AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

Warén, Anders, and M. R. Crossland, 1991. Revision of *Hypermastus* Pilsbry, 1899 and *Turveria* Berry, 1956 (Gastropoda: Prosobranchia: Eulimidae), two genera parasitic on sand dollars. *Records of the Australian Museum* 43(1): 85–112. [22 March 1991].

doi:10.3853/j.0067-1975.43.1991.42

ISSN 0067-1975

Published by the Australian Museum, Sydney

Records of the Australian Museum (1991) Vol. 43: 85–112. ISSN 0067-1975

Revision of *Hypermastus* Pilsbry, 1899 and *Turveria* Berry, 1956 (Gastropoda: Prosobranchia: Eulimidae), Two Genera Parasitic on Sand Dollars

ANDERS WARÉN[1] & MICHAEL R. CROSSLAND[2]

[1]Swedish Museum of Natural History,
Box 50007, S-10405 Stockholm, Sweden

[2]Department of Marine Biology, School of Biological Sciences,
James Cook University, Townsville, Qld 4811, Australia

ABSTRACT. Nine new eulimid gastropods belonging to the genera *Hypermastus* Pilsbry, 1899 and *Turveria* Berry, 1956 are described. Fifteen more eulimids, previously mainly classified in *Eulima* Risso, 1826 and without known hosts are transfered to *Hypermastus* based on shell characters. The species with known hosts are parasitic exclusively on clypeasteroid sea urchins (sand dollars) and parasitise the hosts by penetrating the test with their proboscis and ingesting fluid from the vascular system or the gonads of the host. The snails live on their hosts for periods of a few days and dwell in the sediment most of the time.

WARÉN, A. & M.R. CROSSLAND, 1991. Revision of *Hypermastus* Pilsbry, 1899 and *Turveria* Berry, 1956 (Gastropoda: Prosobranchia: Eulimidae), two genera parasitic on sand dollars. Records of the Australian Museum 43(1): 85–112.

Contents

Gastropods of the family Eulimidae are well known to be parasites of echinoderms and numerous species are known to parasitise and to a varying degree be host specific on all kinds of echinoderms (Warén, 1984). Most species are fairly normal looking prosobranchs, but some have become so adapted to their parasitic life that they can only be recognised as molluscs from the veliger larva.

The species discussed here belong to the former group and retain most of the organs present in Caenogastropoda, except a radula.

Classification of eulimids is difficult since the shell is very featureless and many of the most conspicuous features of the shell (e.g. a mucronate larval shell and inflated, thin-shelled whorls) are the result of adaptations to a parasitic life which have evolved independently many times. The mucronate larval shell, for example, is the result of good protection on the host for newly settled snails. This allows rapid growth up to a certain size, when the protection becomes less efficient. Then the snail instead has to produce a shell that can resist attacks by shell cracking predators. When the protection by the host lasts the whole life of the snail (e.g. when the parasite lives in galls or protected among spines) the globular, thin-walled shell morphology is kept also by adult specimens (Warén, in preparation).

The shape of the aperture (not the size) has, however, proved to be a fairly reliable character for generic classification, but is very difficult to describe.

Examination of several hundred species with known hosts (mostly unpublished) has shown that species with similar apertures live on related host echinoderms. It has also become evident that most members of a group of species with similar host choice and morphology of the aperture show other similarities (e.g. fine structure of the proboscis or micro-sculpture of the shell). As a working hypothesis, Warén (1984) has therefore used host choice and shape of aperture for classification, sincc in most cases preserved material has not been available for detailed anatomical work.

Three of the species discussed in this paper, *Hypermastus placentae*, *H. tenuissimae* and *H. auritae* have been serially sectioned. The anatomy of the proboscis was found to be identical, but this will be discussed in another paper.

Many groups of eulimids are known to parasitise sea urchins and were reviewed by Warén (1984). However, the vast majority of these parasites are associated with species of the Regularia. Only very few species have been reported from the Irregularia.

Habe (1976) described *Curveulima echinocardiaphila* (Japan, parasitic on *Spatangus purpureus* (Pennant)) and *Balcis clypeastericola* (Japan, on *Clypeaster japonicus* Döderlein, 1885). Based on shell morphology, these two species cannot be included in *Hypermastus* or *Turveria*.

There is also one case of a spatangoid sea urchin from the Early Cretaceous (Kiaer, 1981) which had been

parasitised by a supposed eulimid gastropod. The test had been penetrated in a way similar to that described here for *Hypermastus*, and in one case the echinoid had partly repaired the damage, indicating that it was probably not caused by a predator. If this case is correctly assigned to the Eulimidae, it is somewhat surprising since the earliest snails known with certainty to be eulimids are of Late Cretaceous age (e.g. Sohl, 1964).

A few records of eulimids on sand dollars are also found in the echinoderm literature. Guille *et al.* (1986:44) figured *Clypeaster oshimensis* Ikeda, 1935 from New Caledonia, with a eulimid attached on the aboral side. In his large monograph of the sea urchins, Th. Mortensen has some notes on damage of the tests of different species of clypeasteroid sea urchins of the group Laganina, to which suborder the sand dollars belong. He reported (1948:107) that two specimens of *Clypeaster ochrus* H.L. Clark, 1914 were corroded on the aboral side and the spines of this area had regenerated in one of the specimens. Furthermore, (Th. Mortensen, 1948: 262), specimens of *Peronella peroni* L. Agassiz, 1841 were reported to have been drilled by gastropods, but since they were empty tests, it may have been done by a predatory snail. Finally (Th. Mortensen, 1948: 279), specimens of *Peronella japonica* (Mortensen, 1948) collected from 50 m depth, off Misaki Biological Station (Japan) had holes in the test with a tube protruding. The tube is almost certainly a torn-off proboscis of a eulimid.

Material and Methods

The material on which this paper is based has been accumulated over about ten years of searching museum collections, and more importantly, through collaboration with people who have encountered cases of parasitism and recognised the interest of their findings. The final impetus to produce this paper was Crossland and his collaborators' study of *Hypermastus placentae* (in press) and its biology, which enabled interpretation of observations on other species.

When determining species of Eulimidae, the seemingly featureless shells require that every detail be taken into consideration. This includes a careful examination of the surface structure to find any micro-'sculpture'. This 'sculpture' is often very indistinct and can be seen only in certain illumination. Often it is a refractive phenomenon caused by the structure of the most superficial, partly transparent shell layers and not a real sculpture or unevenness of the surface, visible by SEM. This is the case with all spiral sculpture mentioned in the descriptions. The easiest way to find it is to place the shell at an angle at which the incident light is reflected off the shell, and examine the spots where the light is reflected. By small changes in the angle of the shell in relation to the light, critical areas of the shell, for example the subsutural zone, can be examined. The microsculpture is not visible in the figures, except the subsutural riblets, which are shown in Figure 13B and incremental lines, which can be seen on most specimens of Figure 13.

Eulimids have a strongly periodical growth. Usually they grow 0.5 to 1.5 whorls during a very short period of time. The number of whorls added during each such period is to some extent species specific and varies with the size and the sex. This means that a detailed histogram will show several peaks, corresponding to the different number of growth periods the specimens have passed through. For example, an average adult female *Hypermastus placentae* has about 8.7 teleoconch whorls and is 6.3 mm high, not 6.8 mm as said in Table 3. Actually there are almost no specimens 6.8-7.4 mm high, since this size corresponds to a considerable disturbance of the normal growth pattern. Because of this complicated size distribution, there is little use of measuring a few specimens of a eulimid with periodical growth. The height of a single specimen, combined with information about the growth pattern from the incremental scars is more useful. However, if numerous specimens are available it is useful to measure them for sex and size distribution.

The different proportions of the shells, for example shell height/shell breadth, shell height/aperture height, aperture height/aperture breadth, etc., are extremely constant in the species discussed in this paper and the variation is usually less than ±2% in specimens of the same sex. There are, however, some species, where they are quite variable; perhaps the selective pressure on this character is smaller. Despite that only very few specimens have been examined of *Hypermastus colmani* this is quite obvious. Such case are pointed out in the text.

Because of this small variation it is very important that all figures are prepared with the shells in standardised positions. All photos have therefore been taken with the film plane exactly parallel to the columellar axis of the shells, and all proportions of interest can be obtained from the figures.

Because of a pronounced sexual dimorphism, we have tried to base the descriptions on the females, which are larger and usually easier to determine specifically. In some cases this has not been possible since too few specimens were available to allow recognition of the sexes on a statistical basis. This is pointed out in the descriptions.

Specimens designated as paratypes have as far as possible been selected from the same locality, date and host species as the holotype in order to reduce the risk of mixed lots.

Author names are to be quoted as in the headings of the species.

The location of the material studied is listed under each species, and the reference to collections is made with an abbreviation: AMINZ – Auckland Museum and Institute, New Zealand; AMS – Australian Museum, Sydney; ANSP – Academy of Natural Sciences, Philadelphia; BMNH – British Museum (Nat. Hist.), London; LACM – Los Angeles County Museum of

Natural History, Los Angeles, Ca.; MNHN – Museum National d'Histoire Naturelle, Paris; NM – Natal Museum; NMNZ – National Museum of New Zealand; NMV – National Museum of Victoria; NMW – National Museum of Wales; SAM – South Australian Museum; SBMNH – Santa Barbara Museum of Natural History; SMF – Senchenbergisches Museum und Forschungsinstitut; SMNH – Swedish Museum of Natural History, Stockholm; USNM – U.S. National Museum of Natural History, Washington D.C.; ZMA – Zoological Museum Amsterdam; ZMC – Zoological Museum of Copenhagen; ZMHU – Zoologisches Museum der Humboldtuniversität, Berlin.

Tables referred to throughout the text are in Appendix 1.

Biology

Here some observations and conclusions about the biology are summarised. They refer almost exclusively to species of *Hypermastus* since virtually nothing is known about those classified in *Turveria*, except that they are found on species of the sand dollar genus *Encope*.

Host specificity. In this paper, nine new species of *Hypermastus* are described, bringing the number of species with known hosts up to twelve. Three of these are described from undetermined 'sand dollars', two are known from *Peronella leseuri*, three are known exclusively from *Echinodiscus bisperforatus*, and two from both *E. bisperforatus* and *E. auritus*. The apparently high number from *E. bisperforatus* may be surprising considering that there are about 122 known species of the order Clypeasterida (Mortensen, 1948), but the explanation for this may be that *E. bisperforatus* is a very common species, and the material available originates from a few intertidal localities with *Echinodiscus bisperforatus* occurring at least four of these (possibly more since some hosts were not determined). The two species of *Turveria* have both been found on two species of *Encope* which occur sympatrically.

From this sparse material it is difficult to draw any conclusions about the host specificity of the species of *Hypermastus*, but it seems that they follow the same pattern as in other species of Eulimidae with most species occurring on a few related hosts with similar biology. Often the main occurrence is on a single host species with rarer occurrences on the other host species (Warén, 1984).

Infestation rates and life on host. Nothing is known about the infestation rates for most of the species since most of the material is 'second hand'. At one occasion there were specimens of *H. auritae* on every fourth host. Nine specimens of *H. sauliae* were obtained from 45 hosts. Crossland *et al.* (in press) found the rate for *H. placentae* to vary, at the same site, from 25% to close to zero between April 1988 and March 1989. Two possible explanations of this variation were suggested: recruitment and seasonal variation in time spent on the host.

Large specimens of *H. placentae* spend a longer time on the host than do small ones. Ten females (height range 6.12-8.14 mm, mean 7.46 mm) spent an average 8.9 days on the host, during an 18 day period. Eight smaller specimens (height range 3.64-6.96 mm, mean 4.69 mm) spent on an average 2.2 days attached during the same period. It is possible that they were males with empty gonads, after having mated several times.

Feeding biology. No species of *Hypermastus* have a radula and feeding must therefore take place by ingesting coelomic fluid, or by (less likely) dissolving gonadal tissues and ingesting the resulting fluid. Of 19 specimens of *H. placentae* examined, six were found with the proboscis ending in gonadal tissues, 13 with the proboscis ending in the coelomic cavity (Crossland *et al.*, in press). The high frequency of parasitism on the gonads may be due to the body fluids there being richer in nutrients.

Penetration of the host. When species of *Hypermastus* parasitise their hosts, they make a hole in the porous skeleton which constitutes the test. Such penetrations made by *H. boschorum*, *H. placentae* and *H. tenuissimus* have been examined and are described in more detail below. It is rare to find these holes in the process of healing, suggesting that they are repaired by the host in a short time compared with the time that the parasites spend on the host. The time spent on the host is, in the case of females of *Hypermastus placentae*, about nine days (Crossland *et al.*, in press), and the scars must therefore heal in a few days.

The method used for penetrating the skeletal network of the test is not known, but the structure of the skeletal network surrounding the holes (all elements tapering to fine points or rounded, Fig.11) clearly indicates that it has been dissolved. This is probably also the case with the tissues. Where large parasites are found attached to the test, it is denuded of pedicellariae and spines around the hole.

The holes characteristically consist of a large pit, with a fine hole in the bottom. The pit is filled by the pseudopallial collar of the proboscis, which probably aids in the attachment of the parasite to the host, so it is not easily dislodged.

This structure of the sides and the shape of the pit with a much narrower hole for the final penetration of the test, may be of help in recognising the origin of scars in fossil clypeasterids.

Sexual conditions. *Hypermastus placentae* is a gonochorist with males of a smaller average size. Crossland *et al.* (in press) found the males of *H. placentae* to have an average length of 4.17 ± 1.69 mm, while the females were 6.82 ± 0.92 mm. The sex of these specimens had been histologically determined, and no specimens with both testis and ovary were found, which suggests that protandry is not involved. Crossland *et al.* (in

press) occasionally found large males of a shell height corresponding to mature females. This can perhaps be explained by scattered females changing sex to males or more likely that some males continue growing after their reproduction. There is an indication that the same happens in *H. tenuissimae*, where a large, sectioned specimen proved to be a male, but it has not been encountered in other, typically gonochoristic eulimid genera like *Melanella* and *Vitreolina* where hundreds of specimens have been sexed by external sexual characters and/or histology of the gonads (Warén, unpublished).

An attempt to determine the sex from shell morphology based on the paratypes of *Hypermastus placentae* gave very similar results regarding the height of the sexes and the height distribution (see Table 3). It can therefore be assumed that similar attempts on *H. boschorum* and *H. auritae* based on shell morphology only, are reliable.

The bimodality of the size frequencies of several other species fits with this and also with the fact that most species of the Eulimidae have a strong sexual dimorphism, with males smaller than two thirds of the height of the females.

Measurements of 26 *Turveria encopendema* and 23 *T. schwengelae* did not reveal any noticeable bimodality in the height frequency, and therefore it is unlikely that they have a distinct sexual dimorphism. However, this needs confirmation by examination of the soft parts. (The two species may be protandrous or simultaneous hermaphrodites, which is common among eulimids, while equal height of the sexes is unknown in the family.)

