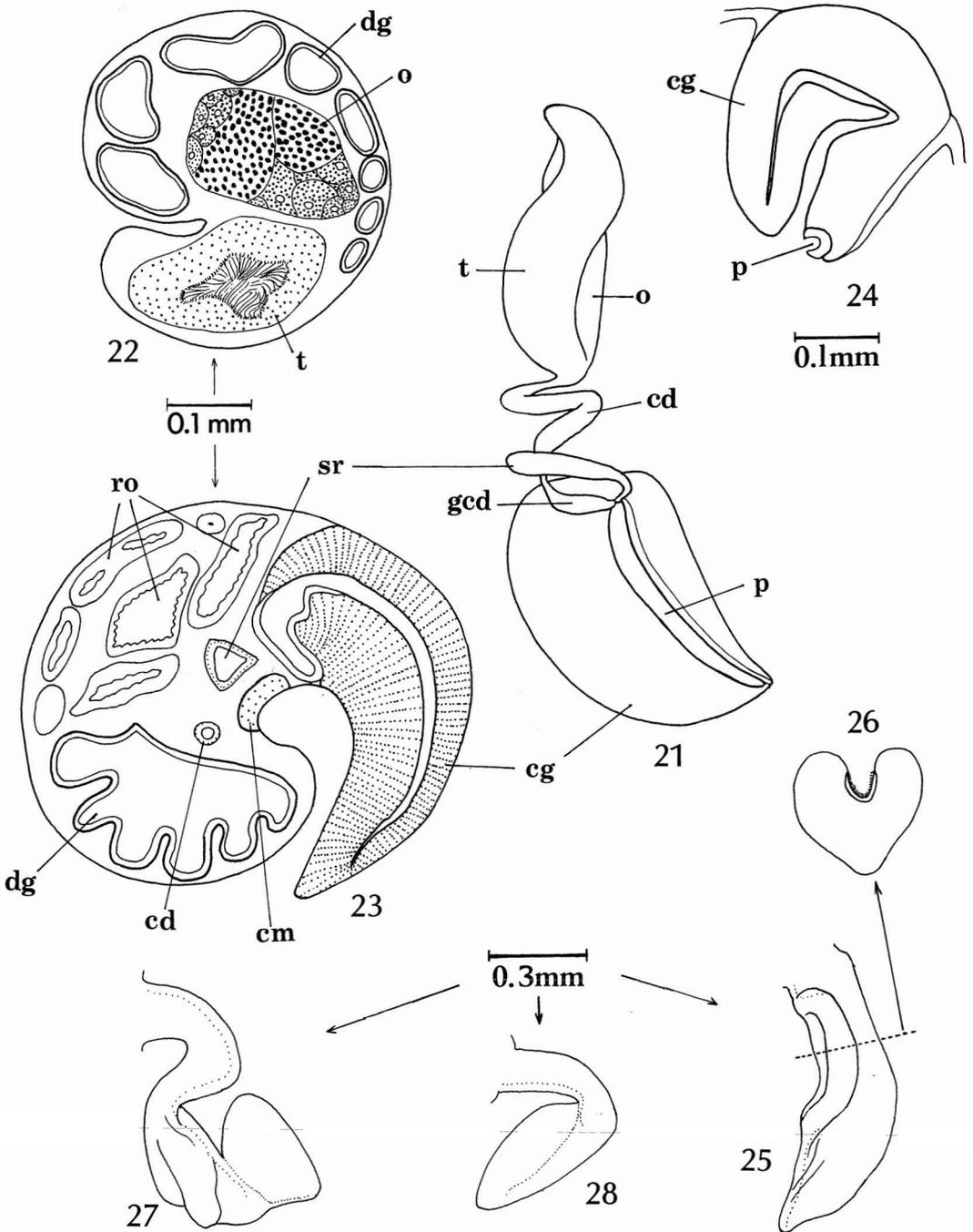
FIGURE 20. Anterior alimentary canal of *Pulicicochlea (Pu.) calamaris*. A diagrammatic longitudinal section of the anterior alimentary canal with transverse sections (b-f) of the main regions. Longitudinal muscle is represented in black and circular muscle as stipple in part a, but this is reversed in parts b-d. For further explanation see text.

ABBREVIATIONS: ao, anterior esophagus; br, buccal region; gr, glandular region; m, mouth; pa, posterior area; po, posterior esophagus; rm, retractor muscles.

York Island, 2 meters, 10 October 1969 (2/34). *New Caledonia*: 500 meters east of Ile Noutié and 300 meters north of small cape, near Touaourou, southeast corner of New Caledonia, near inner edge of reef rampart, 27 January 1970 (3/12). *Western Samoa*: fringing reef on west side of Falefa Harbor, north coast of Upolu Island, 1-2 meters, 29 June 1970 (4/24); 2 July and 8 July 1970 (in Bouin's fluid). Southwest of Matāutu, southeast coast of Upolu Island, in reef lagoon, 1-2 meters, 3 and 8 July 1970 (5/16). *Hawaiian Islands*: off Kahe Point near southwest corner

of Oahu Island, on submerged reef, 3-5 meters, 26 May 1971, collected with W. Milisen (5/13). Off Kalaipalaoa Point, northeast coast of Oahu Island, on fringing reef, 1-2 meters, 9 June 1971 (6/1). South of Palea Point, near southeast corner of Oahu Island, on rocky coral flat, 27 meters, 14 June 1971, collected with W. Milisen (8/12). Off Kaneohe Bay, southeast Oahu Island, on rocks and coral, 9 meters, 17 June 1971 (4/7).

REMARKS: *Pu. (Pu.) calamaris* has a higher, narrower spire than the other two species in the typical subgenus. It has been found only



FIGURES 21-28. 21-26, *Pulicicochlea (Pu.) calamaris* reproductive system: 21, diagram of the reproductive tract, excluding the penis. 22, transverse section of the upper visceral mass showing the gonads and digestive gland. 23, transverse section of the lower visceral mass showing some reproductive structures, the stomach, and the renal organ. 24, transverse section of the pallial oviduct. 25, penis. 26, transverse section of penis. 27, *Pulicicochlea (Pseudoretusa) faba* penis. 28, *Pulicicochlea (Pu.) fusca* penis.