Spawning and larval development. *Hypermastus placentae* spawns in August–September, perhaps also later (Crossland *et al.*, in press). No egg capsules have been found on the hosts, so it seems likely that these are deposited in the sand where the sea urchins live. It is usually difficult to interpret the mode of larval development from larval shells of eulimids, because protoconch 1 is not very clearly demarcated in species known to have planktotrophic development. This is true also for species of *Hypermastus*, but it seems very likely that most of the species, have planktotrophic larvae.

Hypermastus Pilsbry, 1899

Type species. *Hypermastus coxi* Pilsbry, 1899 by original designation (Fig.4A-B).

Description. Eulimids parasitic on sand dollars, with a small to large (3-30 mm), colourless, cylindrical or slender and conical shell with slowly increasing diameter of the flat or very slightly convex whorls. Aperture rather small with the line columella-parietal wall almost straight, slightly arched or with a very weak angle at the transition from columella to parietal wall. Profile of outer lip straight or curved with the median part protruding. Proboscis fully retractile and equipped with a small pseudopallial collar.

Remarks. The genus *Hypermastus* was described by Pilsbry (1899) for a new species of Eulimidae known from shells from New South Wales (Australia). Since then specimens with soft parts have been found at several localities in New South Wales (unpublished material in the Australian Museum), but no specimens have been found associated with their host and we have seen no specimens with preserved soft parts good enough to be examined anatomically.

Warén (1980) used this genus for two new species which were described from Borneo (*H. sauliae* and *H. echinodisci*). They had been found on the sand dollar *Echinodiscus bisperforatus* (Leske, 1778) (Echinoidea, Irregularia, Clypeasteroidea, Scutellidae). The assignment of these two species to *Hypermastus* was based on shell characters only, and the present use of this generic name is still not more firmly founded.

Nevertheless, additional species found later have not disturbed this, but rather have formed a more continuous series, from species similar to *H. coxi* with a cylindrical shell and strongly set off larval shell, via those with an evenly conical spire, to those with a slightly irregular shell and almost *Lymnaea*-like (Pulmonata) aperture. All these species have been found on sea urchins of the order Clypeasterida; no species known from other echinoderms closely resemble *Hypermastus*.

The two genera treated in this paper, *Turveria* and *Hypermastus*, are quite similar in shell morphology but as no specimens of *Turveria* have been available for anatomical examination, we have preferred to keep them apart since *Turveria* has a coloured shell. A coloured shell is uncommon in the Eulimidae and is mostly restricted to the most unmodified taxa, such as *Eulima* Risso, 1826, *Niso* Risso, 1826, and *Hemiliostraca* Pilsbry, 1918. It can therefore not be excluded that *Turveria* is an earlier branch from an ancestral stock of coloured species. There is also a difference in the microsculpture. *Turveria* has a dense coating of sharp and uniform incremental lines, while in *Hypermastus* there are occasional, scattered, irregular and indistinct lines only, which by no means cover the surface as in *Turveria* (Fig.13A,B).

We have in this paper also included a number of eulimids known only from the shell, but from shell morphology they can be placed together with those of which we know the host.

Hypermastus acutus (Sowerby, 1834)

Fig.1A,B

Eulima acuta Sowerby, 1834: 8.

Type material. HOLOTYPE (Fig.1A,B) BMNH 1967989.

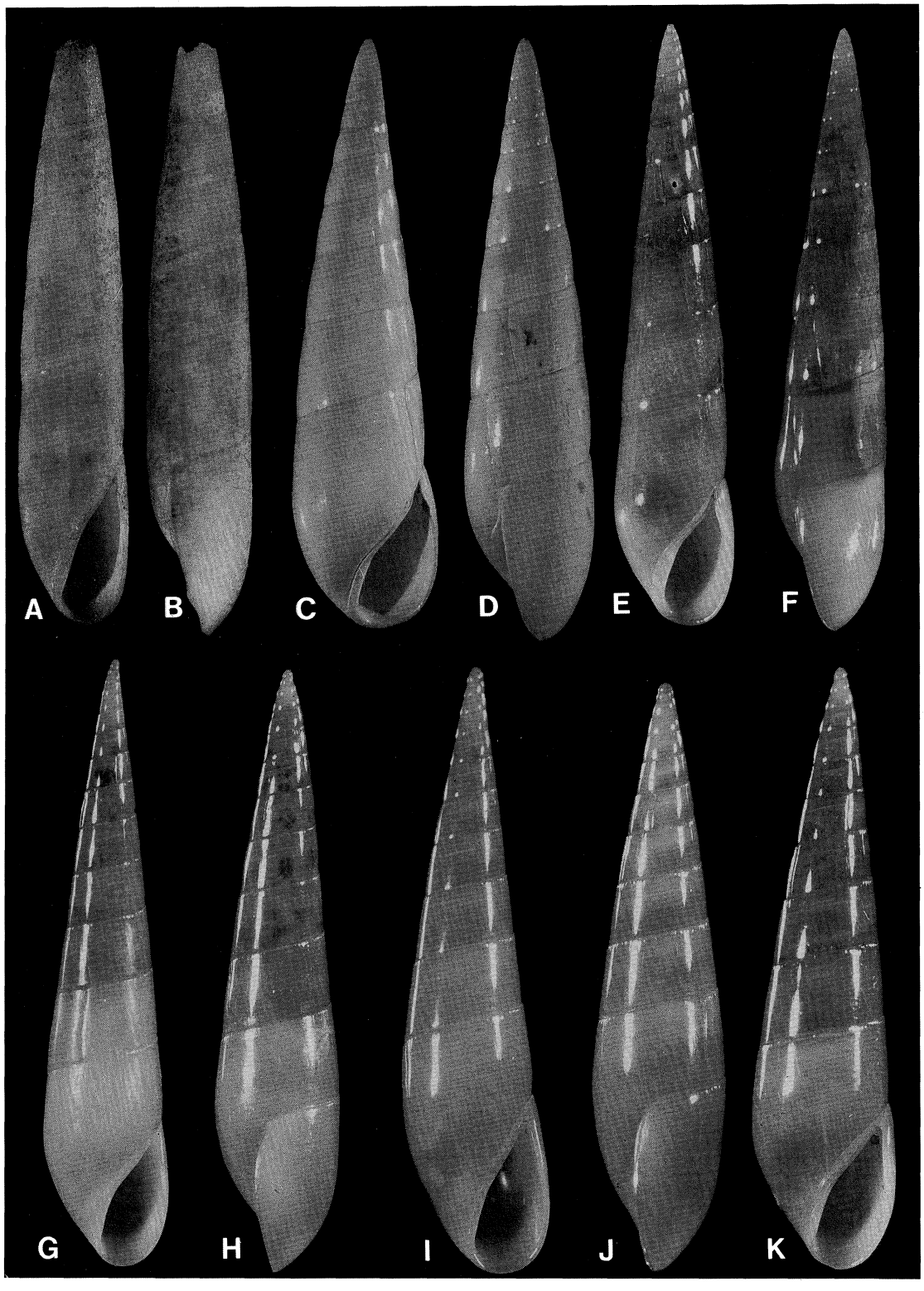

Fig.1. A–B. *Hypermastus acuta* (Sowerby, 1834), holotype, BMNH 1967.989, 7.9 mm. C–F. *H. acuta* (A. Adams, 1851), syntypes. C–D. BMNH 1962.289, 23.7 mm. E–F. BMNH 1962.289, 17.4 mm. G–K. *H. auritae*. G. holotype, female, 12.2 mm. H. paratype, female, SMNH 4114, 11.1 mm. I. paratype, male, SMNH 4114, 7.50 mm. J. paratype, male, SMNH 4114, 7.25 mm. K. female, from *Echinodiscus bisperforatus*, SMNH, 7.96 mm.

Type locality. Bay of Montijo, Pacific side of Panama, 24 m. Host species unknown.

Material examined. The holotype.

Distribution. No reliable additional records exist.

Remarks. The holotype (Fig.1A,B) is in poor condition, corroded and without apex. The aperture is very similar to the most slender species of *Hypermastus*, and we provisionally place it here.

Hypermastus acutus (A. Adams, 1851)

Fig.1C–F

Eulima acuta A. Adams, 1851: 276 (not Sowerby, 1834).

Type material. Two SYNTYPES (Fig.1C-F) BMNH 1968269.

Type locality. Philippines, Luzon, "prov. Cangisanan, Sual", 13 m. Host species unknown.

Material examined. The type material.

Distribution. No reliable additional records exist.

Remarks. This is a large species of *Hypermastus*, one of the syntypes measuring 23.8 mm. It resembles *H. producta* and *H. epepterion*, but differs from them by having a much more rapidly increasing diameter of the apical whorls. In some species, however, this is subject to variation within a species (see *H. auritae*), and richer material will be needed to solve the problem with the relations between the specimens on which these names are based.

Hypermastus acuta A. Adams also resembles the holothurian parasite *Melanella teinostoma* (A. Adams, 1851) in the general shape of the shell, but that species has a sinuated, opisthocline outer lip.

Hypermastus acuta A. Adams is a homonym of *H. acuta* Sowerby, but the species of Eulimidae are poorly known presently and there may very well exist another name for A. Adams' species. We have therefore preferred not to suggest a replacement name until the problems above are solved.

Hypermastus auritae **n.sp.** Warén

Figs 1G–K, 13I

Type material. HOLOTYPE (SMNH 4114, Fig.1G) and 45 PARATYPES; SMNH 4115, AMS C160819, BMNH 1989153, USNM 860502 and coll. D. Bosch, all from type locality.

Type locality. Oman, Masirah Island, just above low tide, 22 Dec. 1988, in fine clean sand, on *Echinodiscus auritus* (Leske, 1778). About every fourth host infested.

Material examined. The types and Quram Beach, near Muscat, water edge at extreme low tide, muddy sand, on *Echinodiscus bisperforatus* (Leske, 1778), leg. D.T. Bosch, 6 Nov. 1987, 1 specimen, SMNH.

Same locality and host, Mar. 1987, leg. D.T. Bosch, 1 female, SMNH.

Description. Shell (Fig.1G-H) tall, slender, conical, fairly solid, semitransparent, with crenulated suture and small aperture. Larval shell (Fig.13I) distinctly set off, sometimes mucronate, consisting of about 1.5 distinctly convex whorls; height 0.24-0.32 mm depending on how much is concealed by the subsequent whorl. Teleoconch of holotype has 12.6, very flat, almost perfectly smooth and polished whorls. Unsculptured except for some very short but rather conspicuous and regularly spaced incremental lines just below suture, giving the uppermost part of the whorls a crenulated appearance (similar to *H. kilburni*, see Fig. 13B). These lines are situated about 0.03-0.05 mm apart on top whorls, 0.15 mm apart on body whorl. Holotype with about 8 incremental scars, 1.3, 2.0, 4.0, 5.3, 6.6, 9.0, 10.0, and 11.5 whorls from outer lip, but their number and position subject to a good deal of individual variation. Height of subsutural zone 20% of height of whorls. Aperture small, with parietal wall and columella forming distinct angle. Outer lip distinctly retracted at suture, evenly curved, and approximately orthocline.

Dimensions. Height of holotype 12.2 mm.

Male (Fig.1I-J). About two thirds the height of the female and has more narrow aperture with less distinct angle between parietal wall and columella.

Remarks. The diameter of the apical whorls is quite variable since in one female they are rapidly increasing their diameter, almost like in *H. coxi*, while in the other specimens they are very slender.

Forty one specimens of the type sample were measured and Table 1 shows the height and sex distribution.

Hypermastus auritae closely resembles *H. kilburni* from Mozambique, but that species has more convex whorls and more conspicuous and distant growth lines below the suture.

The smallest females examined, both from *E. bisperforatus*, are 6.1 and 7.9 mm high and are thus smaller than, or of the same height as the largest males. Nevertheless they can easily be recognised as females from the broader shape of the aperture (compare Fig. 1I and 1K).

Hypermastus boschorum n.sp., Warén

Figs 2A–C, 11E, 13J

Type material. HOLOTYPE (SMNH 4116, Fig.2A) and 20 PARATYPES; SMNH 4117, AMS C160816, BMNH 1989152, USNM 860500, and coll. D. Bosch, all from type locality.

Type locality. Muscat, Quram Beach, extreme low tide, muddy sand, 6 Nov. 1987, leg. D.T. Bosch, all on *Echinodiscus bisperforatus*.

Material examined. The types and Muscat, 0.6 m depth, on *Echinodiscus bisperforatus*, Mar. 1987, leg. D.T. Bosch, 4 specimens, SMNH. Muscat, Quram Beach, extreme low tide, muddy sand, on *Echinodiscus bisperforatus*, Nov. 1988, leg. D.T. Bosch, 3 specimens, SMNH. Muscat, Quram Beach, on a young *Echinodiscus auritus* (46 mm diameter), Nov. 1988, leg. D.T. Bosch, 1 specimen, SMNH.

Description. Shell (Fig.2A,B) straight, slender, glossy, transparent with small, indistinctly off set larval shell and constricted aperture. Larval shell (Fig.13J) 0.35 mm high and consisting of almost 2 slightly convex whorls. Holotype with 9 1/4 almost flat teleoconch whorls sculptured by 50-80 barely visible (at 50x) spiral lines of rows of granules (not visible by SEM) and by close set, indistinct incremental lines. Adult specimens have about 10 irregularly disposed, straight, not very strong incremental scars. Suture shallow, indistinct, well visible only at incremental scars and in reflected light. False suture distinct. Width of subsutural zone corresponding to one third of height of whorls. Aperture small and narrow, its upper part constricted by deflected outer lip.

Dimensions. See Table 2. Height of holotype 5.93mm.

Male (Fig.2C). Three quarters the height of female and more slender. No difference in shape of aperture.

Remarks. *Hypermastus boschorum* resembles *H. sauliae*, but that species is smaller (3.5-5.5 mm high) and has about half a whorl more in the larval shell. The diameter of the protoconch of *H. sauliae* is smaller and its shape is more conical (see Fig.13K). The maximum diameter of the shell corresponds to 23% of the height in *H. sauliae* while *H. boschorum* is slightly broader at 25%.

The specimens were found attached to the host both ventrally and dorsally, and remained attached when the host was shaken in sea water.

Cleaning the test of one parasitised host revealed several perforations (Fig.11E).

The height of 27 specimens was measured and two distinct size classes, presumably males and females, were found (Table 2).

Hypermastus bulbula (Murdoch & Suter, 1906)

Fig.2D–G

Eulima bulbula Murdoch & Suter, 1906: 297.
Balcis pervegrandis Powell, 1940: 233.
Balcis (*Hypermastus*) *bulbula*.–Powell 1979: 141.

Type material. *Eulima bulbula*, HOLOTYPE (Fig.2F,G), NMNZ M 1774; *B. pervegrandis*, in AMINZ, not available. Host species unknown.

Type localities. *Eulima bulbula*, off Great Barrier Island, New Zealand, 200 m; *B. pervegrandis*, off Ahipara, New Zealand, 44 m.

Material examined. The holotype of *E. bulbula* and New Zealand, north of the Cook Strait, 40°33.5'S 174°59.5'E, 86-88 m, 2 specimens, NMNZ M 52710.

Distribution. Only known from New Zealand.

Remarks. On shell characters *Hypermastus bulbula* is most appropriately classified in the genus *Hypermastus*.

We have not been able to examine the type of *B. pervegrandis*, but follow Powell's synonymisation (1979).

There are several possible host urchins in New Zealand. Most likely is perhaps *Peronella hinemoae* Mortensen, 1921.

Hypermastus casta (A. Adams, 1861)

Figs 2H–J, 3A–D

Leiostraca casta A. Adams, 1861: 240.
Leiostraca constantia A. Adams, 1861: 240.
Leiostraca maria A. Adams, 1861: 240.

Type material. *Leiostraca casta*, SYNTYPE (Fig.2H,I) NMV 31376; *L. constantia*, SYNTYPE (Fig.2J) NMV 31352, is the young of *L. casta*; *L. maria*, SYNTYPES (Fig.3A-D) NMV 31373. This is also the young of *L. casta*.

Type locality. *Leiostraca casta*, Shan-tung (Hwan) and Lian-tung (Hulu-shan Bay), 5.5 m; *L. constantia*, Lian-tung (Hulu-shan Bay), 5.5 m, sand and shells; *L. maria*, Gulf of Pe-chili, 5.5 m, mud (all localities in northern China). Host species unknown.

Material examined. The types listed above.

Distribution. No reliable additional records exist.

Remarks. This species has not been recorded since the original description, and we have not seen any further specimens that safely can be assigned to it. We have not figured any larval shell of this species since it

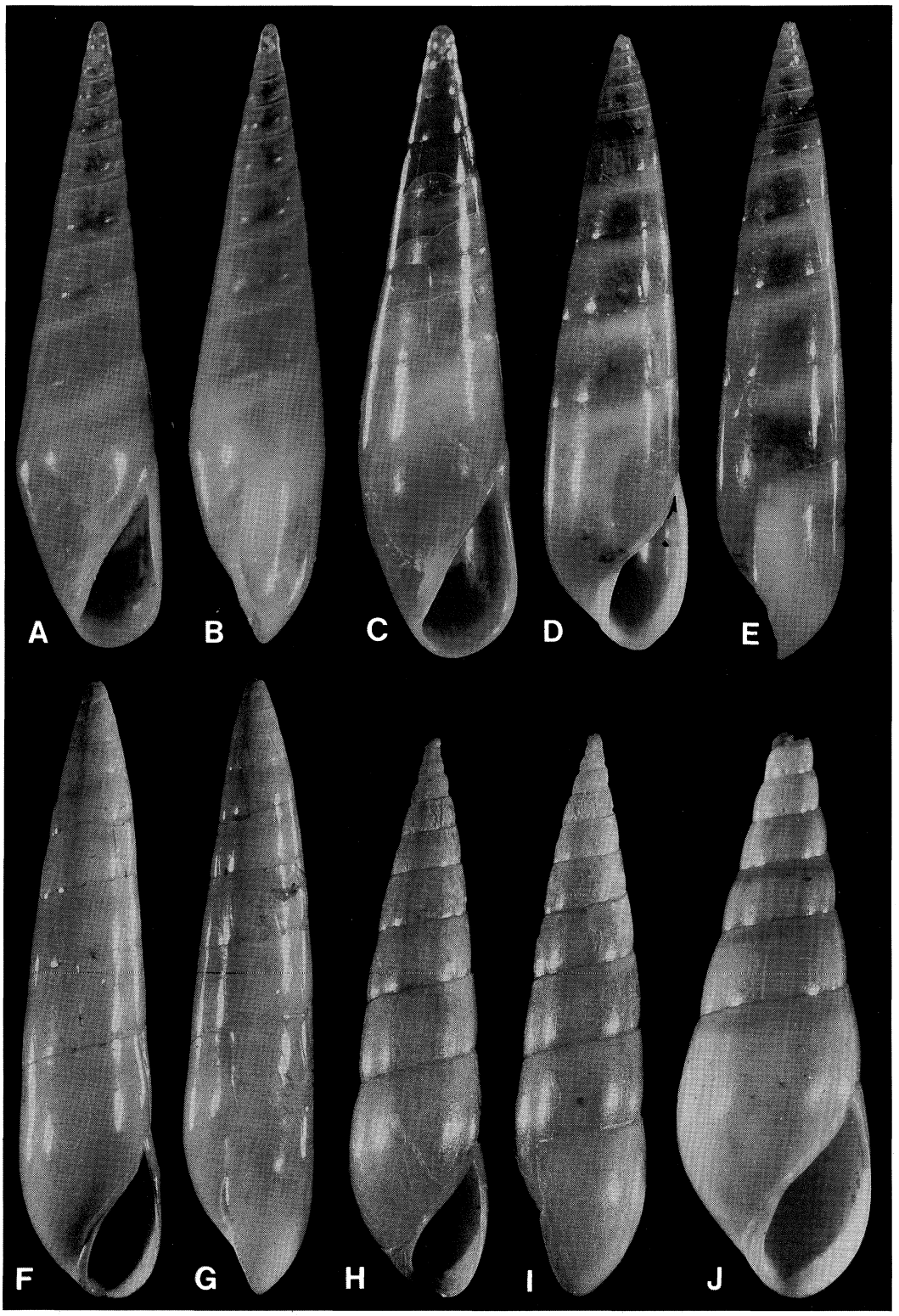

Fig.2. A–C. *Hypermastus boschorum*. A. holotype, 5.93 mm. B. paratype, female, SMNH 4117, 6.26 mm. C. paratype, male, SMNH 4117, 4.29 mm. D–G. *H. bulbula*. D–E. New Zealand, 40°33.5'N 174°59.5'E, 86-88 m, NMNZ M 52710, 11.6 mm. F–G. holotype, NMNZ M 1774, 12.4 mm. H–I. *H. casta*, syntypes, NMV F 31376. 9.88 mm. J. *Eulima constantia*, syntype, NMV F 31352. 5.6 mm.

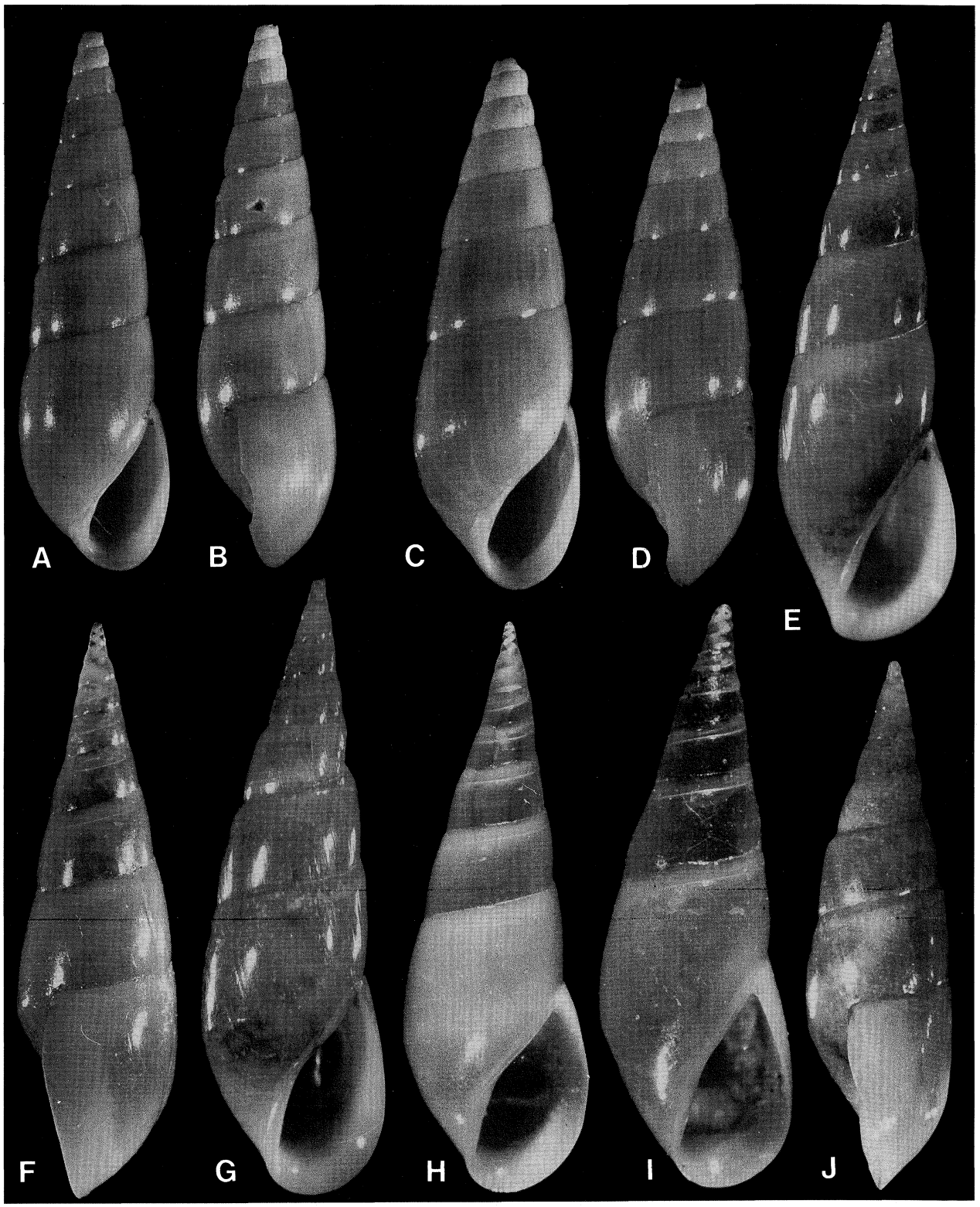

Fig.3. A–D. *Eulima maria*, syntypes, NMV F 31373, A–B 6.81 and C–D 9.96 mm. E–F. *Hypermastus colmani*, holotype, AMS C69735. 8.4 mm. G–J. *H. colmani*. G. J. paratype, female, AMS C160814, 8.0 mm. H. female, SMNH 4118, from AMS C117597, 7.3 mm. I. male, SMNH 4118, from AMS C117597, 3.60 mm.

was broken in all syntypes. It should be possible to recognise *L. casta* from the distinctly convex whorls and rounded aperture.

The presence of this type material in the National Museum of Victoria is somewhat surprising, but Warén has seen no types in other collections. A list of possible types of species described by A. Adams and present in that collection was published by Boyd & Phillips (1985).

Hypermastus colmani n.sp., Warén

Figs 3E–J, 12J

Type material. HOLOTYPE (AMS C69735, Fig.3E,F), 1 PARATYPE, now AMS C160814 (both from AMS C69735) and 2 PARATYPES SMNH 4118 (from AMS C117597).

Type locality. "On large red sand dollar", (presumably *Peronella leseuri* [Valenciennes, 1841]), Urangan, Queensland (AMS C69735).

Material examined. The type material and Dingo Beach, south of Bowen, Northern Queensland, "on oral surface of flat biscuit urchin" (presumably *Peronella leseuri*), leg. P.H. Colman, 30 May 1977, 1 female, broken, 1 female 7.12 mm, 1 male 5.12 mm sectioned, 1 female 7.3 mm, 1 male 3.6 mm, AMS C117597.

Description. Shell (Fig.3E-J) high, straight, conical, transparent and glossy with convex whorls and large expanded aperture. Larval shell (Fig.12J) consisting of about 3 distinctly convex whorls, height 0.46 mm. Holotype has 7.5 unusually convex whorls, which are almost perfectly smooth, sculptured only by some weak and irregular traces of incremental and spiral lines. Incremental scars situated 3.3, 2.1 and 1.0 whorls from larval shell; rather strong and straight. Suture distinct. False suture distinct on the apical whorls, hardly visible on lower ones. Aperture large and expanded. Outer lip evenly curved, straight and prosocline.

Dimensions. Height of holotype 8.4 mm.

Male (Fig.3I). Height about two thirds of height of female and shell of more slender shape and with less distinct angle between parietal wall and columella.

Remarks. *Hypermastus colmani* is characterised by the fairly large and conical shell with unusually convex whorls and the large, expanded aperture. It resembles *H. echinodisci*, but the shell of that species is smaller (about 5 mm high), has a rougher surface, and a larval shell of about two whorls, (height 0.38 mm). *Hypermastus obliquistomum* differs in having a more cylindrical shell with a smaller larval shell of about 2.5 whorls and a height of 0.42 mm.

Hypermastus coxi (Pilsbry, 1900)

Figs 4A–D, 13D

Eulima (Hypermastus) coxi Pilsbry, 1899: 258.
Hypermastus mucronata.–Laseron 1955: 86 (not Sowerby, 1866).

Type material. HOLOTYPE (Fig.4A,B) ANSP 71306. Host species unknown.

Type locality. Port Stephens, NSW, Australia.

Material examined. The holotype and Twofold Bay, NSW, 27-128 m, 1 specimen, AMS C120739; Twofold Bay, NSW, 9 m, 1 specimen, AMS C66118.

Remarks. This species is so far only known from shells, with dried, rotten soft parts. It resembles a miniature of *H. mucronata*, and from the beginning we were inclined to consider it a dwarf male of that species, but since the larval shells are different this is most unlikely. We have never seen rich material with both species present.

Hypermastus coxi can be recognised from the small, cylindrical shell and the mamillate larval shell of slightly more than 1.5 whorls and a height of about 0.20 mm. The position of the larval shell in relation to the following sutures is very variable, as often is the case in eulimids with small mamillate protoconchs and rapid post larval growth. This makes the measurements uncertain.

Hypermastus cylindrica (Sowerby, 1900)

Figs 4E,F, 12E

Mucronalia cylindrica Sowerby, 1900: 127.

Type material. HOLOTYPE (Figs 4E-F,12E) BMNH 1900.11.18.40.

Type locality. Cebu, Philippines. Host species unknown.

Material examined. The type material.

Distribution. No reliable additional records exist.

Remarks. No additional specimens are known of this species, but the shape of the aperture and the outer lip make it likely that this species belongs to *Hypermastus*.

Hypermastus echinodisci Warén, 1980

Figs 4G,H, 13C

Hypermastus echinodisci Warén, 1980: 291.