ABBREVIATIONS: *cd*, common duct; *cg*, capsule gland; *cm*, columellar muscle; *dg*, digestive gland; *gcd*, glandular section of common duct; *o*, ovary; *p*, prostatic sperm groove; *ro*, renal organ; *sr*, seminal receptacle; *t*, testis.

on *E. calamaris*. A large number (39) of collections of the host were made that apparently did not harbor any *Pulicicochlea*. These collections were obtained from Thousand Islands, Indonesia; Waterwitch Reef, northeast Queensland, Australia; Madang, New Guinea; Buka Passage between Buka and Bougainville Islands, New Guinea; Manus Island, Admiralty Islands; Rabaul area, New Britain; Duke of York Islands, New Britain; Solomon Islands (Nissan Islands; Green Islands; New Georgia Island; Santa Ana Island; Reef Islands; Santa Cruz Islands; Guadalcanal Island); Port Vila, Efaté Island, New Hebrides; Nouméa, New Caledonia; Fiji (Suva Harbor, Viti Levu; Lau Group; Ha'apei Group); Tonga (Vavau Island; Tongatapu Island); Western Samoa (Apia Harbor; Falefa Harbor, Upolu Island; Pago-Pago Harbor, Eastern Samoa; Society Islands (Tahiti, Moorea Island); Gambier Islands; Mataiva Atoll, Tuamotu Islands; Pitcairn Island; Rapa Island, Austral Islands; Line Islands (Christmas Atoll; Fanning Atoll); Kaneohe Bay, Oahu Island, Hawaiian Islands; Marquesas Islands (Ua-Huka Island; Nuku-Hiva Island).

Pulicicochlea (Pulicicochlea) fusca sp. nov.

Figures 2, 3, 8, 9, 28

Shell small, fragile, semitransparent, glossy, dark brown, with short spire. Spire externally straight. Protoconch grayish or colorless, of two whorls; last whorl largely enveloped by latter part of penultimate whorl of teleoconch; first whorl large, swollen, making up most of visible protoconch. Teleoconch of one and three-quarter convex whorls, the last very large, making up about seven-eighths of the total length of the shell. Initial portion of first spire whorl and last whorl of protoconch largely enveloped by asymmetrical growth of latter part of penultimate whorl. Aperture large, expanded, about five-eighths of the length of shell. Outer lip with a deep sinus posteriorly; anterior end broadly rounded, not expanded but dished forward; middle part slightly curved forward. Edge of outer lip darker brown than rest of shell. Inner lip a thin glaze, distinct in mature

shells. Columella thin, simple. There is no sculpture.

DIMENSIONS OF HOLOTYPE: Height 1.00 mm; diameter 0.43 mm. Dimensions of Magnetic Island, Queensland, specimen: height 1.10 mm; diameter 0.60 mm.

TYPE LOCALITY: On five *Diadema setosum*, on wreckage and sea floor, off Yacht Club, Rabaul Harbor, New Britain, 12°12.5' S, 152°11.1' E, 1–2 meters, 18 October 1969, collected by Gooding. Holotype (C.102047) and four paratypes (C.102046, Australian Museum, Sydney). One paratype each held by Bernice P. Bishop Museum, Honolulu; U.S. National Museum, Washington; National Science Museum, Tokyo; Western Australian Museum, Perth; National Museum of Victoria, Melbourne; and National Museum of New Zealand, Wellington. On ten *D. setosum*, Madang Harbor, Madang, New Guinea, 5°10.6' S, 145°50' E, between Burns Philp's and Custom's wharves, about 1 meter, 25 August 1969, collected by Gooding, 13 paratypes (C.102291, Australian Museum, Sydney).

ADDITIONAL MATERIAL: The number of *D. setosum* sampled, followed by the number of specimens of *Pu. fusca* collected, is given in parentheses after each locality. All material was collected by Gooding.

Indonesia: Pulau Tjipir, Djakarta Bay, Java, on reef flat near reef edge, about 1 meter, 12 March 1969 (5/25). South side of Pulau Rambut, north of Djakarta, off beach, 1/2 meter, 23 March 1969 (5/several). Near Pulau Tikus, Pulau Pari Group, Thousand Islands (northwest of Djakarta), on reef flat, 1/2 meter, 6 March 1969 (5/"few," not retained). *Australia*: close to edge of reef, landward side of isolated reef opposite Nobby Head, south end of Magnetic Island, off Townsville, Queensland, about 2 meters, 16 July 1969, collected with P. Vine (13/7). Bay on southeast side of Goode Island, northern Queensland, 1–5 meters, 21 July 1969 (16/18). Yonge Reef, northeast Queensland, on coral reef and sand flat, 1–3 meters, 22 July 1969 (10/4). *Papua*: near outer edge of reef near the Department of Agriculture Stock and Fisheries, Fisheries Research Laboratory, Kanudi, near Port Moresby, Papua, 0 m, 30

July 1969 (16/7). Under main wharf at Samarai, 0–3 meters, 12 August 1969 (5/4). *New Britain*: southeast side of small reef between The Beehives (=Dawapia Rocks), Simpson Bay (= Rabaul Harbor), 1/2–2 meters, 30 September 1969 (5/6). Near Davaun, Karavia Bay, Gazelle Peninsula, on wreck, about 1 meter, 1 October 1969 (5/5) (plus *D. savignyi*). On outer edge of reef at south end, east side of Atliklikun Bay, Gazelle Peninsula, about 1/2 meter, 8 October 1969 (5/3). North side of southwest tip of Mioko Island, Duke of York Islands, 1/2–2 meters, 16 October 1969 (3/12) (plus two *D. savignyi*). *Solomon Islands*: west side of Sohano Island, Buka Passage, on rocks and coral at edge of fringing reef, 1–2 meters, 30 October 1969 (7/8). Near pier at Lambeti, Munda region New Georgia Island, near shore, 1 meter, 4 November 1969 (4/14). Just south of wharf at Tulagi Harbor, Tulagi Island, Florida Islands (= Nggela Group), about 1 meter, 2 December 1969 (6/8). *New Caledonia*: reef west of north end of Ilot Maître, Nouméa region, on sand between coral heads, about 2 meters, 12 January 1970 (4/7). North side of rocks off point between Baie de Citrons and Baie de l'Anse Vata, Nouméa, on rocks and sand at edge of reef, 1–2 meters, 6 January 1970 (5/1). Reef off northwest corner of Ilot aux Canards, Nouméa region, 1½–2 meters, 9 January 1970 (4/2). On northeast corner of Ilot Brun, Nouméa, about 2½ meters, 10 January 1970 (4/7). Bay on northwest side of Ile Nou, Nouméa, on sandy silt bottom between coral, about 2 meters, 10 January 1970 (4/2). Five hundred meters east of Ile Noutié and 300 meters north of small cape, near Touaourou, southeast corner of New Caledonia, near inner edge of reef rampart, 1–1½ meters, 27 January 1970 (6/2) (all *D. savignyi*). *Fiji*: near edge of fringing reef southwest of Toberua Inlet, east coast, Viti Levu, about 2 meters, 19 April 1970 (13/19).

REMARKS: This minute species has a shorter spire than *Pu. (Pu.) calamaris* and is dark brown rather than red-brown. There is some variation in size; Australian and New Caledonian specimens tend to be larger than the typical form. It has been found almost ex-

clusively on *D. setosum*, although there are two badly damaged (but collected alive) specimens from *D. savignyi* that are tentatively identified as *Pu. (Pu.) fusca*, and on two occasions it was found in a sample with both species (*D. setosum* and *D. savignyi*) mixed. In these latter cases, it is highly probable that the sample originated from *D. setosum* alone.

Most of the *D. savignyi* sampled from 60 stations did not contain any *Pulicicochlea*. These collections ranged from northwest Australia, through New Guinea, Solomon Islands, New Hebrides, New Caledonia, Norfolk and Lord Howe Islands, Fiji, Tonga, Samoa, Tahiti, Marquesas Islands, Austral Islands, Tuamotu Islands, Gambier Islands, Easter Island, Pitcairn Group, and Line Islands.

About 20 samples of *D. setosum* did not contain *Pulicicochlea*. These included specimens from near Point Quobba, northwest Australia; Houtman Abrolhos, Western Australia; northern Stradbroke Island, off Brisbane, Queensland, Australia; Round Island, off Hammond Island, north Queensland, Australia; Duke of York Island, New Britain; Nissan Island, Green Islands, Solomon Islands; Honiara, Guadalcanal Island, Solomon Islands; Port Vila, Efaté Island, New Hebrides; Nouméa area, New Caledonia; Viti Levu, Fiji; Tonga; Pulau Jong, southwest of Singapore; and Gulf of Suez.

Pulicicochlea (Pulicicochlea) astropyga sp. nov.

Figures 4, 10–12

Shell small, semitransparent, glossy, reddish-brown, with short globose spire. Spire externally straight. Protoconch colorless, transparent, of nearly two whorls; last one and one-half whorls strongly tilted down (anteriorly) and immersed in penultimate whorl; remainder projecting, but not swollen. Teleoconch with two convex whorls; penultimate whorl bulging in the portion above the outer lip of the aperture; remainder immersed in body whorl. Body whorl cylindrical, making up nearly the total length of the shell. Aperture large, not expanded be-

yond spire, about three-fifths of length of shell. Outer lip with a moderately deep sinus posteriorly; anterior end broadly rounded, not expanded but markedly dished forward; middle part also curved forward. Edge of outer lip darker brown than rest of shell. Inner lip a thin glaze. Columella thin, simple. There is no sculpture.

DIMENSIONS OF HOLOTYPE: Height 1.22 mm; diameter 0.47 mm.

TYPE LOCALITY: On four *Astropyga radiata*, on muddy sand slope off beach on west side of Nukulau Islet, southeast coast of Viti Levu, Fiji, 18°10.5' S, 178°31.13' E, 18 meters, 26 April 1970, collected by Gooding and T. Gilbert. Holotype (C.102044) and one collapsed paratype (C.102045, Australian Museum, Sydney).

ADDITIONAL MATERIAL EXAMINED: On two *Astropyga radiata*, on muddy sand slope off Mahaena Village, east coast of Tahiti, in about 30 meters, 25 March 1971, collected by Gooding and J. Bennett (one specimen now lost).

REMARKS: The swollen spire of *Pu. astropyga* readily distinguishes this species from the two described above, and although only one complete specimen is now extant, the opportunity is taken to describe it so that this revision might be as complete as possible. It has been found only on *A. radiata* in the two localities given above. The host echinoid was not sampled at any other localities.

***Pulicicochlea (Pseudoretusa) faba* sp. nov.**

Figures 5, 13, 14, 18, 19, 27, 29, 30

Shell thin but not very fragile, semitransparent, dark red-brown, glossy with no spire, somewhat flattened dorso-ventrally. Whole visible shell consisting of only the body whorl, which is twisted so that the apertural side is strongly concave. Protoconch and spire completely immersed, and small "umbilicus" is present at the posterior end of the shell. Aperture narrow posteriorly, where it forms a deep sinus that extends for about one-quarter of a whorl. Outer lip curved forward in middle section, where it lies close to parietal area, this giving appearance of a narrow slit in upper half of aperture. Lower

half of outer lip expanded sideways; not extended forward. Inner lip prominent in lower half of aperture, where it forms a clearly separated plate over the short columellar area. Lower expanded part of aperture with a nonpigmented patch, which serves as a window for the eyes. There is no sculpture.

DIMENSIONS OF HOLOTYPE: Height 2.76 mm; diameter 1.15 mm.

TYPE LOCALITY: On 28 *Echinothrix diadema*, among rocks and coral on flat rocky reef, just south of Kapapa Island, Kaneohe Bay, southeast side of Oahu Island, Hawaii, 21°28'44" N, 157°48'03" W, in 1 meter, 7 June 1971, collected by Gooding and W. Milisen. Holotype (C.102048) and 6/17w paratypes (C.102049, Australian Museum, Sydney). Same data, on 28 *E. diadema*, 14 June 1971, 10/7w paratypes (C.102290), and on 28 *E. diadema*, 23 June 1971, three paratypes (C.102289, Australian Museum, Sydney). Two paratypes each are held by Bernice P. Bishop Museum, Honolulu; U.S. National Museum, Washington; National Science Museum, Tokyo; Western Australian Museum, Perth; National Museum of Victoria, Melbourne; and National Museum of New Zealand, Wellington.

ADDITIONAL MATERIAL: The number of *E. diadema* sampled, followed by the number of specimens of *Pu. (Ps.) faba* collected, is given in parentheses after each locality. All material was collected by Gooding.