Type material. HOLOTYPE and several PARATYPES,

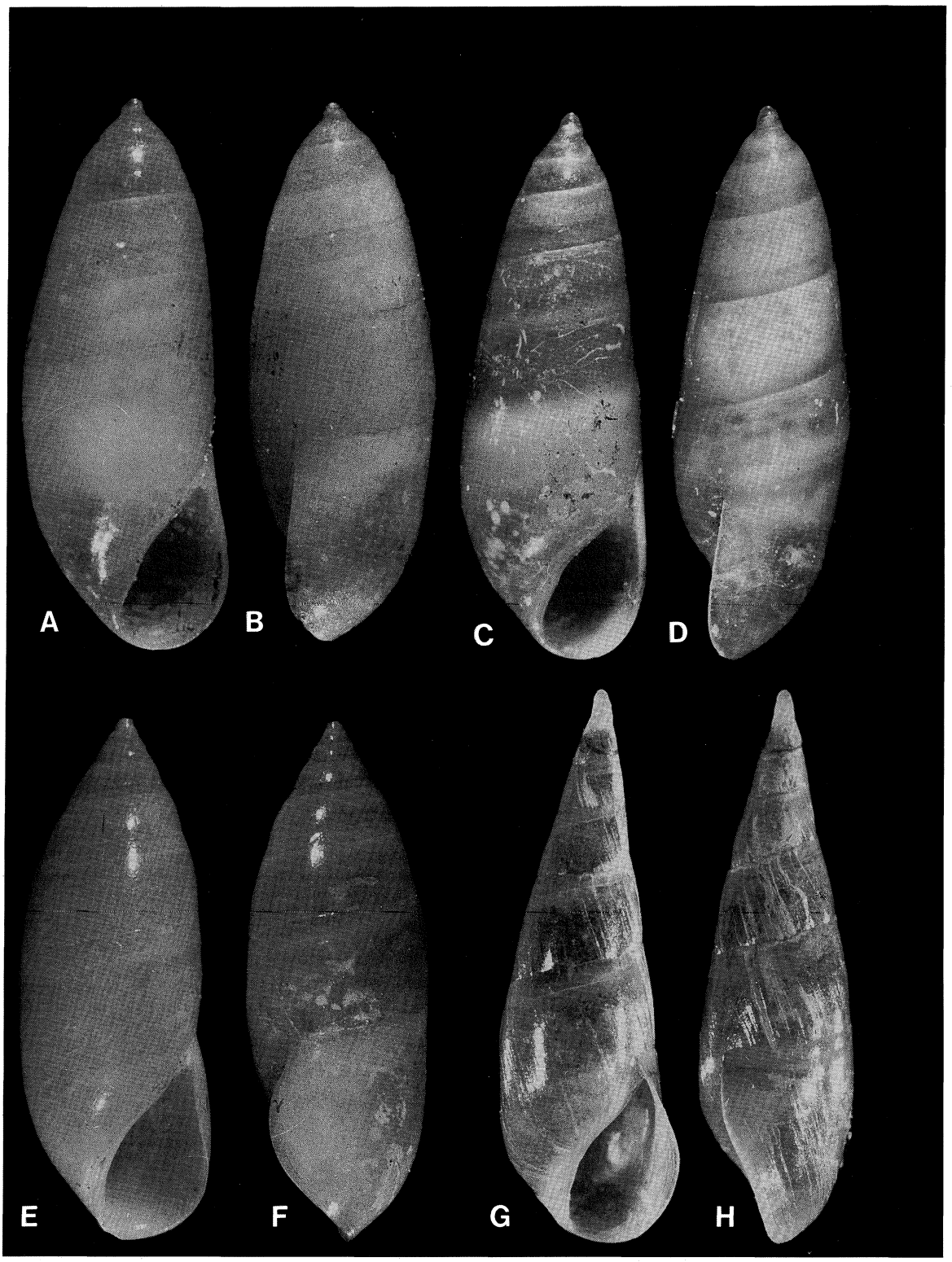

Fig.4. A–D. *Hypermastus coxi*. A–B. holotype, ANSP 71306, 4.0 mm. C. Twofold Bay, New South Wales, 27-128 m, AMS C120739, 4.32 mm. D. same locality, 9 m, AMS C66118, 4.16 mm. E–F. *H. cylindrica*, holotype, BMNH 1900.11.10.40, 6.95 mm. G–H. *H. echinodisci*, MNHN ex M. Saul, 4.8 mm.

ANSP 349451 and 349452.

Type locality. Tanjong, Aru, Jesselton, Sabah (North Borneo), on *Echinodiscus bisperforatus*.

Material examined. The type material and Merang Beach, Trengganu State, Malaysia, 5°32.3'N 102°56.8'E, lowest intertidal zone, "sparse sand dollars heavily infested", leg. T.E. Yancey 13 Aug. 1974, 3 young specimens, USNM 853989; Tanjong, Aru, Jesselton, Sabah (North Borneo), leg. M. Saul, 1 specimen, MNHN.

Distribution. Only known from the material examined, from Malaysia and Borneo, intertidal.

Remarks. *Hypermastus echinodisci* may be recognised by the expanded, *Lymnaea*-resembling aperture, which is more irregular than in *H. obliquistomum* and *H. colmani*, both of which are also considerably larger.

Hypermastus epeterion (Melvill, 1889)

Figs5A–B,12I

Eulima epeterion Melvill, 1889: 31.

Type material. HOLOTYPE (Figs 5A-B, 12I) in NMW.

Type locality. Mauritius. Host species unknown.

Material examined. The holotype.

Distribution. No reliable additional records exist.

Remarks. No additional information is available about this species. It is so far known only from the type. It resembles *H. epiphanes*, but that species has flatter apical whorls. It is unusually large for the genus, 16 mm high.

Hypermastus epiphanes (Melvill, 1897)

Fig.5C,D

Eulima epiphanes Melvill, 1897: 13.

Type material. Several SYNTYPES in NMW, 1 SYNTYPE AMS C40863, 1 SYNTYPE SMNH 4124 (Fig.5C,D), all from type locality.

Type locality. Linjah, Persian Gulf, 9 m, soft mud. Host species unknown.

Material examined. The type material.

Distribution. No reliable additional records exist.

Remarks. Very similar to *H. epeterion*, but *H. epiphanes* has flatter apical whorls. Also this is an unusually large species, 14 mm high.

Hypermastus georgiregis (Cotton & Godfrey, 1932)

Figs5E–F,12A

Eulima georgiregis Cotton & Godfrey, 1932: 37.

Type material. HOLOTYPE (Figs 5E-F,12A) SAM D 10631

Type locality. King George Sound, SA, 40-50 m. Host species unknown.

Material examined. The type material.

Distribution. No reliable additional records exist.

Remarks. *Hypermastus georgiregis* is, judging from shell characters, an unquestionable member of this group of sand dollar parasites. The profile of the outer lip and the weak angle between the columella and parietal wall is very similar to all other species with known hosts. Nothing is known about its biology. It resembles *H. mucronata*, but has more convex whorls and a larger larval shell (about 0.23 mm diameter instead of 0.18 mm). However, it cannot be excluded that they are synonyms.

Hypermastus indistincta (Thiele, 1925)

Fig.5G–I

Eulima indistincta Thiele, 1925: 309.

Type material. HOLOTYPE and 6 PARATYPES (Fig.5G-I) in ZMHB, all no 101928.

Type locality. Padang, Sumatra. Host species unknown.

Material examined. The type material.

Distribution. No reliable additional records exist.

Remarks. We have seen only the type material of this species, which resembles *H. tenuissimae* but has a less straight spire and attains a larger height (at least 9 mm). *Hypermastus indistincta* also resembles *H. boschorum*, but that species has a more straight spire and a proportionally larger aperture.

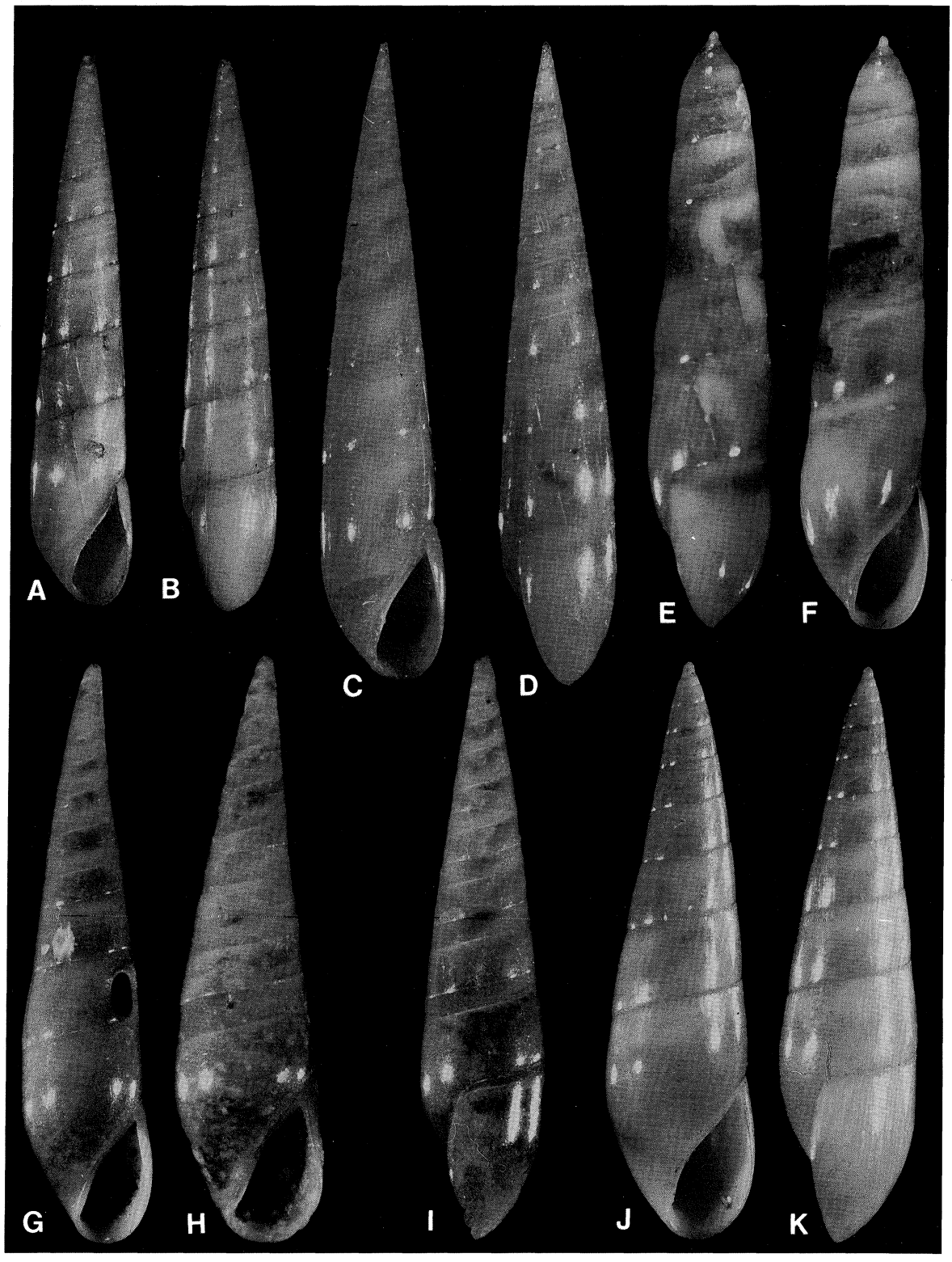

Fig.5. A–B. *Hypermastus epeterion*, holotype, 16.1 mm. C–D. *H. epiphanes*, syntype, 13.8 mm, SMNH 4124. E–F. *H. georgiregis*, holotype, SAM D 10631, 12.0 mm. G–I. *H. indistincta*. G. holotype (drilled) 9.3 mm. H–I. paratypes, H. (male?) 4.7 mm and I. 7.9 mm. J–K. *H. kilburni*, holotype, NM G 3676/T70, 9.00 mm.

Hypermastus kilburni n.sp., Warén

Figs5J–K,13B,E

Type material. HOLOTYPE (Fig.5J-K) NM G 3676/T69; paratypes, 11 young specimens, NM G 2106/T70, from the same locality, "on sand dollars", and 3 young specimens SMNH 4119, from NM G 2106/T70.

Type locality. Mozambique, Bazaruto Island, parasitic on an 'echinoid'.

Material examined. The type material.

Distribution. No additional records exist.

Description. Shell (Fig.5J-K) tall, conical, slightly convex, solid, with mucronate larval shell. Larval shell (Fig.13E) distinctly set off, with about 1.5 perfectly flat whorls and height of about 0.26 mm. Holotype has 9.3 indistinctly convex teleoconch whorls, of which first 2 whorls increase their diameter much faster than subsequent ones. Sculpture consisting of some irregularly scattered incremental lines and 6 incremental scars situated 1.5, 2.7, 3.5, 4.5, 5.4 and 7.4 whorls from outer lip. In addition, there are numerous, regularly appearing short incremental riblets at the suture, about 0.1 mm long and with intervals of 0.1-0.04 mm. Suture distinct. Aperture rather high and slender, slightly excavated in its lower part. Outer lip retracted at suture, slightly and evenly convex and orthocline.

Dimensions. Height of holotype 9.05 mm.

Male. Not known. Specimen described assumed to be female.

Remarks. *Hypermastus kilburni* is based on two lots from the same locality, collected by different collectors. The description is based on the holotype, which comes from a lot of a single adult specimen, the paratypes come from a sample of 14 young specimens (NM G 2106).

Hypermastus kilburni resembles *H. auritae*, but has more crowded incremental riblets at the suture, a rougher surface with more distinct growth lines and distinctly convex whorls. It also resembles *H. serratus*, but that species has more distinctly convex whorls and a more strongly convex profile of the outer lip.

Hypermastus minor n.sp., Warén

Figs6A,B,12F

Type material. HOLOTYPE (Fig.6A,B) USNM 778727.

Type locality. "On juvenile echinoids, *Echinodiscus bisperforatus*, mid-intertidal area of very wide sand beach" (label, presumably T.E. Yancey), Konchung Laut Village, 32 km south of Klang, Selongor State, Malaysia, leg. T.E. Yancey, 10 Mar. 1974, 1 adult specimen, USNM 778727.

Material examined. The holotype and Tanjong Aru, Jesselton, Sabah (North Borneo), leg. M.Saul, on *Echinodiscus bisperforatus* (together with numerous *H. sauliae*), 1 specimen, SMNH.

Distribution. Only known from the material examined.

Description (sex not known). Shell (Fig.6A,B) small, solid, and glossy. Left side evenly convex, right side straight with proportionally large aperture. Larval shell (Fig.12F) consisting of almost 3 slightly convex whorls (height 0.45 mm). Holotype has about 4.7 almost perfectly flat whorls, with very fine and indistinct spiral microsculpture. Suture very shallow but distinct. Teleoconch with 4 straight, not very distinct incremental scars on lower 3 whorls. Aperture large with almost perfectly straight parietal wall, reaching far over to the left side. Outer lip slightly prosocline, indistinctly retracted at suture, slightly and evenly convex below suture.

Dimensions. Height of holotype 3.68 mm (larval shell missing).