Admiralty Islands: north side of Hawaii Island, off north coast of Manus Island, 1/3 meter, in surf zone, 30 August 1969 (13/4). *New Ireland*: reef just south of Cape Nuan, Kavieng, just outside surf zone, 1/2–2 meters, 18 September 1969 (9/5). *New Britain*: at south end, east side of Atliklikun Bay, Gazelle Peninsula, on outer edge of coral reef, about 1/2 meter, 2 October 1969 (11/1). *Solomon Islands*: on reef off Lavanggu, Lughu (= Kanggava) Bay, Rennell Island, just inside surf zone, 1 meter, 27 November 1969 (5/1). Off northeast end of reef on west side of Port Mary Bay, Santa Ana Island, in surf zone, 1–2 meters, 4 December 1969 (4/1). At edge of fringing reef off Navale Village, west side of Graciosa Bay, Ndeni Island, Santa Cruz Islands, about 1 meter, 6 Decem-

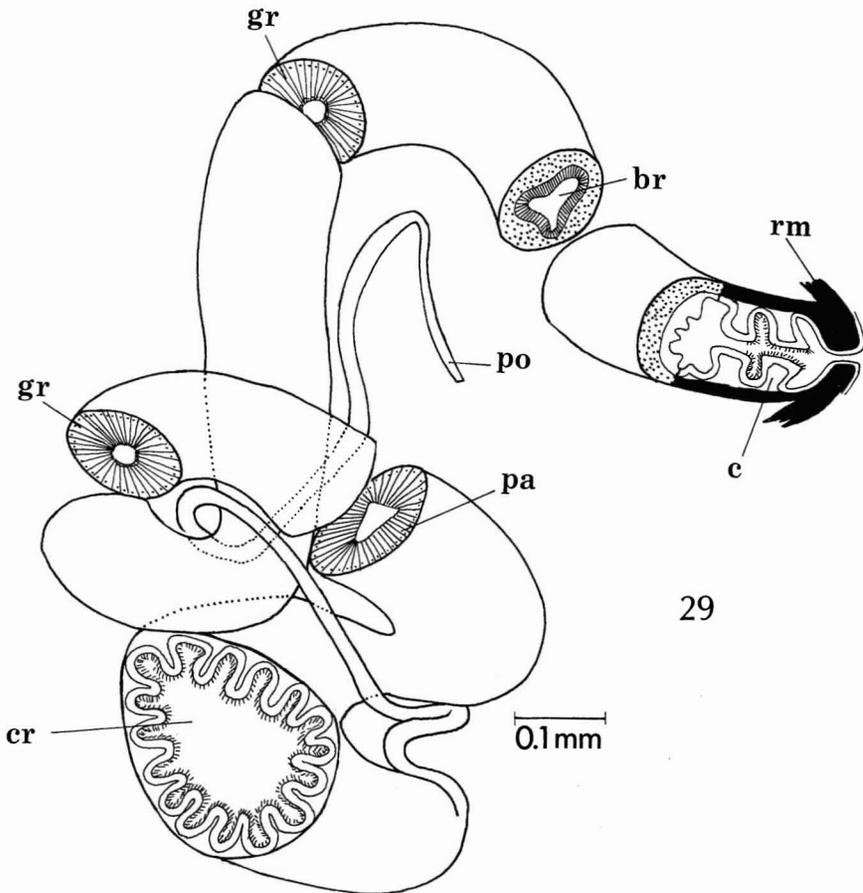


FIGURE 29. Anterior alimentary canal of *Pulicicochlea (Pseudoretusa) faba*. A diagrammatic reconstruction with transverse sections to show the main regions. ABBREVIATIONS: *br*, buccal region; *c*, collar; *cr*, crop; *gr*, glandular region; *pa*, posterior area; *po*, posterior esophagus; *rm*, retractor muscles.

ber 1969 (5/1). On reef in bay just west of hill with Mission, Marovovo, Guadalcanal Island, just in or outside surf zone, 1 meter, 6 December 1969 (5/2). *New Caledonia*: 500 meters east of Ile Noutié and 300 meters north of small cape, near Touaourou, southeast corner of New Caledonia, on surface reef rampart just inside surf zone, 27 January 1970, collected by A. Michel and R. Grandperrin (2/1). *New Hebrides*: off Groupe Scolaire Nord Vaté, Takara District, northeast corner of Efaté Island, just inside surf zone on narrow, fringing reef, 1/2 meter, 27 December 1969 (one in Bouin's fluid). *Fiji*: Mbalavu Reef, off Levuka, Ovalau Island, just inside surf zone, 1/2 meter, 4

May 1970 (3/1). Outer reef west of Ongea Levu, Lau Group, just inside surf zone, 1/2 meter, 6 May 1970 (5/1). *Tonga*: between Lifuka and Uoleva Island, Ha'apei Group, in reef channel, 1/2 meter, 21 May 1970 (5/2). *Western Samoa*: fringing reef on west side of Falefa Harbor, north coast of Upolu Island, 1-2 meters, 26 and 29 June 1970 (2/1). Section of West Reef opposite Cape Horn and off Casino Hotel, Apia Harbor, near reef edge, 1-2 meters, 27 June 1970 (6/2). *Tuamotu Archipelago*: narrow fringing reef just east of jetty off Tuuhora Village, north coast of Anaa Atoll, 1/4-1/2 meter, 10 August 1970 (4/3). Narrow fringing outer reef west of Ngnarumaova Village, Raroia