Remarks. Despite being known from only two specimens, and we find this species characteristic enough

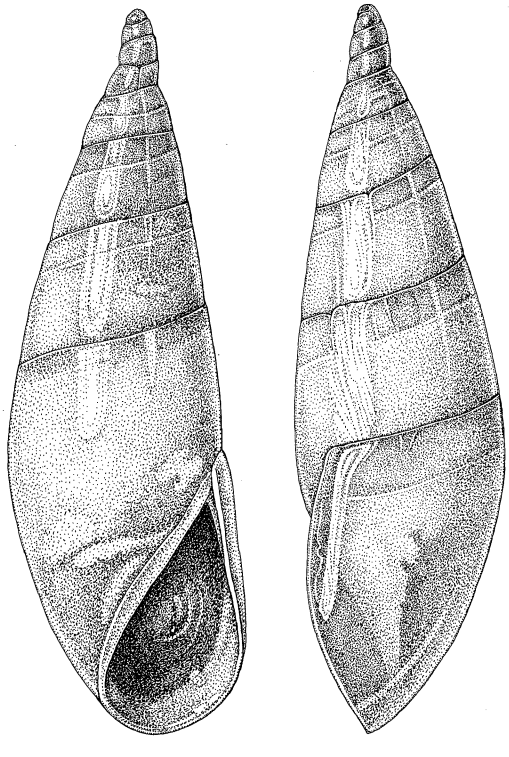

Fig.6. *Hypermastus minor*, holotype, 4.0 mm.

to be described. The general shape of the shell with the outer lip and the right side forming a straight line and the left side evenly curved differs from all other species of *Hypermastus*. The aperture on the other hand, especially the straight parietal wall and the shape of the outer lip does not differ from what is normal within the genus.

Hypermastus mucronata (Sowerby, 1866)

Figs 7A–D,12E

Eulima mucronata Sowerby *in* Reeve, 1866: sp. 42.
Hypermastus coxi.–Laseron 1955: 86.

Type material. SYNTYPES (Fig.7A,B) BMNH 1870.10.26.114.

Type locality. Port Jackson, NSW, from G.F. Angas. Host species unknown.

Material examined. The type material and several lots in AMS, from New South Wales and southern Australia.

Distribution. New South Wales and southern Australia, shallow water (material in AMS).

Remarks. No additional information about this species is known, although the species is not rare. It resembles *H. georgiregis*, *H. philippiana* and *H. colmani*, but has flatter whorls than any of these. From *H. colmani* it differs also by having a more blunt larval shell and a strongly prosocline and straight outer lip.

Hypermastus obliquistomum n.sp., Warén

Figs 7E,F,12H

Type material. HOLOTYPE AMS C160815, (Fig.7E,F), from AMS C117611.

Type locality. "From sand dollars", Baie des Isoles, Noumea, New Caledonia, mudflats, ventral side of host, leg. P.H. Colman, 15 May 1971, together with a single specimen of *H. serratus*.

Material examined. The holotype.

Description (sex not known). Shell (Fig.7E,F) straight, conical, somewhat irregularly coiled, transparent and smooth with large aperture. Larval shell (Fig.12H) consisting of about 2.5 slightly convex whorls, height 0.42 mm. Holotype with 8.4 convex teleoconch whorls, constricted at subsutural zone, smooth except for some very weak and fine spiral microstriation, and some irregular incremental lines. Teleoconch with 4 incremental scars 3, 5, 6, and 7 whorls from the larval shell, plus several additional thickenings similar to scars but not marked with a furrow. Aperture is large, broad and expanded. Parietal wall evenly curved and outer lip prosocline with upper part more strongly curved, most projecting at uppermost one fifth.

Dimensions. Height of the holotype 8.3 mm.

Remarks. *Hypermastus obliquistomum* resembles *H. colmani* and *H. echinodisci* in having distinctly convex whorls, a slightly irregularly shaped aperture and a conical shape. However, the larval shell is larger and has more whorls than in *H. echinodisci* and the aperture is much smaller than in *H. colmani*, where its height is about 35% of the total height of the shell compared with 31% in *H. obliquistomum*.

Hypermastus peronellicola (Kuroda & Habe, 1950)

Figs 7G,H,12B

Balcis peronellicola Kuroda & Habe, 1950: 60.

Type material. One SYNTYPE (Figs 7G,H,12B) NSMT 39847.

Type locality. Yura Bay, Wakayama Pref., Honshu, on *Peronella leseuri*.

Material examined. One syntype.

Distribution. Southern Japan (Habe, 1976).

Remarks. This species was described from *Peronella leseuri* (A. Agassiz) and recorded from three other south Japanese localities. We have examined a syntype, which is somewhat similar to *H. colmani*, but has flatter whorls and a smaller and less expanded aperture.

Hypermastus placentae n.sp., Warén & Crossland

Figs 7I–L,8A–C,11C,D,F,13L

Type material. HOLOTYPE (Fig.7I-J) AMS C160817; numerous SYNTYPES AMS C160818, BMNH 1989154, USNM 860501, SMNH 4120, all from type locality.

Type locality. On *Arachnoides placenta* (Linnaeus, 1758), Queensland, 6 km north-north-west of Townsville, Pallarenda Beach, 19°12'S 146°47'E, lower part of intertidal sandflat, leg. M.R. Crossland.

Material examined. The types and Port Douglas, northern Queensland, on *Arachnoides placenta*, 6 females,

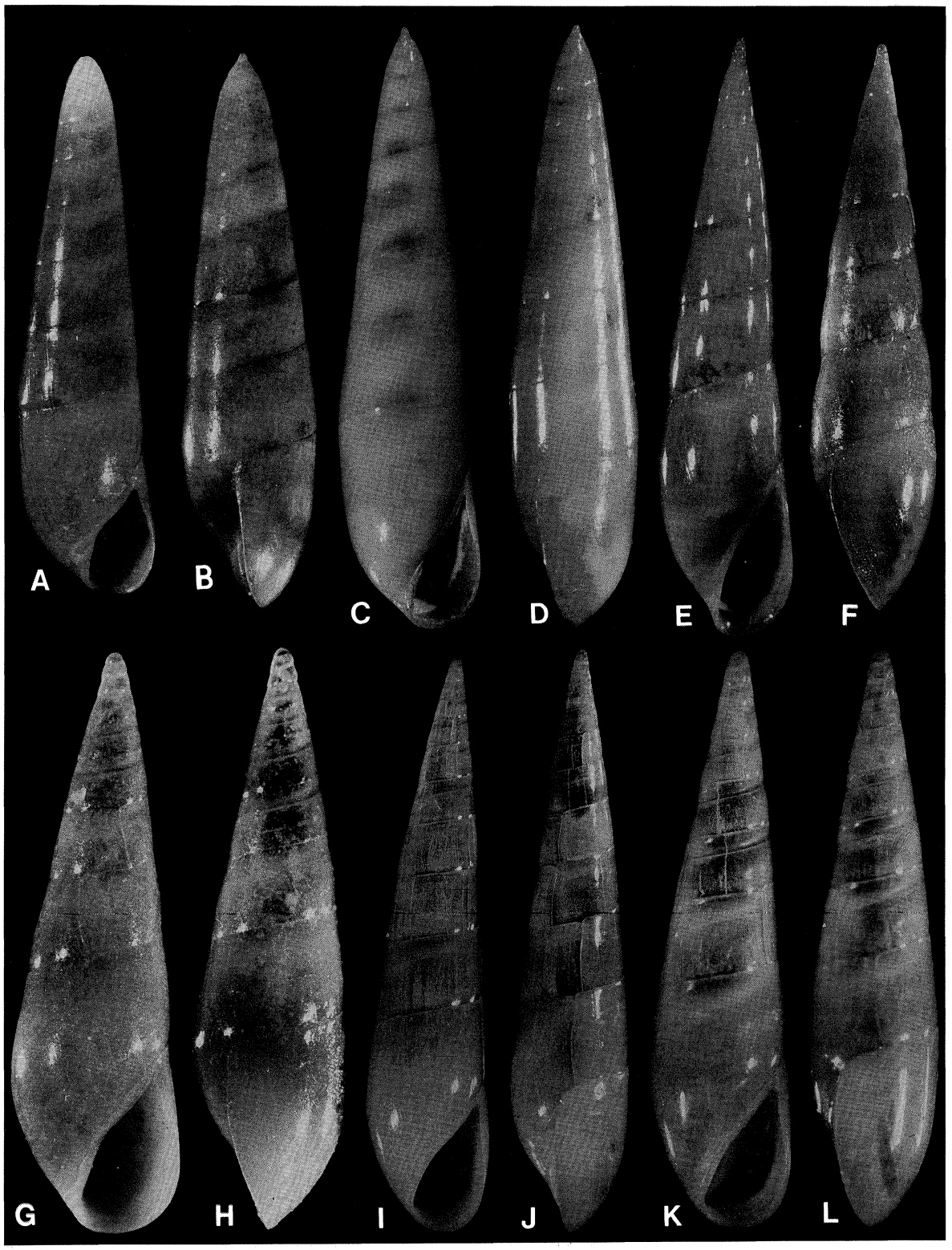

Fig.7. A–D. *Hypermastus mucronata*. A–B. syntypes, 11.4 and 10.5 mm. C–D. Sow and Pigs Reef, Sydney, New South Wales, 10.8 mm. E–F. *H. obliquistomum*, holotype, AMS C117611, 8.3 mm. G–H. *H. peronellicola*, syntype (young ?), NSMT 4.32 mm. I–L. *Hypermastus placentae*. I–J. holotype, 7.89 mm. K–L. paratype, (male) SMNH 4120, 4.29 mm.

8 males, AMS C120754.

Description. Shell (Figs 7I-L,8A-C) tall, straight, solid, smooth, conical with fairly large aperture. Larval shell (Fig.13L) consisting of about 1.5 slightly convex whorls height 0.36 mm. Holotype with 9.8 very flat and smooth teleoconch whorls, with some hardly perceptible and very indistinct traces of spiral lines and slightly more distinct incremental lines. Teleoconch with 10 rather strong, straight incremental scars, more distant on apical whorls, more crowded at half grown size and about 1 whorl apart on lower 4 whorls. Suture is very shallow and indistinct. False suture distinct, occupies two sevenths of the height of the whorls. Aperture rather broad, outer lip prosocline, evenly curved, and retracted at suture.

Dimensions. Height of holotype 7.89 mm.

Male (Figs 7K,L, 8A). 0.59 times height of female, with slightly more slender shell.

Remarks. *Hypermastus placentae* resembles *H. boschorum*, but is broader than that species and the upper part of the outer lip is not constricted in *H. boschorum*. The shape closely resembles that of *H. tenuissimae*, but that species has one whorl more in the larval shell and its surface is rougher with distinct spiral sculpture.

Crossland *et al.* (in press) have described the biology of *H. placentae* in some detail. This is summarised under "Biology". The sexes are separate, with females 1.6 times the shell height of the males. The height and sex distribution is shown in Table 3, where a set of values of specimens sexed from shell morphology is also shown.

Hypermastus productus (Sowerby, 1894)

Fig.8D,E

Eulima producta Sowerby, 1894: 156 (not *Leiostraca producta* Carpenter, 1863: 357, new name for *Leiostraca solitaria* Carpenter, 1857: 439).

Type material. HOLOTYPE (Fig.8D,E) in BMNH.

Type locality. Hong Kong Harbour, 13-20 m. Host species unknown.

Material examined. The holotype.

Distribution. No reliable additional records exist.

Remarks. At a height of 30.5 mm, this is the largest species known of *Hypermastus*. We have seen no additional material and it has not been mentioned in the literature.

It should be possible to recognise *H. productus* by the very slender spire and the large height, but there is a possibility that it is the female of *H. epeterion* or *H. epiphanes*. The larval shell of the type and only known specimen is broken.

Hypermastus productus comes very close to being a homonym of *Leiostraca producta* Carpenter, 1863 since *Leiostraca* is an junior synonym of *Eulima*. *Leiostraca producta*, however, belongs to *Melanella* and no renaming will be necessary.

Hypermastus randolphi (Vanatta, 1900)

Fig.8H,I

Eulima randolphi Vanatta, 1900: 256.
Melanella (*Melanella*) *randolphi*.–Bartsch 1917: 312.
Melanella (*Melanella*) *californica* Bartsch, 1917: 313.

Type material. *Eulima randolphi*, SYNTYPES ANSP 73729, BMNH 1929.6.6.56-59 (Fig.8H); *M. californica*, HOLOTYPE USNM 56911.

Type locality. *Eulima randolphi*, Unalaska Island, Alaska; *M. californica*, Catalina Island, California. Host species unknown.

Material examined. The material listed by Bartsch (1917).

Distribution. Alaska to California, usually in shallow water, 0-50 m (Bartsch, 1917).

Remarks. The types of the two names mentioned in the synonymy have been compared side by side and no difference could be seen.

The short, stout shell of *H. randolphi* looks quite different from most species of *Hypermastus*, but the aperture shows some similarity and there is no other group where it fits better. The larval shell consists of slightly more than one whorl and is 1.2 to 1.4 mm high. It has a diameter of 1.1 to 0.9 mm and *H. randolphi* must have very large and yolk-rich eggs. This may be a part of the reason why *H. randolphi* looks different, since a coiling starting with a large and irregular protoconch often gets a different appearance (Warén, unpublished).

A possible host for *H. randolphi* (if it really belongs to *Hypermastus*) is *Dendraster excentricus* (Eschscholtz, 1829) (Scutellidae), which is the only sand dollar common from Lower California to Alaska, in 0 to 90 m (Mortensen, 1948).

Hypermastus sauliae Warén, 1980

Figs 8F,G, 13K

Hypermastus sauliae Warén, 1980: 291.

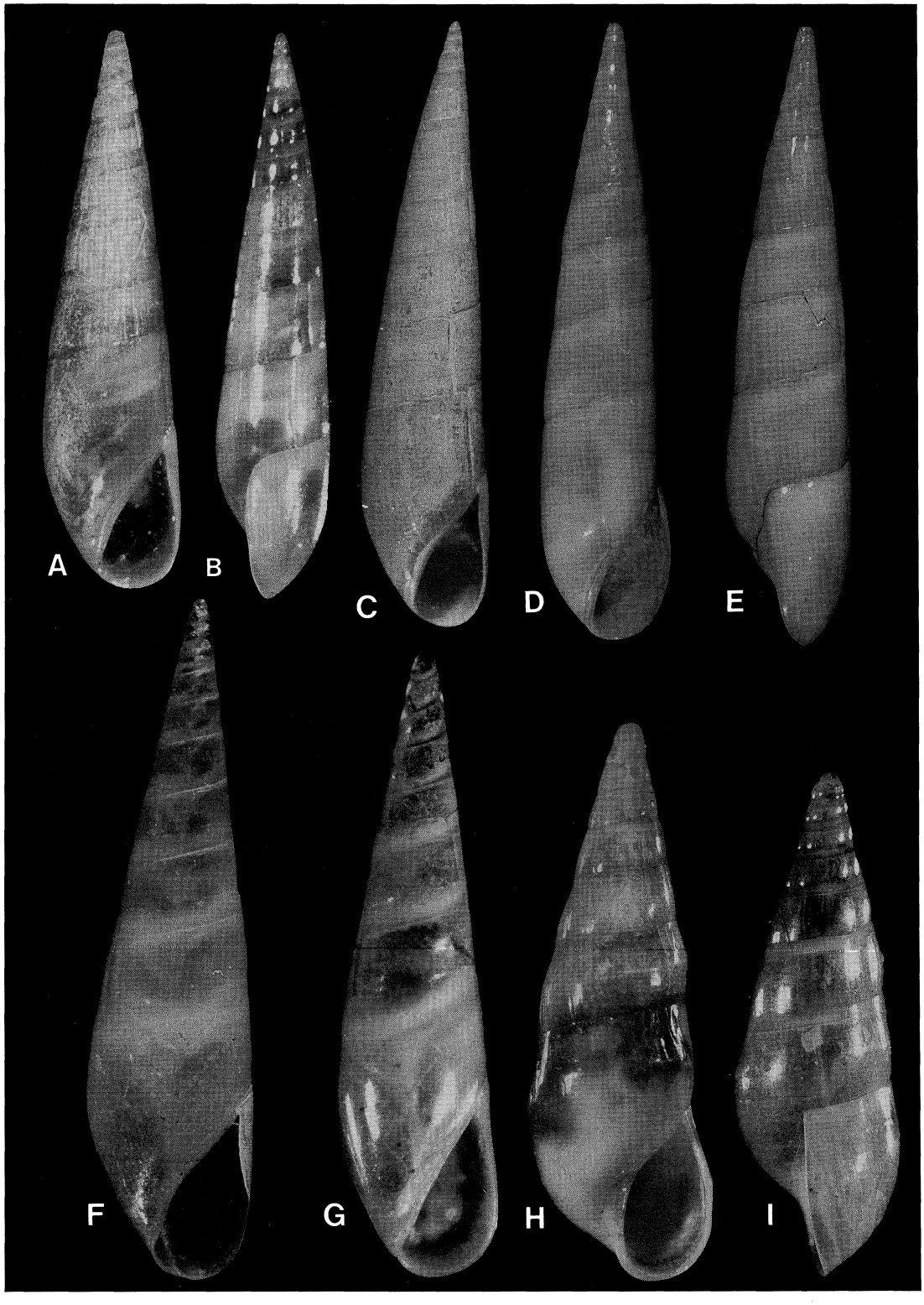

Fig.8. A–C. *Hypermastus placentae*. A. male, AMS C120754, 4.0 mm. B-C. females, AMS C120754, 7.04 mm and 6.56 mm. D–E. *H. producta*, holotype, 30.5 mm. F–G. *H. sauliae*, USNM 775663. F. female, aperture slightly damaged, 5.5 mm. G. male, 2.80 mm. H–I. *H. randolphi*. H. syntype, BMNH 1929.6.6.56-59, 7.5 mm. I. Alaska, SMNH, 7.8 mm.