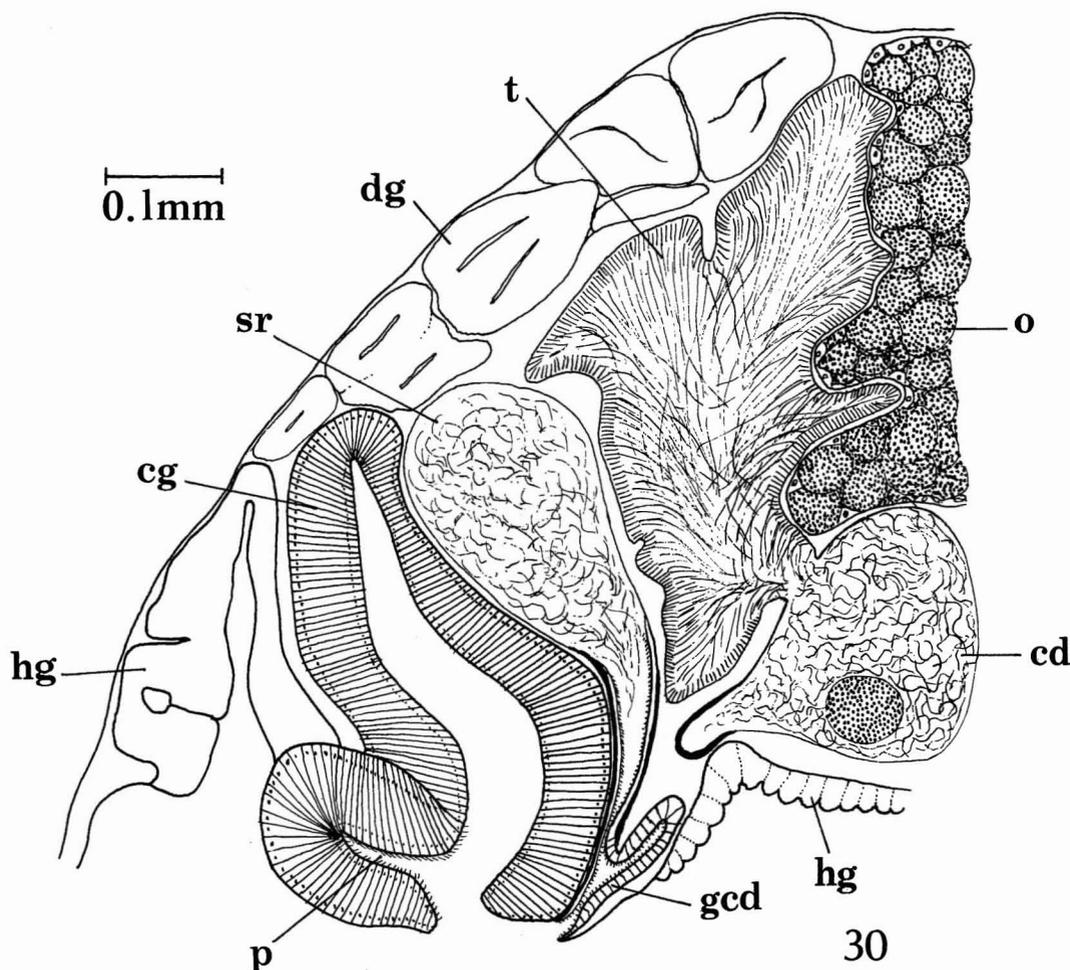


FIGURE 30. *Pulicicochlea (Pseudoretusa) faba*. A semidiagrammatic drawing of a section through some of the structures of the reproductive system. ABBREVIATIONS: *cd*, common duct; *cg*, capsule gland; *dg*, digestive gland; *gcd*, glandular section of common duct; *hg*, hypobranchial gland; *o*, ovary; *p*, prostatic sperm groove; *sr*, seminal receptacle; *t*, testis.

Atoll, 1/4–1/2 meter, 13 August 1970 (10/3). Narrow fringing outer reef just north of stone jetty on west side of Fangatau Atoll, 1/4 meter, 14 August 1970 (6/1). Narrow fringing outer reef just north of stone jetty off Teonemahina Village, northwest side of Pukapuka Atoll, 0–1/3 meter, 16 and 27 August 1970 (17/8). Outer reef flat, in pass area just north of only large islet, north coast of Marutea Nord Atoll, about 1 meter, 11 November 1970 (10/1). Pouheva Village, northeast part of lagoon, near Arikitamiro Pass, Makemo Atoll, on flat of spit reef,

about 1 meter, 12 November 1970 (9/2). Reef flat just east of village, Vahitahi Atoll, 1/2 meter, 19 November 1970 (?/1) (in Bouin's fluid). Small easternmost channel, south side of Mataiva Atoll, under beach rock and coral, 1 meter, 8 February and 23 March 1971 (15/?). Near outer edge of narrow fringing reef just north of main passage into lagoon, northwest coast of Mataiva Atoll, 1/3 meter, 3 February 1971 (14/7). Main passage, northwest side of Mataiva Atoll, 0–1 meter, 19 February 1971 (10/3). *Society Islands*: near southwest edge of Récif de

Vaipou (east side of Passe Tareu), Baie de Papetoai (= Oponu), north coast of Island of Moorea, 0–2 meters, 29 March 1971 (10/1). Outer reef off lighthouse on Pointe Venus, north coast of Tahiti, behind algal ridge, 1 meter, 3 August and 16 October 1970 (15/6); 8 August 1970 (in Bouin's fluid). On narrow outer reef off south end of outer protective wall for harbor, Papeete, Tahiti, just behind algal ridge, 1 meter, 26 January 1971 (20/3). About halfway between beach and outer edge of fringing reef, east side of Baie de Popote, Mahaiatea, Atimaono District, south coast of Tahiti, 1 meter, 5 January 1971, 9 March 1971 (18/7) (one in Bouin's fluid). Just behind surf zone on outer reef off Faaa Airport, Tahiti, 1 meter, 11 and 16 March 1971 (12/6). Close to east side of Passe de Teavaraa, off Mataiea District, south coast of Tahiti Island, just behind algal ridge of outer reef, 1 meter, 27 October 1970 (9/5) (specimens disintegrated). Just east of small indentation in Récif Vaihirere, southwest of Pointe Pufarataiai (near southeast corner of Presquile de Tairapu), Tahiti, just behind surf zone, 1 meter, 4 March 1971 (12/5) (specimens disintegrated). *Marquesas Islands*: west of small-boat landing, north side of Baie de Vaitahu, Tahuata Island, in crevices on rocky cliff with coral, just under surge zone, 1/2–1 meter, 19 August 1970 (7/2). *Gambier Islands*: reef flat on north side of small channel to Tauna Motu (middle of southeast section of barrier reef), about 1 meter, 2 December 1970 (7/1). Channel between two small islets (motus), northeast section of barrier reef between Puaumu and Vaiatekeue Motus, about 1 meter, 18 December 1970 (10/9). *Line Islands*: near east edge of sandy patch reef northeast of point north of English Harbor, in lagoon at Fanning Atoll, 1/2–1 meter, 2 May 1971 (10/2). Near outer side of easternmost channel in North Pass complex, Fanning Atoll, 1/2–1 meter, 3 May 1971 (3/1). *Hawaiian Islands*: on fringing reef off Kalaipalooa Point, northeast coast of Oahu Island, 1–2 meters, 9 June 1971 (6/1). On fringing reef off sewer line at Hauula, northeast coast of Oahu Island, just inside surf zone, 1–2 meters, 15 June 1971

(22/11). Off west end of Waikiki Beach, just outside surf, 3 meters, 21 June 1971 (5/3). Off Kaneohe Bay, in crevices, 9 meters, 17 June 1971 (7/4). On patch reef flat, Kaneohe Bay, 1/2–1 meter, 17 June 1971 (15/12).

REMARKS: The species is immediately recognized by its beanlike shape and completely inverted spire. It was found only on *E. diadema*. Gooding did not find it present in 32 samples taken from *E. diadema*. These were obtained from Waterwitch Reef, northeast Queensland, Australia; off Port Moresby, Papua; near Kavieng, New Ireland; Rabaul district, New Britain; Duke of York Island, New Britain; Solomon Islands (Nissan Island, Green Islands; Buka Island; New Georgia Island, Santa Cruz Islands); Port Vila, Efate Island, New Hebrides; Suva Harbor, Viti Levu, Fiji; Vavau Group, Tonga; Upolu Island, Western Samoa; Tutuila Island, Eastern Samoa; Tuamotu Islands (Anaa Atoll; Fangatau Atoll; Niau Atoll; Hao Atoll; Mataiva Atoll; Tatakoto Atoll; Fakahina Atoll); Marquesas Islands (Ua-Pu Island; Ua-Huka Island); Austral Islands (Rurutu Island; Tubuai Island; Raivavae Island); Ile Makarua, Gambier Islands; Christmas Atoll, Line Islands; Oahu Island, Hawaiian Islands.

The host apparently normally harbors only one parasitic gastropod, although in two instances counts have been recorded that suggest two parasites are occasionally present.

GENERAL ANATOMICAL ACCOUNT

The anatomy of only *Pulicicochlea calamaris* and *Pu. (Pseudoretusa) faba* was investigated. The specimens were fixed in Bouin's fluid and the localities from which these were obtained are indicated in the "Additional Material" sections for these species.

Head-Foot

The head-foot (Figures 15–19) consists of a small foot, a head bearing prominent cephalic tentacles (ct) with large eyes at their

outer bases, three pedal flaps [two lateral (lpf) and one posterior (ppf)]. The foot (f) is smaller in *Pu. faba* than in *Pu. calamaris* or *Pu. fusca*. It has, in all three species, a fairly easily distinguished propodial and metapodial portion. The latter has a massive, ventral, longitudinal slit (ms), the opening to the pedal mucous gland (pg) proper. A relatively small slit on the anterior edge of the foot opens into the anterior pedal mucous gland (am). Both these large glands penetrate the anterior body cavities; the anterior gland is found in the snout region and the anterior cephalic cavity below the gut (Figure 17). Most of the posterior gland lies ventral to the anterior gland. Both the ducts (md) of these glands bear long cilia that presumably waft the mucus to the pedal surface where it is used for maintaining the position of the parasite. The lobes bordering the metapodial slit are all that remain of the sole, but in *Pu. calamaris* and *Pu. fusca* ventral lobes (vl) are present that are a modification of the edges of the foot. They are non-pigmented ventrally, often weakly pigmented laterally, and densely ciliated. The lateral parts of the foot bear wide, retractable lateral pedal flaps (lpf), which are presumably homologous to the lateral parts of the opercular lobe of *Balcis* [as shown by Fretter (1955, Figure 1)], while another flap (ppf) extending posteriorly is equivalent to the posterior part of the opercular lobe. No trace of the operculum remains in the species of *Pulicicochlea*.

The pedal flaps cover much of the shell in *Pu. calamaris* when alive (Figure 15), but are relatively small in *Pu. faba* (Figure 18), where they are barely visible dorsally.

The pedal flaps extend dorsally and ventrally from their origins in the sides of the foot (Figure 17). Observations on living animals show that the ventral portion of the lobes tends to fold around the host's spine, presumably aiding the animal in maintaining its position.

Lining the posterior parts of the outer surfaces of each lateral pedal lobe or flap and the right (outer) side of the posterior pedal lobe of *Pu. faba* is an epithelium of tall

glandular cells; ciliated and simple goblet cells are found on the inner sides. These lobes sometimes have patches of black pigmentation developed on their outer surfaces.

The pedal lobes of *Pu. calamaris* and *Pu. fusca* are variably pigmented, some being completely black, others hardly pigmented at all. The nonciliated epithelium is taller on the outer surface and much more densely pigmented.

The posterior lobe of *Pu. calamaris* is a simple flap, but that of *Pu. faba* lies along the long, posterior part of the aperture, its thick, wedge-shaped, glandular edge neatly blocking this in the contracted state (Figure 18).

The cephalic tentacles (ct) of *Pu. faba* (Figure 18) are short and stubby (in preserved material) compared with those of *Pu. calamaris* (Figures 15, 16) and *Pu. fusca*, which are long and relatively large for the size of the animal. The eyes in the three species are very well developed with a spherical lens and a prominent pigmented retina. Pigmentation of the head and tentacles is variable, but usually it is dense (except for a clear space around the eyes) in *Pu. calamaris* and *Pu. fusca* and, in *Pu. faba*, is restricted to a little around the head—mostly posterior to the eyes.

Pallial Cavity

There is a spacious pallial cavity present in the three species and in each there is a monopectinate ctenidium (ctm), an osphradium, and a hypobranchial gland (hg). The pallial cavity of *Pu. faba* is somewhat restricted by its very narrow opening, and about half of the apertural slit does not open to the cavity, housing only a lobe of the mantle and the posterior pedal flap. The ctenidium in the two species sectioned is not strongly developed, ciliation is weak but there are ample blood spaces. A ciliated tract on the left side of the cavity presumably maintains the respiratory current.

The short osphradium has stubby filaments in *Pu. faba* but is simple in *Pu. calamaris*. It is supplied with a prominent ganglion and

is relatively conspicuous. A well-developed hypobranchial gland, simple in *Pu. calamaris* and folded in the larger *Pu. faba* (Figure 30), lies on the posterior roof of the cavity in front of the pallial gonoducts.

Because of the relatively long apertures in these species, the right side of the cavity has been much shortened and the pallial gonoducts run almost at right angles to the main axis of the body.

Alimentary Canal

The most conspicuous parts of the alimentary canal (Figures 20, 29) are the acrembolic proboscis and the anterior esophagus, which together make up the foregut. The foregut is relatively much longer in *Pu. faba* (Figure 29) than in *Pu. calamaris* (Figure 20), while that of *Pu. fusca* is similar to that of *Pu. calamaris* as far as can be judged by dissection.

The proboscis was not sectioned in the fully extended state in either species, nor has it been observed in this state in preserved material. Observations on living animals show that *Pu. calamaris* has a rather short proboscis, whereas *Pu. faba* is capable of extending its proboscis to a length slightly longer than the rest of the body, although this is exceptional.

The proboscis of *Pu. calamaris*, when everted, extends snoutlike in front of the foot (Figure 16). When retracted there remains only a tiny slit between the tentacles. The much more massive proboscis of *Pu. faba* is extruded ventrally, displacing the foot to the right (Figure 18). When retracted there remains a snoutlike ridge that extends below the tentacles to the left of the foot.