Type material. HOLOTYPE 275267 and several PARATYPES, ANSP 349453.

Type locality. Tanjong, Aru, Jesselton, Sabah (North Borneo), on *Echinodiscus bisperforatus*.

Material examined. The type material and Bangan Bay, Kudat River, Sabah (North Borneo), from 45 *Echinodiscus bisperforatus*, leg. P. Bouchet 8 Jan. 1981, 3 females, 6 males, MNHN; Merang Beach, Trenganu State, Malaysia, 5°32'03"N 102°56'08"E, from "sand dollars", leg. T.E. Yancey 13 Aug. 1974, 1 female, 19 males, USNM 778633; 20 miles south of Klang, Selongor State, Malaysia, 2°43.5'N 101°27.3'E, from *Echinodiscus bisperforatus*, leg. T.E. Yancey 10 May 1974, 3 males, USNM 853990; Tanjong Aru, Jesselton, Sabah (North Borneo), leg. M.Saul, 1 specimen MNHN, 20 specimens, SMNH, 48 specimens, ZMA.

Distribution. Only known from the material examined.

Remarks. This species is very similar to *H. boschorum*, but that species has a more constricted outer lip and about half a whorl less in the larval shell.

Hypermastus serratus n.sp., Warén

Figs 9A,B, 12C

Type material. HOLOTYPE (Figs 9A,B,12C) AMS C117611.

Type locality. "From sand dollars", Baie des Isoles, Noumea, New Caledonia, mudflats, ventral side of host, leg. P.H. Colman 15 May 1971.

Material examined. Only known from the holotype.

Description (sex not known). Shell (Fig.9A,B) cylindrical, tall, slender with sharply set off larval shell, glossy and transparent with fairly large and slender aperture. Larval shell (Fig.12C) consisting almost 2 slightly convex whorls. First teleoconch whorl partly covers larval shell and makes it difficult to measure height; estimated to 0.21-0.24 mm. First 2 teleoconch whorls increase their diameter very rapidly. Holotype with 10.3 slightly convex teleoconch whorls with occasional, almost imperceptible traces of distant spiral lines and growth lines covering upper part of subsutural zone and giving it a crenulated appearance. These lines stop abruptly after 0.05-0.1 mm. Four rather strong and deep incremental scars 5.7, 6.7, 7.7 and 9.0 whorls from larval shell. Aperture large and the parietal wall with weak angle just above midpoint of height. Outer lip retracted at suture, slightly prosocline and evenly curved.

Dimensions. Height of holotype 8.7 mm.

Remarks. This species closely resembles *H. auritae*, but differs in having the first two postlarval whorls abruptly increasing their diameter, while in *H. auritae* they are slowly and regularly increasing. It also differs from *H. auritae* in having about half a whorl more in the larval shell despite their similar height.

Hypermastus tenuissimae n.sp., Warén

Figs 9C–E, 10C,D, 11A,B, 12G

Type material. HOLOTYPE (Fig.9C) (female?) in ZMC; 3 PARATYPES, SMNH 4121, all from type locality.

Type locality. West side of Ko Yao Yai, Phuket, Thailand, underside of sand dollars, *Echinodiscus tenuissimus* (L. Agassiz, 1847) (Scutellidae), leg. 5th Thai-Danish Expedition, station 1132, 21 Feb. 1966.

Material examined. The types and 1 male, 5.0 mm, which was sectioned and 1 male 3.9 mm (Fig.9E) which was lost after the photo was taken.

Description (sex uncertain, assumed to be female). Shell (Fig.9C,D) rather small, straight, conical, slender, very smooth and with small aperture. Larval shell (Fig.12G) consisting of almost 3, slightly convex whorls, height 0.40 mm. Holotype with 8.2 almost flat teleoconch whorls, without spiral sculpture but with irregular incremental lines. Holotype having about 10 distinct incremental scars, somewhat more crowded at apical part. Suture very shallow and inconspicuous. False suture distinct, subsutural zone corresponding to one quarter the height of whorls. Aperture small and narrow, not constricted in upper part. Outer lip orthocline, slightly protruding at suture, very shallowly sinuated below the suture, very slightly protruding and evenly curved below sinus.

Dimensions. Height of the holotype 5.68 mm.

Male (Fig.9E). Smaller (although one sectioned specimen of 5.0 mm was male).

Remarks. *Hypermastus tenuissimae* is known from six specimens only, and it cannot be excluded that it reaches a larger height, perhaps 7 to 9 mm, if all the specimens known are males.

This sand dollar parasite closely resembles *H. sauliae*, but that species has one whorl less in the larval shell (height 0.32 mm) and the surface has an indistinct spiral sculpture, which is absent in *H. tenuissimae*. Otherwise they are identical. *Hypermastus boschorum* can be separated by having an indistinct spiral sculpture, the upper part of the aperture being constricted, and by having a larval shell which is 0.35 mm high and consists of about 1.8 whorls.

One specimen of the host sand dollar preserved with the specimens (Fig.10C,D) has three ventral and three dorsal holes in the test. These consist of a shallow

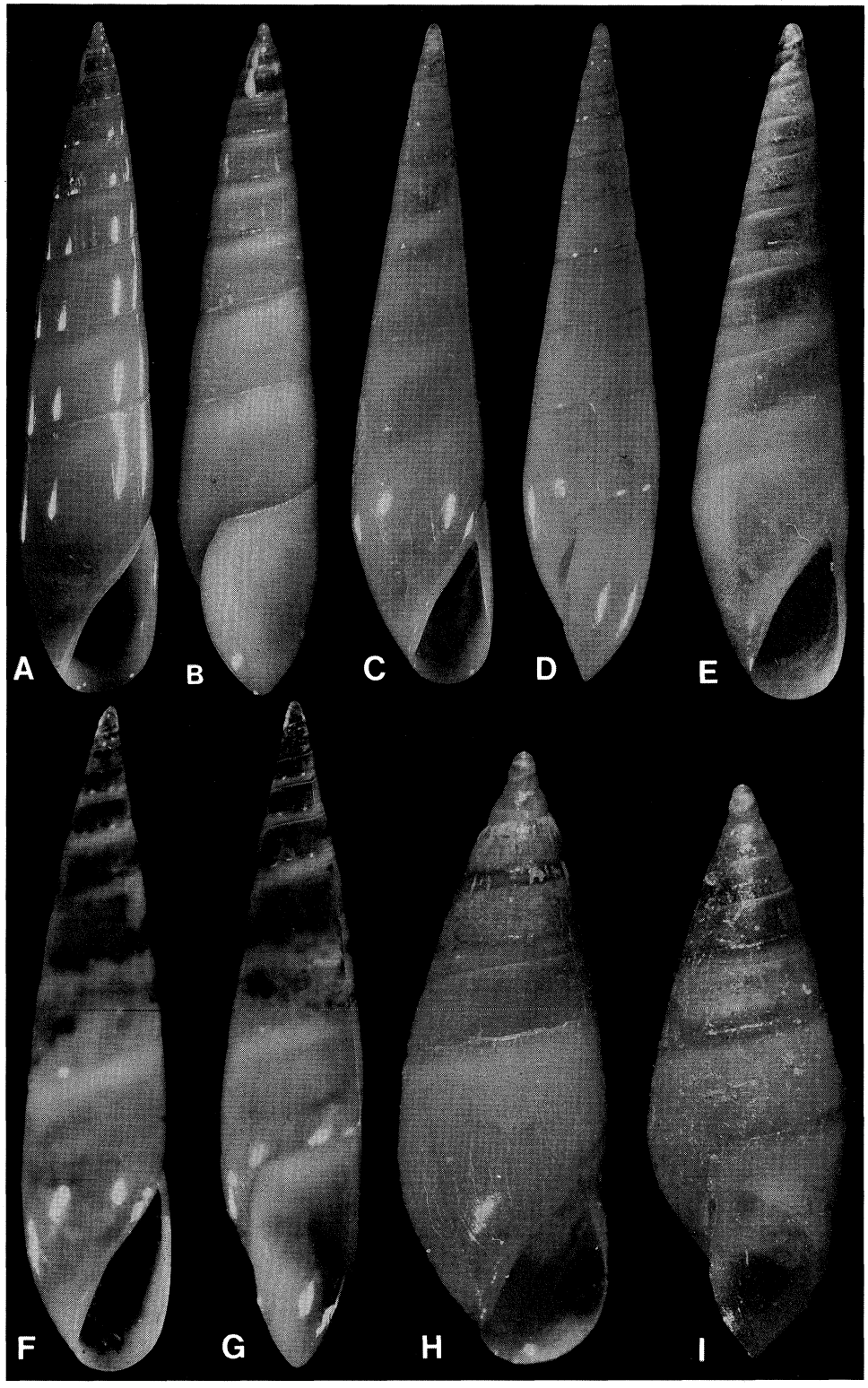

Fig.9. A–B. *Hypermastus serratus*, holotype, AMS 117611, 8.7 mm. C–E. *H. tenuissimae*. C–D. holotype, 5.7 mm and paratype (SMNH 4121), 5.8 mm. E. male, paratype (lost), 3.92 mm. F–G. *H. williamsi*, holotype, SAM D 10637, 6.78 mm. H–I. *Turveria encopendema*, LACM 55556, 4.20 and 3.96 mm.

pit, in the bottom of which there is a final penetration of the test (Fig.11A,B). It is not known if all the specimens in the type material come from this single host specimen, or also from additional ones.

Hypermastus williamsi (Cotton & Godfrey, 1932)

Figs 9F,G, 12D

Strombiformis williamsi Cotton & Godfrey, 1932: 39.

Type material. HOLOTYPE (Figs 9F,G,12D), South Australian Museum D 10637; PARATYPE, 1 shell, South Australian Museum D 16217.

Type locality. St Vincent's Gulf, South Australia, 18 m. Host species unknown.

Material examined. The types.

Distribution. No reliable additional records exist.

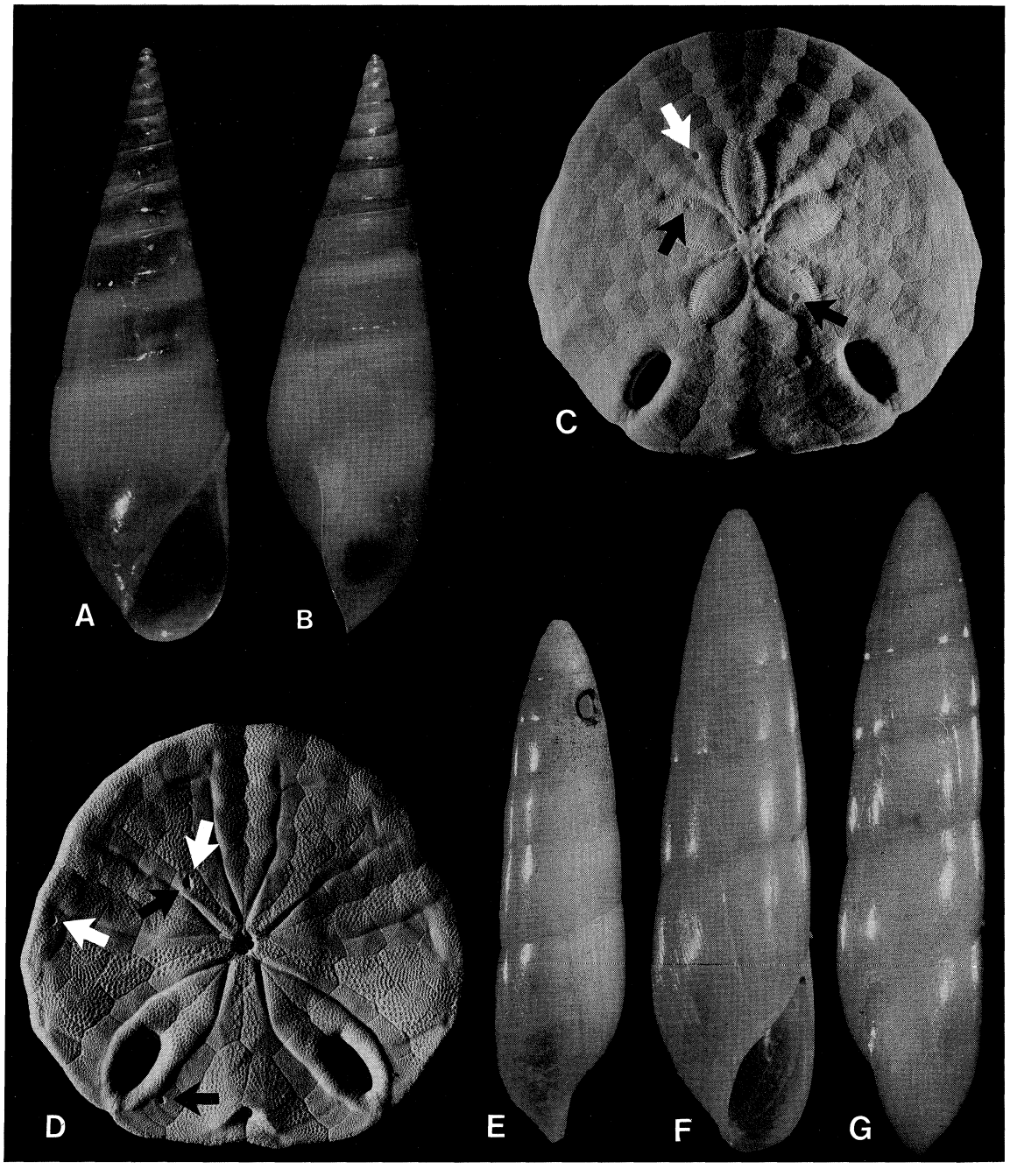

Fig.10. A–B. *Turveria schwengelae*, LACM 55553, 5.23 and 5.06 mm. C–D. *Echinodiscus tenuissimus*, parasitised by *Hypermastus tenuissimae*, scars indicated by arrows. Diameter of host 37 mm. E. *Eulima philippiana*, holotype, 10.4 mm. F–G. *Eulima dunkeriana*, syntypes, ANSP 80637, 10.5 and 12.1 mm.