The proboscis consists of several easily identifiable parts that will be dealt with separately. The first part of the retracted acrembolic proboscis is its sheath. This consists of a short area with retractor muscles (rm) with their origin in the columellar muscle. This portion of the sheath is lined with a columnar epithelium in both species. In *Pu. calamaris* (Figure 20b) the cells have black granules distally, and have dense, purple-staining cytoplasm and are ciliated

in the posterior portion only. The epithelium of the sheath is everted and faces the exterior when the proboscis is extruded; the folded nature of the epithelial lining obviously allows considerable extension. In *Pu. faba* there is a small, bilobed rim (c) located just inside the opening to the sheath; this forms a double ridge around the base of the extruded proboscis. The collar, unlike the rest of the sheath, is ciliated. At the posterior limit of the sheath in both species there is a short, thin-walled zone with simple cuboidal epithelium. This zone, more clearly marked in *Pu. calamaris*, ends abruptly at the mouth (m)—recognized by its columnar epithelial lining which in *Pu. calamaris* has a few goblet cells and is covered with a very thin cuticle (Figure 20c, d). In *Pu. faba* the area has simple pink-staining, weakly ciliated cells thrown into folds. This buccal region (br), is surrounded by a thick coat of longitudinal muscles and, in *Pu. calamaris*, an inner layer of circular muscles, and probably acts as a buccal pump. There is no trace of salivary glands, odontophore, radula, or jaws as is typical of the family. The buccal region opens into the esophagus which makes up the remainder of the proboscidial apparatus. The esophagus appears to be surrounded by a thin layer of elastic tissue throughout, and can be divided into several regions. The first is a glandular region (gr) with tall secreting cells that open, between a lining of cuboidal cells bearing very short cilia, into a narrow lumen. This region, which is short in *Pu. calamaris* (Figure 20e) and long and convolute in *Pu. faba*, is followed by the second region (pa), which has very uniform, tall, eosinophilic cells in *Pu. calamaris* that appear to be regularly arranged as radial muscles (Figure 20f). These cells have near basal nuclei like those of other muscle cells. A very thin lining of pavement cells lines the narrow, triangular lumen of this esophageal bulb. A very similar structure was observed in dissection of *Pu. fusca*. In *Pu. faba* the radial muscles are represented by normal columnar tissue and the pavement epithelial cells are relatively thicker and ciliated. In *Pu. calamaris* the esophagus then abruptly narrows to about a quarter of its diameter

to form a narrow portion (ao) that runs anteriorly alongside the proboscoidal part and then runs posteriorly after becoming even narrower (po) and passing through the nerve ring.

The second part of the esophagus of *Pu. faba* is relatively much shorter than that of *Pu. calamaris* and opens abruptly into a thin-walled sac (cr), the cuboidal, ciliated lining of which is thrown into numerous pockets and folds. This area represents an expansion of the first part of the narrow esophagus in *Pu. calamaris* and probably functions as a storage crop. It has virtually no muscle but is obviously capable of considerable expansion and elongation. The crop suddenly constricts to form a very narrow esophagus (po), which then passes anteriorly as in *Pu. calamaris*. In both species, particularly in *Pu. faba*, the posterior esophagus is exceedingly narrow and even difficult to trace in sections. It terminates at the anterior end of the digestive gland. As is typical of this family, there is no distinct stomach; the esophagus merely opens into the primary lumen of the digestive gland (dg) tubules. These lumina are very wide in *Pu. calamaris* (Figures 22, 23) and extremely narrow in *Pu. faba* (Figure 30).

The digestive cells in *Pu. calamaris* are more or less cuboidal, vacuolate with inconspicuous cilia and dark greenish refringent granules released into the lumen in spherules. Large spiculelike and angular fragments of chitinlike material are seen in the lumina, and these are sometimes surrounded by amoebocytes that appear to be breaking them down. The digestive gland of *Pu. faba* has an altogether different appearance. The cells are filled with large pinkish-staining granules about the size and appearance of the yolk granules of the eggs in the neighboring ovary. The shape of the cells—and usually of the tubules themselves—is almost impossible to determine. The lumina are very narrow and do not contain recognizable food fragments. No dark-colored excretory granules are produced.

The ciliated intestine in both species is very short and opens at the back of the pallial cavity on the right side. *Pullicocochlea*

calamaris voids blackish fecal pellets, whereas those of *Pu. faba* are pale yellow.

Reproductive System

Both species (Figures 21–26, 30) are hermaphrodites and have a separate ovary (o) and testis (t). The ovary of *Pu. faba* is much more extensive than the testis, whereas in *Pu. calamaris* the gonads are about the same size. The eggs are large and yolky in both species. The gonads in *Pu. faba*, particularly the ovary, branch into a number of separate tubules, whereas in *Pu. calamaris* they are more or less simple tubes. In both species they join proximally and form a common duct (cd). This is thin-walled, fairly wide and convolute in both species. Whereas only sperm have been observed in this duct in *Pu. calamaris*, both eggs and sperm have been found in *Pu. faba* (Figure 30), although this may be an artifact produced during fixation.

The common duct narrows, is here lined with cuboidal ciliated cells, and has a thin muscle coat externally (= renal section). After this very short section, the epithelium abruptly thickens and becomes glandular (gcd), the blue-staining gland cells alternating with wedge-shaped ciliated cells. This short section then opens at the posterior end of the pallial cavity at the ventral edge of the pallial glandular genital duct and near the openings of the renal organ and the anus. The sperm passes into a ciliated groove surrounded by prostate tissue (p) which runs along the left ventral side of the oviduct. The prostate is rather well developed in *Pu. faba* (Figure 30) and forms a narrow glandular groove in *Pu. calamaris* (Figure 24). In both species the prostate is confined to the right side of the pallial cavity and is approximately the same length as the oviduct. The barely distinguishable, nonglandular groove continues along the remainder of the pallial cavity, crossing from the base of the right side of the pallial cavity to the penis.

The pallial oviduct is a ventrally open, bilobed gland (cg). In both species it is short, bulky, and crescent-shaped. It is folded on itself in *Pu. calamaris* (presumably to give a

larger secretory surface) (Figure 24) but is simple (U-shaped in section) in *Pu. faba* (Figure 30). The glandular oviduct in *Pu. faba* is swung posteriorly and tapers to a narrow gutter that runs posteriorly for a short distance opposite the posterior part of the aperture. The orientation of this duct in *Pu. calamaris* is nearly at right angles, but the posterior corner of the aperture is slightly anterior to it.