Remarks. The position in *Hypermastus* is concluded solely from shell characters.

Hypermastus williamsi can be recognised from the larval shell (Fig.12D) which is less cylindrical than normal and consists of more than two whorls (height 0.55 mm). The larval development is probably planktotrophic.

Turveria Berry, 1956

Type species. *Turveria encopendema* Berry, 1956, by original designation, Mexico, Baja California, on *Encope grandis* L. Agassiz, 1841 and *E. californica* Verrill, 1870 (Scutellidae).

Description. Medium sized (4-6 mm) eulimids parasitic on sand dollars, with a rather short and broad, conical, shell with a reddish brown colour pattern. Surface covered by a very fine but distinct sculpture of axial lines. Aperture small and narrow with the line columella-parietal wall almost straight. Outer lip slightly sinuated below the suture.

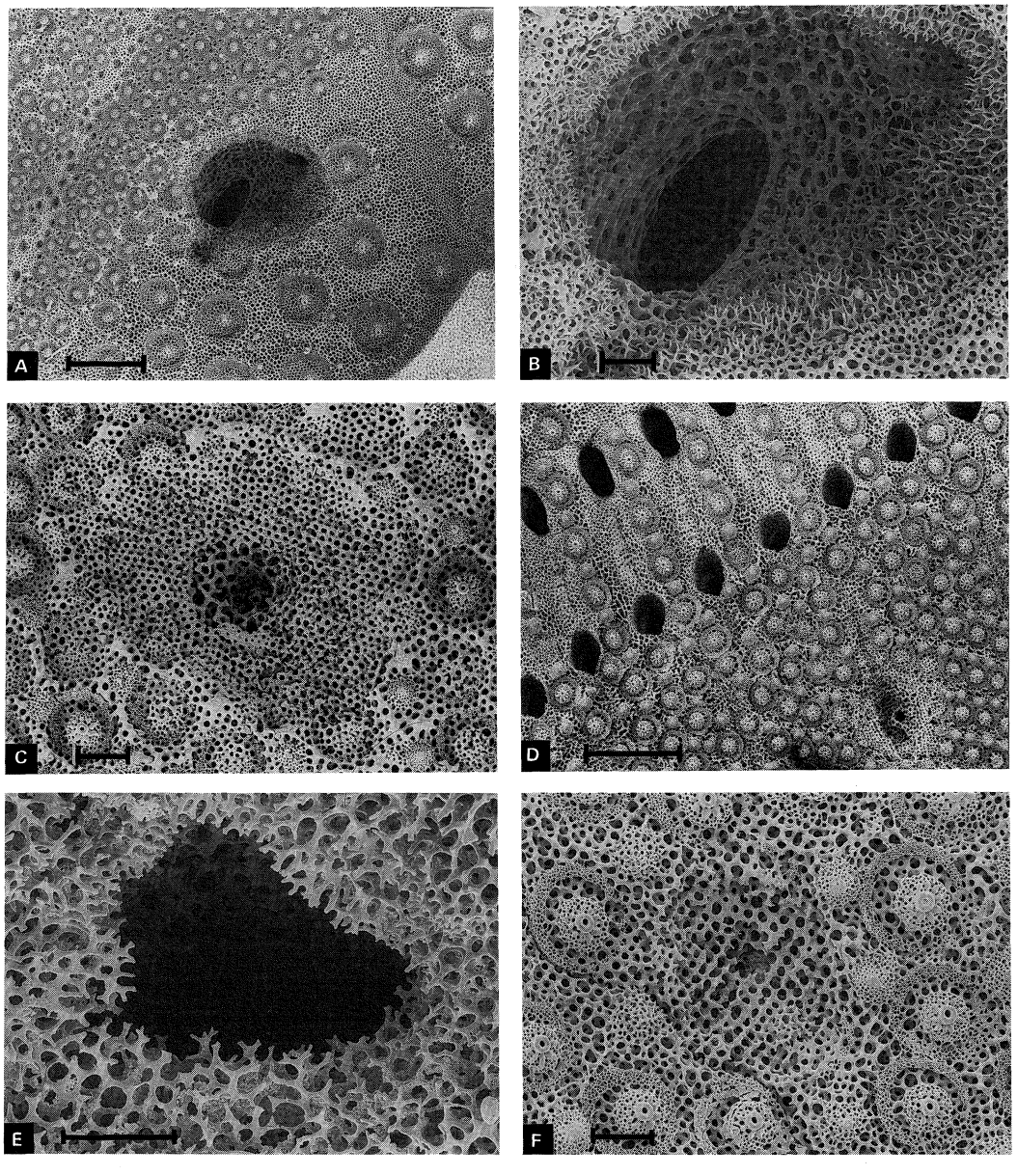

Fig.11. Holes in tests of sand dollars, caused by *Hypermastus* spp. A–B. *Echinodiscus tenuissimus*, parasitised by *H. tenuissimae*. Notice that there are two penetrations by the proboscis. Notice also the pointed structure of the skeletal network which indicates that the hole has been caused by dissolution of the skeleton. C–D. Arachnoides placenta, parasitised by *H. placentae*. C. Shallow attachment. D. Deeper attachment. E. *Echinodiscus bisperforatus*, parasitised by *H. boschorum*. F. *Arachnoides placenta* parasitised by *H. placentae*. Shallow attachment. Scale lines A, D, 0.5 mm; B, C, E, F, 0.1 mm.

Remarks. As mentioned in the introduction, the species of *Turveria* are characterised by having a shell with colour spots and bands, and a distinct microsculpture of dense and sharp incremental lines not occurring in any known species of *Hypermastus*. They also differ by having a sinuated outer lip, while that of *Hypermastus* is evenly curved or straight. Apart from this, the shells are quite similar. In a front view the shape of the aperture is very much the same,.

Turveria encopendema Berry, 1956

Figs 12H,I, 13A,H

Turveria encopendema Berry, 1956: 156.

Type material. In the collection of S.S. Berry, now in SBMNH (not available).

Type locality. Outer strand of Cholla, Bahia de Adaur, Sonora, Mexico, on *Encope grandis* and *E. californica.*

Material examined. Cholla Bay, Sonora, Baja California, on *Encope grandis*, 2 specimens, LACM 55556; El Magote, La Paz Harbor, Baja California, 24°10'N 112°W, intertidal to 2.5 m, 1 specimen, no host, LACM 66-29; Bahia de Adair, Sonora, Mexico, no host, 1 specimen, 5 shells, LACM 55557; Sand flats at Willard Island, Bahia san Luis Gonzaga, Baja California, Mexico, on *Encope grandis*, 1 specimen, LACM 55554; Cholla Bay, Puerto Penasca, Sonora, intertidally down to 1 m, on *Encope grandis*, 43 specimens, coll. D. Shasky.

Distribution. No reliable additional records exist.

Remarks. It has not been possible to examine any type material and Berry's "camera lucida drawing" is too rough to be of any help and is probably based on a young specimen. Berry mentions, however, that the larval shell is mucronate, which clearly distinguishes his species from *T. schwengelae*. For further differences, see *T. schwengelae*.

Turveria schwengelae (Bartsch, 1938)

Figs 10A,B, 13F,G

Strombiformis hemphilli Bartsch, 1917: 344.
Leiostraca schwengelae Bartsch, 1938: 34.

Type material. HOLOTYPE and 3 PARATYPES, USNM 127554.

Type locality. Point Abrejos, Baja California.

Material examined. The types and Concepcion Bay, Baja California, 26°42'N 111°55'W, 1 shell, no host, LACM 63-37; Willard Island, Bahia san Luis Gonzaga, Sonora, Baja California, on *Encope* sp., 4 specimens, LACM 55553; Bahia San Luis Gonzaga, Sonora, Baja California, on *Encope grandis*, intertidal, 36 specimens, leg. D. Shasky.

Description (sex not known). Shell (Fig.10A,B) conically lanceolate, solid, smooth, transparent, with brownish markings along suture and on outer lip. Larval shell (Fig.13F,G) consisting of about 2.7 distinctly convex whorls and is perfectly smooth, colourless except for an occasional brownish tint on initial whorl. Visible height of larval shell 0.26 mm, and total height of shell of larva estimated to about 0.29 mm. A specimen of 5.2 mm has 7.25 teleoconch whorls of slowly and uniformly increasing diameter, sculptured by numerous dense and sharp incremental lines. Teleoconch with 9 incremental scars, 1.2, 1.9, 2.8, 3.8, 4.3, 4.8, 5.5, 6.0 and 6.6 whorls from outer lip, but as usual there is some individual variation in this character. Suture is shallow but distinct and makes a distinct turn downwards about 0.3 mm before outer lip. Aperture is distinctly constricted in its upper part as a consequence of this, and pear shaped. Outer lip distinctly prosocline, with shallow sinus below suture. Colour pattern not as bright as in *T. encopendema*, consisting of a brownish spiral band just below periphery of body whorl. Band concealed under, or visible through subsutural zone on earlier whorls; also a large, roundedly triangular blotch at lower part of outer lip and one less distinct, sometimes absent, similar spot just below corner between outer lip and suture.

Dimensions. Maximum height 5.8 mm.

Remarks. *Strombiformis hemphilli* was renamed *Leiostraca schwengelae* because of supposed secondary homonymy with *Eulima* (*Leiostraca*) *hemphilli* Dall, 1883. *Leiostraca schwengelae* is a replacement name proposed before 1961, and thus *S. hemphilli* is permanently invalidated.

Since we have good material of this species and Bartsch's description is not easy to uinderstand, we have redescribed it. *Turveria schwengelae* differs from *T. encopendema* by having a regularly conical spire, flatter whorls, less vivid colour pattern, and by being about one fifth higher (4.91 ± S.D. 0.27 mm among 23 mature specimens; 4.18 ± S.D. 0.27 mm among 26 specimens of *T. encopendema*).

Doubtful Species

Eulima philippiana Dunker, 1860

Fig.10E–G

Eulima philippiana Dunker, 1860: 226.
Eulima dunkeriana Pilsbry, 1901: 395.

Type material. *Eulima philippiana*, holotype (Fig.10E) SMF, Frankfurt a. M. (ex Heidelberg no. 2773); *E. dunkeriana* (Fig.10F,G), syntypes ANSP 80637.

Type locality. *Eulima philippiana*, Japan, Harbour of Decima; *E. dunkeriana*, Hindo, Japan. Host species unknown.

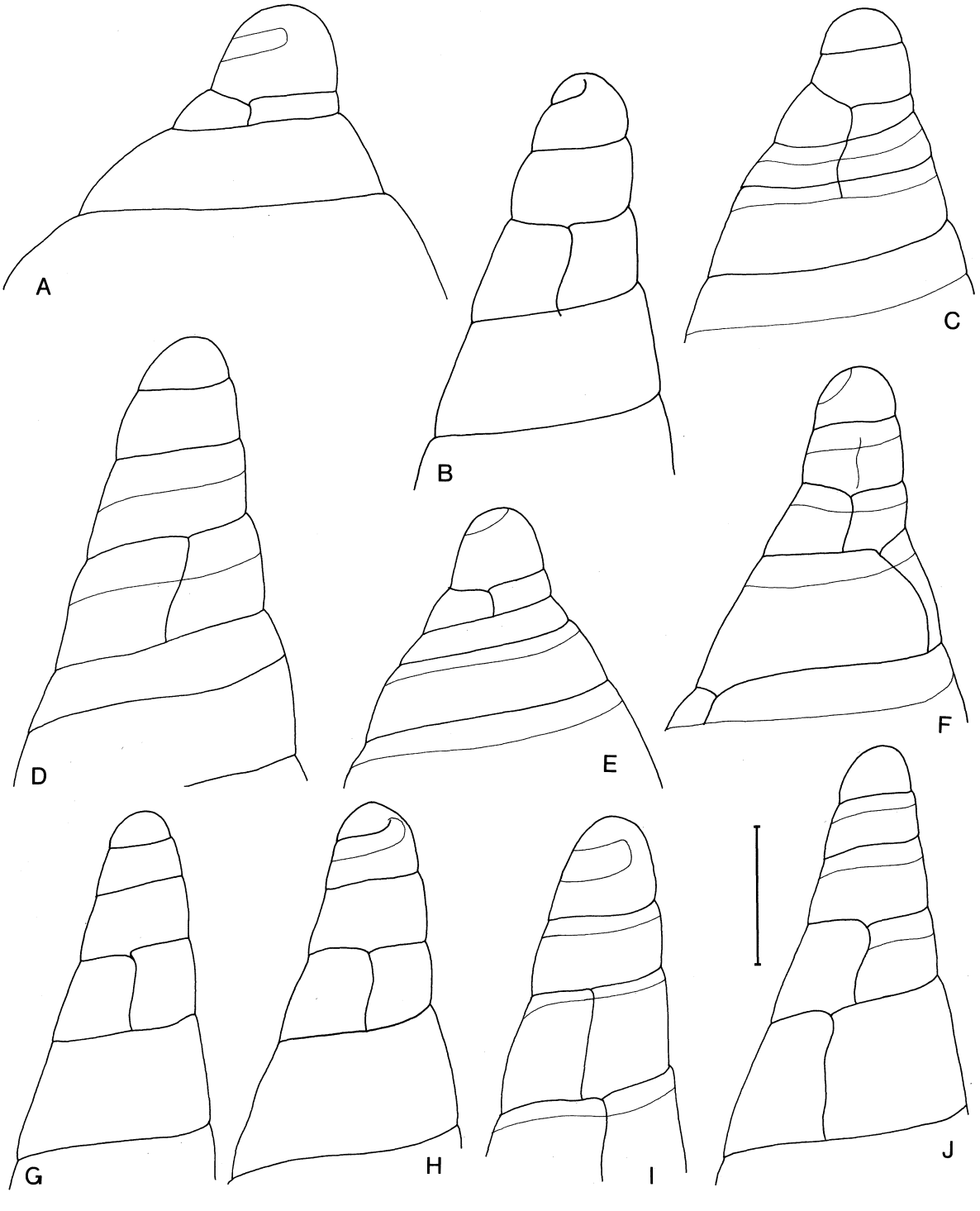

Fig.12. A–J. Larval shells, all at the same magnification. A. *Hypermastus georgiregis*, holotype. B. *H. peronellicola*, syntype. C. *H. serratus*, holotype. D. *H. williamsi*, holotype. E. *H. mucronata*, Sydney. F. *H. minor*, holotype. G. *H. tenuissima*, holotype. H. *H. obliquistomum*, holotype. I. *H. epepterion*, holotype. J. *H. colmani*, holotype. Scale line 0.25 mm.

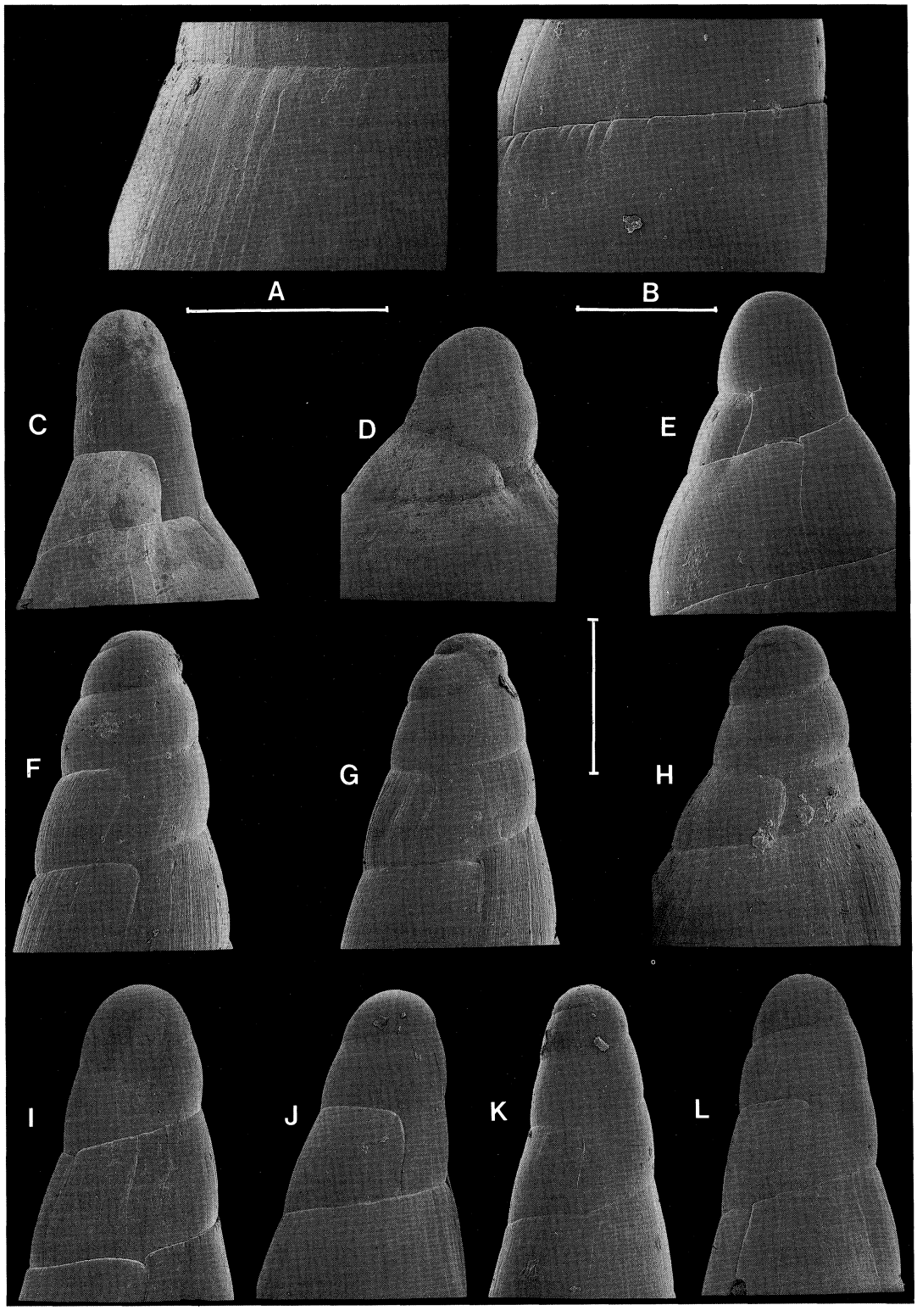

Fig.13. Sculpture and larval shells. A. *Turveria encopendema*, incremental lines, LACM 55557. B. *Hypermastus kilburni*, paratype SMNH 4119, sutural incremental lines. C–L. larval shells, all at the same magnification. C. *H. echinodisci* USNM. D. *H. coxi* AMS C120739. E. *H. kilburni*, paratype, SMNH 4119. F–G. *T. schwengelae*, LACM 55553. H. *T. encopendema*, LACM 55557. I. *H. auritae*, paratype, SMNH 4115. J. *H. boschorum*, paratype, SMNH 4117. K. *H. sauliae*, USNM 778633. L. *H. placentae*, paratype, SMNH 4120. Scale line 0.25 mm.

Material examined. The type material.

Distribution. No reliable additional records.

Remarks. The holotype of *E. philippiana* is in very poor condition. It is worn and both the apex and the aperture are broken. The holotype of *E. dunkeriana* is not much better. We are, however, convinced that they are conspecific.

Our impression is that *E. philippiana* does not belong to *Hypermastus*, since the outer lip is almost perfectly straight, forms an angle of slightly more than 90° with the suture and is distinctly prosocline. In *Hypermastus* it is usually convex, often with a small, blunt angle shortly below the suture. We are, however, not sure and figure it for comparison.

Summary of Taxonomic Changes

The following new species are described: *Hypermastus auritae* n.sp., Warén is a parasite of *Echinodiscus auritus* from Oman; *H. boschorum* n.sp., Warén is a parasite of *E. bisperforatus*, also in Oman; *H. colmani* n.sp., Warén parasitises *Peronella leseuri* in Queensland; *H. kilburni* n.sp., Warén is described from an undetermined sand dollar in Mozambique; *H. minor* n.sp., Warén is described from *E. bisperforatus* from Malaysia; *H. obliquistomum* n.sp., Warén and *H. serratus* n.sp., Warén are described from undetermined sand dollars from New Caledonia; *H. placentae* n.sp., Warén & Crossland is described from *Arachnoides placenta* from Queensland; *H. teuissimae* n.sp., Warén is described from *Echinodiscus tenuissima* from Thailand.

Fifteen eulimids are transfered to *Hypermastus*, based on shell characters, viz.: *Eulima acuta* Sowerby, 1834 (Pacific Panama); *Eulima acuta* A. Adams, 1851 (Philippincs); *Eulima bulbula* Murdoch & Suter, 1906 (New Zealand); *Leiostraca casta* A. Adams, 1861 (new synonyms *L. constantia* A. Adams, 1861 and *L. maria* A. Adams, 1861) (off northern China); *Mucronalia cylindrica* Sowerby, 1900 (Philippines); *Eulima epeterion* Melvill, 1889 (Mauritius); *Eulima epiphanes* Melvill, 1897 (Persian Gulf); *Eulima georgiregis* Cotton & Godfrey, 1932 (South Australia); *Eulima indistincta* Thiele, 1925 (Sumatra); *Eulima mucronata* Sowerby, 1866 (South Australia and New South Wales); *Leiostraca schwengelae* Bartsch, 1938; *Balcis peronellicola* Kuroda & Habe, 1950 (Japan); *Eulima producta* Sowerby, 1894 (Hong Kong); *Eulima randolphi* Vanatta, 1900 (new synonym: *Melanella californica* Bartsch, 1917) (Alaska); and *Eulima williamsi* Cotton & Godfrey 1932 (South Australia). *Eulima philippiana* Dunker, 1860 is a valid senior synonym of *Eulima dunkeriana* Pilsbry, 1901 and the systematic position of the species is uncertain.

ACKNOWLEDGMENTS. We want to thank P. Bouchet (MNHN), S. Boyd (NMV), P. Colman, I. Loch and W.F. Ponder (AMS), T. Habe (Tokyo), R.S. Houbrick (USNM), R. Janssen (SMF), R. Kilburn (NM), R. Kilias (ZMHB), B.A. Marshall (NMNZ), J.H. McLean (LACM), P.G. Oliver (NMW), R. Robertson (ANSP), T. Schiötte (ZMC); K. Way (BMNH) and W. Zeidler (SAM), who all contributed material to this study.

A special thanks is directed to Dr D. Bosch, Clover, South Carolina, who spent much time collecting eulimids from sand dollars and to Dr D.R. Shasky, Redlands, California who contributed most specimens of the genus *Turveria*.

The work has been financially supported by the Swedish Natural Science Research Council.

References

Adams, A., 1851. Descriptions of new species of *Eulima*, *Triphoris* etc., from the collection of Hugh Cuming Esq. Proceedings of the Zoological Society of London 1851: 276–279.

Adams, A., 1861. On some new genera and species of mollusca from the North of China and Japan. Annals and Magazine of Natural History (3)8: 239–246.

Bartsch, P., 1917. A monograph of West American melanellid mollusks. Proceedings of the United States National Museum of Natural History 53: 295–356.

Bartsch, P., 1938. *Leiostraca schwengelae*, a new name. Nautilus 52: 34.

Berry, S.S., 1956. A new west Mexican mollusk parasitic on echinoids. American Midland Naturalist 56: 355–357.

Boyd, S.E. & J.U. Phillips, 1985. Molluscan types in the Museum of Victoria. Occasional Papers from the Museum of Victoria 2: 37–64.

Carpenter, P.P., 1857. Catalogue of Mazatlan shells in the British Museum. British Museum, London, pp. i-iv + ix–xvi + 552.

Carpenter, P.P., 1865. Diagnoses of new species and a new genus of mollusks from the Reigen Mazatlan collection with an account of additional specimens presented to the British Museum. Proceedings of the Zoological Society of London 1865: 268–273.

Cotton, B.C. & F.K. Godfrey, 1932. South Australian shells. IV. South Australian Naturalist 14: 16–44.

Crossland, M.R., R.A. Alford & J.D. Collins (in press). Population dynamics of an ectoparasitic gastropod: *Hypermastus* sp. (Eulimidae) on the sand dollar *Arachnoides placenta* (Echinoidea).

Guille, A., P. Laboute & J.-L. Menou, 1986. Guide des etoiles de mer, oursins et autres echinodermes du lagon de Nouvelle-Caledonie. Editions de l'ORSTOM, Collection Faune Tropicale no. XXV. 238 pp.

Habe, T., 1976. Parasitic gastropods from echinoderms of Japan. Bulletin of the National Science Museum. Ser.A. (Zoology) 2: 157–168.

Kier, P.M., 1981. A bored Cretaceous echinoid. Journal of Paleontology 55: 656–659.

Kuroda, T. & T. Habe, 1950. Eulimidae in Japan (I). Illustrated Catalogue of Japanese shells (ed. T. Kuroda) 1(9): 53–60.

Laseron, C.W., 1955. Revision of the New South Wales Eulimoid shells. The Australian Zoologist 12: 83–107.

Melvill, J.C., 1889. Descriptions of three new species of

shells. Journal of Conchology, London 6: 31–33.
Melvill, J.C., 1897. Descriptions of thirty-four species of marine Mollusca from the Arabian Sea, Persian Gulf and Gulf of Oman. Memoirs of the Manchester Literary and Philosophical Society 41: 1–25.
Mortensen, Th., 1948. A monograph of the Echinoidea IV.2. Clypeastroida. C.A. Reitzel, Copenhagen, pp. 471.
Murdoch, R. & H. Suter, 1906. Results of dredging on the Continental shelf of New Zealand. Transactions of the New Zealand Institute 38: 278–305.
Pilsbry, H.A., 1899. A new species of Australian *Eulima*. Proceedings of the Academy of Natural Sciences Philadelphia 1899: 258.
Pilsbry, H.A., 1901. New Japanese marine, land and fresh water mollusca. Proceedings of the Academy of Natural Science Philadelphia 1901: 385–400.
Powell, A.W.B., 1940. The marine mollusca of the Aupourian Province, New Zealand. Transactions of the Royal Society of New Zealand 70: 205–248.
Powell, A.W.B., 1979. New Zealand Mollusca. Collins, Auckland, Sydney, London. 500 pp.
Sohl, N.F., 1964. Neogastropoda, Opisthobranchia and Basommatophora from the Ripley, Owl Creek, and the Prairie Bluff formations. U.S. Geological Survey, Professional Papers 331B: i–iv, 153–343.
Sowerby, G.B., 1834. Genus *Eulima* Risso. Proceedings of the Zoological Society of London 2: 6–7.
Sowerby, G.B., 1866. Monograph of the genus *Eulima*. **In** L. Reeve. Conchologia Iconica. 15. London.
Sowerby, G.B., 1894. Descriptions of new species of marine shells from the neighbourhood of Hong-Kong. Proceedings of the Malacological Society of London 1: 153–159.
Sowerby, G.B., 1900. Descriptions of new species of marine Mollusca collected by the late Otto Koch at the Island of Cebú, Philippines. Proceedings of the Malacological Society of London 4: 126–129.
Thiele, J., 1925. Gastropoda. II. Teil. Wissenschaftliche Ergebnisse der deutschen Tief-See Expedition auf dem Dampfer "Valdivia" 1898–1899 17(2): 37–382.
Vanatta, E.G., 1900. West American Eulimidae. Proceedings of the Academy of Natural Science, Philadelphia 1899: 254–257.
Warén, A., 1980. Descriptions of new taxa of Eulimidae (Mollusca, Prosobranchia), with notes on some previously described genera. Zoologica Scripta 9: 283–306.
Warén, A., 1984. A generic revision of the family Eulimidae (Gastropoda, Prosobranchia). Journal of Molluscan Studies, Supplement 13, pp. 96.

Accepted 30 May 1990

APPENDIX 1

Table 1. Height and sex distribution of *Hypermastus auritae*.

	male	female
number	31	10
max height mm	7.9	12.3
min height mm	6.2	10.4
mean height mm	7.0	11.2
S.D. mm	0.5	0.6

Table 2. Height and sex distribution of *Hypermastus boschorum*.

	male	female
number	14	13
maximum height mm	4.64	6.39
minimum height mm	4.02	5.07
mean height mm	4.26	5.75
S.D. mm	0.20	0.46

Table 3. Height and sex distribution of *Hypermastus placentae*.

	male	female	indet.
number, A.W.	21	13	
number, M.C.	20	45	55
maximum height, A.W., mm	4.4	7.7	
maximum height, M.C., mm	7.4	8.1	
minimum height, A.W., mm	3.6	6.1	
minimum height, M.C., mm	1.8	4.0	
mean height, A.W., mm	4.0	6.8	
mean height, M.C., mm	4.2	6.8	
S.D., A.W., mm	0.21	0.41	
S.D., M.C., mm	1.69	0.92	

Comments. A.W., values based on specimens sexed according to shell morphology, by A. Warén. – M.C., based on values published by Crossland *et al.* 1990. – S.D., standard deviation