A thin-walled seminal receptacle (sr) opens at the ventral side of the pallial oviduct next to the end of the common duct in both species. This is wide distally in *Pu. faba* (Figure 30) and contains a mass of unorientated sperm, although the proximal portion sometimes contains orientated sperm, some with their heads embedded in the epithelium. The seminal receptacle in *Pu. calamaris* (Figure 21) is a narrow, almost straight tube and contains bundles of sperm orientated lengthwise along the tube. In both cases the tube narrows to a duct lined with irregular cuboidal cells, ciliated in *Pu. faba*, and with a thin external muscle coat.

The penis lies on the right side of the head and is usually bent back into the pallial cavity. The spermatozoa are transmitted to its tip by way of a ciliated gutter (Figure 26) that runs along the posterior edge of the flattened proximal portion (when at rest). The proximal part of the penis of *Pu. faba* is narrower than the expanded bladeliike distal end (Figure 27). The groove opens onto the posterior face of this blade. *Pulicicochlea calamaris* has a rather simple, tapered penis (Figure 25), but that of *Pu. fusca* is intermediate in shape (Figure 28), having a slightly expanded, flattened distal end. The penis of *Pu. calamaris* has a low lobe in its proximal half, which is not present in the other species. The outer surface of the penis in both species is nonciliated and is not particularly muscular; much of its bulk consists of blood spaces crossed by diagonal muscle fibers.

Renal Organ

The renal organ (Figure 23 ro) is similar in both species and lies behind the pallial

cavity. It is somewhat diffuse, giving off a number of short tubules, and is lined with vacuolate cuboidal cells that bud off spherules nearly equal in size to the cells themselves. Some spherules contain dark excretory granules. The renal organ discharges into the posterior end of the pallial cavity near the anus.

Nervous System and Circulatory Systems

These systems were not studied in any detail. The circumesophageal ganglia in both species are large and concentrated and a prominent ganglion lies beneath the osphradium.

The heart lies posterior to the gill and encroaches into the left mantle wall. It consists of a large ventricle and an auricle enclosed in a narrow pericardium, the ventricle relatively larger in *Pu. calamaris*. In *Pu. calamaris* some blood spaces have aggregations of large amebocytes filled with brownish-black granules. There is a minute renopericardial opening.

OBSERVATIONS ON THE LIVING ANIMALS

Position on Host

Pulicicochlea calamaris has been observed in situ on the aboral side of a fresh host and is found on or near the distal ends of the large primary and the fine secondary spines. Specimens pipetted onto a host move to the spines. They probably prefer the distal portions of the spines because these are out of reach of most pedicellariae and tube feet. *Pulicicochlea calamaris* crawls about readily and can hang upside down on the surface film.

Pulicicochlea faba has not been observed in situ but does crawl about independently when washed from the host. It does not seem to be capable of hanging upside down on the surface film. Movement appears to be effected by a combination of foot and proboscis.

Both species attach themselves to the host by producing a strong mucous thread with its origin in the pedal mucous glands. When detached from their position on the host they

can quickly pull themselves into position on this thread.

Feeding Behavior

When living *Pu. calamaris* were presented with the secondary spines of *E. calamaris* they immediately climbed on and moved along them, stopping at intervals to feed. Constant testing of the surface of the spines with the proboscis occurred as the animals crawled. They would then stop, apply the proboscis like a suction cup to the epidermal tissue of the spine and pull backward and forward until a piece of epidermis was detached. Once the detached tissue was swallowed the suction process would be repeated. Two or three "bites" were taken in any one spot, and each time the animal paused for a couple of minutes and then crawled to the next spot.

Living *Pu. faba* was much more difficult to observe. The mobile proboscis is used as a sensory structure as in *Pu. calamaris*. It probably feeds by thrusting its proboscis into the body cavity of the host, either through a gill flap or tube foot, or through the test. One was observed possibly feeding on the anal cone of a specimen of *E. calamaris* after being pipetted onto it. Further evidence for the two species feeding on different tissues of the host is the different colored fecal material and different details in the structure of the gut.

Breeding/Life Cycle

No young specimens of *Pu. faba* have been collected, although these are reasonably common in the other two species. It does not seem likely that *Pu. faba* infects its host at the late stage, but intensive searching, including the remains from crushed tests, have failed to reveal the juveniles. The egg capsules of both species are unknown.

DISCUSSION

The known distributions of the hosts and *Pulicicochlea* species are shown in Figures

1–5. The samples available to us do not allow a definitive statement on the relative distributions of the hosts and their parasites, because in all cases they do not encompass the entire range of the host. In the case of *E. calamaris* in the extreme eastern part, and probably the western part, of its range *Pu. calamaris* appears to be absent. *Echinothrix diadema*, on the other hand, harbors *Pu. (Ps.) faba* in most of the sampled areas. Similarly, samples from *D. setosum* contained *Pu. fusca* over most of its range although the ectoparasite may be absent in southern Queensland, Western Australia, and Tonga. Little can be said about the distribution of *Pu. astropyga* because of the very small number of samples available.

Pulicicochlea seems to be restricted to the tropical Indo-Pacific, there being no trace of it in samples from any of the warm temperate species of the Diadematidae sampled or from tropical species in the Atlantic-Caribbean region.

The degree of adaptation of *Pulicicochlea* species to their ectoparasitic life shows a progression within the genus. All four species have retained their mobility and have developed cryptic coloration. The minute size and the pedal lobes of the typical subgenus are presumably additional modifications to meet the requirements of life on long, slender spines. *Pulicicochlea (Pseudoretusa) faba* has advanced beyond being a probable epidermal feeder like its congeners, and presumably feeds by plunging its much longer proboscis through the integument of the host. This modification has been accompanied by some loss in mobility (a smaller foot) and in the reduction of the pedal flaps, as this species probably spends its life on the test of the host. The tendency toward the inversion of the spire is a feature of the genus, which shows a series through *Pu. calamaris*, *Pu. fusca*, *Pu. astropyga*, and culminates in a completely inverted spire in *Pu. (Ps.) faba*.

The evolution of a number of different species of one genus of eulimid on species of a single family of echinoderm is of interest because most other genera of the Eulimidae seem to be rather indiscriminate in their choice of hosts. Any further discussion on

host-parasite relationships in the Eulimidae must, however, await a more detailed analysis of eulimid taxonomy.

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